

AN ABSTRACT OF THE THESIS OF

Thomas H. Young for the degree of Honors Baccalaureate of Science in Zoology presented August 12, 2004.

Title: Patterns of Age and Growth in Young-of-Year Rockfish, *Sebastes spp.*, Along the Oregon Coast.

Abstract approved:

Bruce A. Menge

Rockfish of the genus *Sebastes* are important components of Oregon reef communities. I examined patterns of age and growth in young-of-year rockfish across two nested spatial scales – local and regional – along the Oregon coast. Using otolith microstructural examination, I examined the relative importance of local versus regional factors for larval and juvenile growth and development; I investigated the effects of larval growth and development on juvenile growth; and I tested predictions of two hypotheses: the Single Process Concept and the Growth-Mortality Hypothesis. My results suggest that larval growth rates varied on a regional spatial scale, whereas juvenile growth rates varied on a local spatial scale. I found that faster growing larvae metamorphosed at younger ages, corroborating a prediction of the Single Process Concept. Larval growth rates exhibited a negative effect on juvenile growth rates, signifying a trade-off in growth between larval and juvenile stages. There was no evidence of directional growth-selective mortality during the juvenile stage, disproving the Growth-Mortality Hypothesis. Future research should involve long-term studies that focus on temporal patterns of growth and recruitment in young-of-year rockfish across multiple spatial scales, in relation to variability in habitat, biological interactions, and oceanographic conditions.

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**Patterns of Age and Growth in Young-of-Year Rockfish,
Sebastes spp., Along the Oregon Coast**

by

Thomas H. Young

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

Thomas H. Young, Author

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Thank you to all of the fish whose lives were sacrificed for this study, and to the mighty Pacific Ocean for allowing me to explore her profound, unfathomable depths. Sometimes a gracious host, often frustratingly belligerent and uncooperative, may she nonetheless always remain wild and untamed.

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DEDICATION

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**Patterns of Age and Growth in Young-of-Year Rockfish,
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INTRODUCTION

Background

Adult population dynamics and year-class strength in marine fish with pelagic larvae is thought to be primarily determined by processes occurring during the larval and early juvenile stages and thus is predicted by variation in recruitment to the juvenile stage (Recruitment Limitation Hypothesis, Hjort 1914, Lasker 1978, Houde 1987, Sale 1990, Doherty and Fowler 1994). The processes that influence the survivorship of fish larvae and juveniles are therefore essential to understanding adult population dynamics (Myers and Cadigan 1993, Caley et al. 1996, Doherty and Williams 1998), and spatial variability in the fitness of larval and juvenile marine fish may forecast cohort persistence (McCormick 1998). I examined spatial patterns of growth rates and metamorphosis ages in larval and juvenile young-of-year rockfish along the Oregon coast. I also tested some key hypotheses that implicate the growth and development of early life history stages as critical factors for adult population dynamics in marine fishes.

Rockfish of the genus *Sebastes* are dominant fish in temperate rocky reef and kelp forest communities of the northeast Pacific (Love et al. 2002). Rockfish constitute one of the most abundant and diverse taxon of fishes in the nearshore environment of the Oregon coast and are thought to be ecologically important components of Oregon's

coastal ecosystems (Gaines and Roughgarden 1987, Love et al. 2002, Stephens et al. *In Press*). Rockfish have historically comprised a significant proportion of Oregon's commercial and recreational fisheries landings (Love et al. 2002, PFMC 2000, PFMC 2002). However, dramatic declines in several species of rockfish and the collapse of rockfish fisheries (Ralston 1998, Murray et al. 1999, Love et al. 2002) precipitated a long-term ban of all bottom fishing in 2003 along the entire U.S. Pacific continental shelf by the Pacific Fisheries Management Council, in order to protect the remaining rockfish populations (PFMC 2004a).

Although most rockfish are not classified as overfished, and many that are commercially and recreationally harvested are listed as having healthy populations (PFMC 2003, 2004b), all rockfish share common life history characteristics that make them highly vulnerable to overfishing and slow to recover from declines (Love et al. 2002). Therefore, the overfished and "recovering" status of several Oregon rockfish species (PFMC 2003, PFMC 2004b) underscores the need to monitor key demographic parameters in rockfish in order to better understand the ecological factors that influence rockfish population sizes. Many prominent fisheries hypotheses implicate ages at metamorphosis, (i.e., larval durations), and the growth rates of larval and juvenile young-of-year fishes as critical factors for determining subsequent adult population sizes and recruitment to fisheries (Cowan and Shaw 2002, Houde 2002). The purpose of this study was to investigate patterns of age at metamorphosis and larval and juvenile growth rates of young-of-year rockfish at two nested spatial scales, local and regional, along the Oregon coast.

Rockfish are characterized by internal fertilization and viviparity, with larvae born live from their mother in an event called parturition (Love et al. 2002). As in many other marine fish, rockfish exhibit a biphasic life cycle, consisting of a planktonic larval stage followed by metamorphosis into a juvenile stage and thigmotactic settlement from the plankton as the fish associate with a structural habitat (Love et al. 2002, Ammann 2004). The planktonic larval stage is typically one to two months duration in most rockfish (Love et al. 2002), during which fish may undergo long-distance dispersal as currents carry the larvae away from their location of parturition (Roberts 1997). Larvae then metamorphose and either remain in the plankton as pelagic juveniles, or settle as demersal juveniles onto a structural bottom habitat (Love et al. 2002). Many species of rockfish settle onto nearshore rocky substrates and vegetated habitats, such as shallow rocky reefs and the canopy fronds of kelp forests (Hoelzer 1988, Carr 1991, Nelson 2001, Love et al. 1991, Love et al. 2002, Ammann 2004).

Pelagic larval and juvenile rockfish are zooplanktivorous, while demersal juveniles consume both zooplankton and small benthic invertebrates, predominantly arthropods (Love et al. 1991, Love et al. 2002). Young-of-year rockfish may be subject to competition with one another for potentially limiting food resources and habitat refuges from predators (Hoelzer 1987). Predators include a diversity of marine taxa, such as ctenophores, cnidarians, and a wide array of planktivorous and piscivorous fish. Predation rates and other forms of mortality in young-of-year rockfish, such as disease or starvation, may be determined by the growth rates and ages at metamorphosis of larval and juvenile fish (Fuiman 2002, Houde 2002), emphasizing the importance of identifying patterns in these fundamental demographic parameters.

In general, larger marine fish have been demonstrated to be more successful at evading predators (Fuiman 1989, Fuiman 1994, Cowan et al. 1996), to exhibit greater dietary flexibility (Fuiman 2002), to compete more effectively for limiting resources such as food and space (Buchheim and Hixon 1992, Webster and Hixon 2000, Webster 2004), and to better tolerate starvation and environmental stress (Fuiman 2002) compared to smaller con-specifics (Bigger-is-Better Hypothesis, Miller et al. 1988, Bailey and Houde 1989, Houde 1997). Faster-growing marine fish attain size refuges from multiple significant sources of mortality at an earlier age when compared to slower-growing fish, thereby decreasing the total time integrated mortality experienced up to a given size class, *ceteris paribus* (Pfister 1997). Faster growth rates may be due to more favorable environmental conditions (Fortier and Gagné 1990, Hakala et al. 2003) and resources (Booth and Hixon 1999, McCormick and Molony 1992), genetic factors (Anderson and Sabado 1999) and behaviors influencing growth (Magnuson 1962, Koebele 1985, Ochi 1986), or optimal maternal contributions to growth in early life history stages of fish (Jones 2002, Berkeley et al. 2004).

Similarly, faster-growing fish are presumably in better physical condition than slower-growing conspecifics of the same size, and are likely better able to escape predators, compete for resources, and survive environmental extremes (Growth-Mortality Hypothesis, Anderson 1988, Booth and Hixon 1999, Takasuka et al. 2003). Consequently, both larger and faster-growing fish are thought to experience lower daily mortality rates than smaller and slower-growing conspecifics (Hare and Cowen 1997). Such ecological correlates of size and growth are especially pronounced for the early life stages of fish, particularly larvae and young-of-year juveniles, when daily mortality rates

from predation and starvation are an order of magnitude higher than adult mortality rates and extremely variable (Cushing 1975, Houde 1987, Houde 1989).

The Single Process Concept predicts that the highest mortality rates for marine fish occur during the pelagic larval stage, prior to metamorphosis into juveniles and settlement to a reef habitat (Cushing 1975, Houde 1987, Houde 1989). In addition, the Single Process Concept explicitly predicts that the age of metamorphosis should be determined primarily by larval growth rates, with faster-growing larvae metamorphosing at younger ages, corresponding to younger ages of settlement from the plankton to a benthic habitat. Therefore, faster larval growth rates should presumably result in younger metamorphosis ages, producing disproportionately higher larval survivorship and higher recruitment rates to the juvenile population (Cushing and Horwood 1994).

Similarly, the Stage Duration Hypothesis states that small changes in the duration of the larval stage of fish can explain large fluctuations in juvenile and adult population sizes (Houde 1987, Fuiman 1994, Leggett and DeBlois 1994). For faster-growing larvae, accelerated ontogeny and early settlement ages may result in decreased duration of exposure to the highly vulnerable pelagic and planktonic existence that characterizes the larval stage (Miller et al. 1988, Beyer 1989, Houde 1994). The average age at which a fish cohort metamorphoses and settles from the plankton onto a benthic habitat can thus be a key factor in determining the total survivorship of that cohort and the magnitude of recruitment to the reproductive adult population. If larval growth rates are indeed a major determinant of metamorphosis age, then this relationship highlights the potential influence of larval growth rates on recruitment (Bergenius et al. 2002) and thus the persistence and replenishment of rockfish populations (Doherty and Fowler 1994).

Spatial patterns in growth rates and metamorphosis ages of larval and juvenile rockfish along the Oregon coast have important implications on the fitness of different rockfish populations in their early life history stages and consequently may help to understand spatial patterns in adult population sizes (McCormick 1998). Previous research has shown that various ecological factors operating at multiple spatial scales may be important for determining growth rates of young-of-year fish. For instance, habitat type (Tupper and Boutilier 1997) and structural complexity (Levin et al. 1997), predation intensity (Metcalf et al. 1987), competitor density (Booth 1995), temperature (Love et al. 1991, Francis 1994, McCormick and Molony 1995), timing of settlement (Cowen 1991), currents and hydrographic properties (Iles and Sinclair 1982, Fortier and Gagné 1990), upwelling and productivity (Lasker 1978), and food availability (Love et al. 1991, McCormick and Molony 1992) all have been demonstrated to be important for determining growth and developmental rates for different fish taxa (Jones 2002). Understanding the spatial scale at which differences in growth rates and metamorphosis ages occur will provide clues and allow inferences as to the relative effects of local and regional processes on rockfish growth and development.

The Oregon coast occurs within the larger California Current system and consists of two distinct latitudinal regions, separated by an abrupt, bathymetrically induced, oceanographic discontinuity located near Cape Blanco (42°50'N) (Appendix V: Fig. A) (Huyer 1983, Barth and Smith 1998, Barth et al. 2000). North of Cape Blanco is characterized by summer upwelling frequently alternating with periods of relaxation or downwelling (Huyer 1983). South of Cape Blanco, summer upwelling is stronger and more persistent (Parrish et al. 1981, Barth and Smith 1998). Summer sea-surface

temperatures north and south of Cape Blanco reflect these differences in upwelling intensity and frequency, with warmer and more variable sea-surface temperatures typically north of Cape Blanco and consistently colder sea-surface temperatures typically south of Cape Blanco (Appendix V: Fig. A).

The oceanographic dissimilarities between these two regions are hypothesized to be responsible for corresponding biological differences in nearshore and intertidal marine communities (Freidenburg 2002). Previous research has discovered that intertidal invertebrate recruitment, growth, and predation rates are higher in the region north of Cape Blanco as compared to south of Cape Blanco (Freidenburg 2002). Likewise, Parrish et al. (1981) found that spawning success of major coastal fisheries was correlated with spatial variation in nearshore ocean surface drift conditions. A review by Love et al. (1991) identifies variation in growth rates of demersal juvenile rockfish at scales ranging from regional (100's of km), to local (1-10's of km), to the microhabitat scale (10-100's of meters). However, an investigation of spatial patterns in growth and age of young-of-year rockfish along the Cape Blanco oceanographic boundary has to date been absent from the scientific literature.

Selective mortality may be an important confounding factor in observed patterns of age and growth (Sogard 1997), as predicted by the Bigger-is-Better (Miller et al. 1988, Bailey and Houde 1989, Fuiman 1994, Cowan et al. 1996, Houde 1997) and Growth-Mortality Hypotheses (Anderson 1988, Booth and Hixon 1999, Takasuka et al. 2003). The use of temporally discrete (single point-in-time) fish collections to estimate the growth rates of a cohort fails to account for the presumably disproportionate loss of smaller and slower-growing individuals throughout the larval and early juvenile stage.

Selective mortality could potentially skew the measured growth rates of a cohort towards the larger and faster-growing individuals that survive to be sampled in the juvenile stage (Ricker 1969, Levin et al. 1997, Takasuka et al. 2003). Dissimilar growth rates between sites or regions may result from size- and/or growth-selective mortality occurring at different intensities or over different durations of time between locales. Therefore, different average growth rates may be more representative of a surviving cohort's average age and time of exposure to changing predation pressures through different life stages, or may be indicative of different suites of predators to which sites and regions are exposed, rather than intrinsically distinct growth rates. To address this potential sampling bias towards faster growing survivors, it is necessary to test for the possible presence and direction of growth-selective mortality in fish collected for age and growth analyses.

Objectives

The objective of this study was to conduct a comparison of larval and juvenile growth rates and metamorphosis ages of young-of-year rockfish on two nested spatial scales on the central and southern Oregon coast. Spatial comparisons were conducted between individual sites on the local level, approximately one to ten kilometers apart, and between groups of sites on the regional level, hundreds of kilometers apart, in order to test whether patterns of age and growth vary on a local or regional spatial scale along the Oregon coast. In addition, I observationally tested some central predictions of hypotheses addressing the age, growth, development, and mortality of the early life history stages of marine fishes. Using otolith microstructural examination and analyses

(Jones 1992, Jones 2002), I asked six questions related to the patterns of age and growth in young-of-year rockfish along the Oregon coast:

- 6) Do parturition dates, metamorphosis dates, or metamorphosis ages (i.e., larval durations) vary between regions or among local sites along the Oregon coast?
- 7) Do larval, juvenile, or total growth rates vary between regions or among local sites along the Oregon coast?
- 8) Do juvenile physical conditions (mass-length relationships, or condition factors) vary between regions or among local sites along the Oregon coast?
- 9) Do faster growing larvae metamorphose at younger ages, as predicted by the Single Process Concept?
- 10) Do larval growth rates, size at metamorphosis, or larval duration (i.e., age at metamorphosis) predict juvenile growth rates?
- 11) Does growth-selective mortality occur during the early juvenile stage of young-of-year rockfish along the Oregon coast, as predicted by the Growth-Mortality Hypothesis?

METHODS AND MATERIALS

Fish Collection

Juvenile young-of-the-year rockfish (*Sebastes* sp., Appendix V: Fig. B) were collected between August 19 and September 10, 2002 from the emergent *Nereocystis luetkeana* kelp canopy at collection depths of 0 to 3 meters (Appendix V: Fig. C). Total water bottom depths were approximately 10 to 15 meters. Fish collections were made haphazardly by SCUBA divers using Benthic Ichthyofaunal Nets for Coral and Kelp Environments (BINCKE, Anderson and Carr 1998), which consisted of knotless nylon netting of 3/16" mesh dyed red and sewn onto a closable PVC frame. Captured fish were immediately sealed within plastic Ziploc bags and placed into an ice cooler. Fish were transported within a day of capture to a -20°C freezer for storage (Butler 1992).

A total of 135 fish were collected from five local sites nested within two regions of the Oregon coast (Fig. 1, Appendix V: Table A). Collections were made from three southern Oregon sites located immediately south of Cape Blanco (42°50'N): Orford Reef, Nellie's Cove, and East Island Rock; and from two central Oregon sites located near Cape Foulweather (44°46'N): Otter Crest (Appendix V: Fig. C) and Depoe Bay (Fig. 1). Depoe Bay fish were collected on September 10, and fish from all other sites were collected between August 19 and August 23.

Fish Identification

Fish were examined for general morphological characteristics and pigmentation patterns (Matarese et al. 1989, Laidig and Adams 1991). The scientific literature was searched for known juvenile rockfish geographic distributions and juvenile rockfish recruitment habitats (Love et al. 2002). Collected specimens were compared to the visual identification of juvenile young-of-year rockfish from the literature for those species that were found to occur in the nearshore environment along the Oregon coast and are known or suspected to settle to *Nereocystis* kelp canopy.

Fin ray counts were conducted on all fish and compared to known meristics for rockfish species (Matarese et al. 1989, Laidig and Adams 1991, Love et al. 2002). Unstained fin rays were counted for pectoral, dorsal, and anal fins on each fish. Counts were made repeatedly on each fin until three consecutive counts were equal. Left pectoral fins rays were counted in all fish with the exception of two from East Island Rock (southern). In one fish from East Island Rock, right pectoral fin rays were counted due to a heavily damaged left pectoral fin. In another fish from East Island Rock, both pectoral fins were sufficiently damaged to preclude reliable pectoral fin ray count without staining the rays.

Ten fish, the largest and smallest individuals from each site, were sent to the National Marine Fisheries Service (NMFS) Santa Cruz Laboratory for further examination and species identification. The ten fish were genetically analyzed at the NMFS La Jolla Laboratory. Tissue samples were removed from the caudal fin of each fish and DNA was sequenced using cytokine b site analysis.

Fish Measurements

Frozen fish were thawed until tissues softened, and standard lengths (SL) were measured from the most anterior tip of the head with the mouth closed to the most posterior tip of the caudal peduncle (Appendix V: Fig. B). SL were measured to the nearest 0.1mm in a haphazardly selected order using dial calipers. After the SL of each fish was measured, the fish were assigned alphanumeric identification codes and preserved with 95% ethanol in individual vials (Butler 1992).

The blotted dry masses of fish were recorded after removal of otoliths. Fish were removed from ethanol vials and individually blotted on both left and right sides with a dry paper towel. Blotting was repeated until both sides of the fish were completely dry and no more ethanol was absorbed into the towel. Dry fish were then immediately weighed on a Denver Instrument Company A-200DS digital scale. Masses were rounded to the nearest 0.001g.

Several heavily damaged fish, some with missing body parts, were excluded from the study due to a suspected high degree of inaccuracy in length and/or mass measurements. These fish included five from Otter Crest, three from Orford Reef, one from Nellie's Cove, and one from East Island Rock (Appendix III: Table A).

Otolith Selection

Sub-samples of 15 fish from Orford Reef and 20 fish from each of the two central sites, Otter Crest and Depoe Bay, were randomly selected for otolith analyses (Appendix V: Table A). All fish from Nellie's Cove and East Island Rock were used for otolith

analyses with the exception of the two heavily damaged fish that were not measured (one from each site). Sub-samples were used to approximately equalize the sample sizes between regions and among sites within each region, and to guarantee feasibility and timely completion of otolith preparation, examination, and analyses. Randomized selection of fish was conducted in order to ensure proportional representation across the size distribution of fish sampled from each site and to eliminate any size-selection bias.

Otolith Preparation

Right-side sagittal otoliths, the largest otolith pair in *Sebastes spp.*, were extracted from all preserved fish and were mounted onto glass microscope slides using Aremco Crystal Bond 509, a thermoplastic glue, so that either the medial or lateral face of the otoliths were parallel to the slide (Neilson 1992, Secor et al. 1992). In order to make visible the daily growth increments, the medial and lateral faces of otoliths selected for examination and analyses were alternately ground and polished by hand in the sagittal plane while viewed through a compound light microscope at 100x magnification (Secor et al. 1992). Otoliths were placed onto a Thermolyne hotplate set to approximately 150°C, melting the thermoplastic glue. The otoliths were then flipped over to expose the opposite face, remounted on the slide, and removed from the hotplate to cool. After the glue hardened, otoliths were ground on the opposite face in the sagittal plane. Grinding was conducted using 1500 grit wet/dry sandpaper, and polishing was conducted with a Buehler Microcloth polishing cloth and Buehler 0.05 micron Alumina B polishing gel (Micropolish Gamma Number 3). Progress of otolith preparation was monitored by

intermittently viewing otoliths through a compound light microscope at 100x magnification in between cycles of grinding and polishing. Otoliths were repeatedly flipped, ground and polished on both medial and lateral faces in the sagittal plane until the nucleus and all daily growth increments became visible (Fig. 2).

Otolith Microstructure Examination

In order to estimate ages at capture and metamorphosis (i.e., juvenile transformation), daily otolith increments were counted in OPTIMAS 4.1, a micro-computer-based image analysis system (Campana 1992). The image analysis system consisted of a compound microscope connected to a video camera, computer, and a monitor. A 25x objective lens (a working magnification of 250x) and a polarizing filter were used to view microstructural details on the otoliths and for otolith increment counts. The increments of each selected otolith were counted from the nucleus to the edge to estimate age at capture, and from the nucleus to the first accessory primordium to estimate age at metamorphosis (Fig. 2).

Accessory primordia were identified as points peripheral to the nucleus (also referred to as the “primordium”) from which new daily increments began to radiate outwards (Campana 1992). The first accessory primordium formed on each otolith – the accessory primordium closest to the nucleus of the otolith – was recognized as marking the time of juvenile transformation, and therefore provided a reference point for the age of metamorphosis (Laidig et al. 1991). The otoliths of two fish from East Island Rock did not exhibit accessory primordia.

Counts were conducted three independent times for all otoliths in three randomized blind orders in order to eliminate site-specific reader biases (Neilson 1992). Otolith order was re-randomized between each of the three, repeated counts in order to account for possible effects of otolith order on reader accuracy and to ensure independence of repeated counts for each otolith.

Three otoliths selected for examination and analysis were unreadable due to overpolishing and indistinguishable daily increments or to excessive cracks and obscurities around the nucleus. These otoliths, consisting of two from Depoe Bay and one from Nellie's Cove, were not examined, and the fish were excluded from the study, lowering the number of fish examined for Depoe Bay and Nellie's Cove to 18 and 12, respectively (Appendix V: Table A).

Ages and Dates

To estimate the age of each fish at time of capture, the three otolith increment counts from the nucleus to the otolith edge were averaged for each otolith. To estimate the age of each fish at time of metamorphosis, the three otolith increment counts from the nucleus to the first accessory primordium were averaged for each otolith. Otolith increment counts were averaged in order to reduce variation due to counting errors (Campana and Jones 1992). Since all fish had undergone or were undergoing metamorphosis at the time of capture, the age at capture was also used inferentially as the age of metamorphosis for fish whose otoliths did not exhibit accessory primordia.

The parturition date for each fish was estimated by subtracting the age at capture from the collection (capture) date (Campana and Jones 1992). The metamorphosis date for each fish was estimated by adding the metamorphosis age (larval duration) to the parturition date. The daily formation of otolith growth increments was validated by searching the scientific literature for validation studies of otolith increment deposition rate in young-of-year *Sebastes spp.* In addition, fish ages were validated by comparing the range of parturition dates and metamorphosis dates estimated from otolith increment counts with known parturition times and settlement dates in the literature for the species collected (Geffen 1992).

Data Analyses and Statistics

All data were analyzed in JMP 4.0 using a Nested ANOVA design with terms for region and site[region] to test for the effects of nested spatial scales on patterns of age and growth (Sokal and Rohlf 1995, Zar 1999). Region was modeled as a fixed effect and site[region] was modeled as a random effect. Age, size, and growth rates were used as covariates in some analyses, and an interaction term between the covariate and Region was included in each ANOVA model with a covariate. Terms for region and site[region] were maintained within the ANOVA models for questions of interest that did not relate specifically to spatial patterns of age and growth in order to test whether relationships of age and growth were consistent across regions and local sites.

I used $p=0.05$ as my critical p-value for assessing statistical significance. I considered p-values between $p=0.05$ and 0.1 as marginally significant. Parameter

estimates were reported from the full ANOVA models for terms with $p < 0.10$. P-values from two-sided t-tests, with a null model of $t=0$, were reported for parameter estimates of Region and Site[Region] with $p < 0.10$.

Regression lines and p-values were included in figures for significant terms with $p < 0.10$. Simple linear regression lines were fit to the data using a Least Sum-of-Squares method. Multiple linear regression lines were fit to the data by eye. For more detail, see Appendix I.

Otolith Radial Measurements

Otolith post-rostral radii and radii to the first accessory primordia were measured using OPTIMAS 4.1. OPTIMAS 4.1 was calibrated to 4x and 10x objective lenses prior to measuring using a 1.0 millimeter micrometer. All radial measurements were conducted twice, independently, in two randomized blind orders. Otolith radii were measured consistently along standardized posterior, or post-rostral, transects because an overwhelming majority of the first accessory primordia appeared within the posterior region of the otoliths (Campana 1992).

Otolith radii were measured twice for each otolith, and the two measurements were conducted independently from one another in a randomized blind order and then averaged. Post-rostral radius was measured at 40x magnification from the nucleus to the posterior tip of the post-rostrum (Fig. 2). Radius to the first accessory primordium was measured at 100x magnification along a standardized posterior radial transect, from the nucleus to the location of the increment marking the time, or age, of formation of the first

accessory primordium (Fig. 2). The posterior radial transect consisted of a straight line between the nucleus and the posterior-most tip of the post-rostrum.

Otolith sizes were compared between regions and among sites within each region using an ANOVA of otolith post-rostral radius on region and site[region] (Sokal and Rohlf 1995, Zar 1999), in order to detect possible systematic biases in otolith increment counts. Larger otoliths tended to exhibit more sub-daily increments and be more difficult to age compared to smaller otoliths. Spatial variation in otolith sizes may indicate differences in the degree of error for fish age estimates between sites and regions.

Fish Size Back-calculations

Fish sizes were back-calculated to the age of metamorphosis by modeling the otolith-somatic growth relationships with an ANOVA of SL at capture on otolith post-rostral radius, region, and site[region]; and an ANOVA of $\ln(\text{blotted dry mass})$ on $\ln(\text{otolith post-rostral radius})$, region, and site[region] (Sokal and Rohlf 1995, Zar 1999). Appropriate regression equations, of the form:

$$\text{Length} = A * (\text{Otolith Radius}) + B$$

for lengths, and of the form:

$$\ln(\text{Mass}) = A * \ln(\text{Otolith Radius}) + B$$

for masses, were then fit to the relationships between fish sizes and otolith radii after eliminating non-significant terms at a p-value cut-off of 0.05 (Campana and Jones 1992). Measurements of otolith radii to the first accessory primordia were used as proxies for otolith radii at metamorphosis. These values were inputted to the regression equations

describing the otolith-somatic growth relationships in order to back-calculate predicted fish sizes – lengths and masses – at metamorphosis. For more detail, see Appendix I.

Growth Rates

Total growth rates, juvenile growth rates, and larval growth rates were calculated using both standard lengths and blotted dry masses. Length growth rates were calculated using the following equations (Jones 2002):

$$\text{Total Growth Rate} = \frac{(\text{Length at Capture} - \text{Length at Parturition})}{\text{Age at Capture}}$$

$$\text{Juvenile Growth Rate} = \frac{(\text{Length at Capture} - \text{Length at Metamorphosis})}{(\text{Age at Capture} - \text{Age at Metamorphosis})}$$

$$\text{Larval Growth Rate} = \frac{(\text{Length at Metamorphosis} - \text{Length at Parturition})}{\text{Age at Metamorphosis}}$$

Standard length was used for length at capture, back-calculated length was used for length at metamorphosis, and 5.3 mm was used for the length at parturition, based on the values from the literature for *Sebastes maliger* (Matarese et al. 1989), which is thought to comprise an overwhelming majority of the juvenile rockfish collection (estimated 80% *S. maliger* from genetically analyzed subsample of ten fish).

Mass growth rates were calculated using the following equations (Jones 2002):

$$\text{Total Growth Rate} = (\text{Mass at Capture}) / (\text{Age at Capture})$$

$$\text{Juvenile Growth Rate} = \frac{(\text{Mass at Capture} - \text{Mass at Metamorphosis})}{(\text{Age at Capture} - \text{Age at Metamorphosis})}$$

$$\text{Larval Growth Rate} = (\text{Mass at Metamorphosis}) / (\text{Age at Metamorphosis})$$

Blotted dry mass was used for mass at capture, and back-calculated mass was used for mass at metamorphosis. No values for mass at parturition were available from the literature for *S. maliger*, and therefore mass at parturition was not subtracted from mass at capture or metamorphosis in order to derive total and larval growth rates, respectively.

1) Do parturition dates, metamorphosis dates, or metamorphosis ages (i.e., larval durations) vary between regions or among local sites along the Oregon coast?

An ANOVA of estimated parturition date with terms for region and site[region] was conducted to validate age estimates from otolith increment counts (Geffen 1992), with the assumption that all juvenile rockfish collected from each region along the Oregon coast parturated at approximately the same time (T.E. Laidig, personal communication). An ANOVA of estimated metamorphosis date with terms for region and site[region] was conducted to test for spatial patterns in timing of metamorphosis. An ANOVA of estimated metamorphosis age (larval duration) with terms for region and site[region] was conducted to test for spatial patterns in age of metamorphosis. For more detail, see Appendix I.

2) Do larval, juvenile, or total growth rates vary between regions or among local sites along the Oregon coast?

Spatial patterns of larval growth rates were examined using ANOVAs of larval growth rates (by length and by mass) with terms for region, site[region], and size at metamorphosis (length or mass). Juvenile growth rates were examined using ANOVAs

of juvenile growth rates with terms for region, site[region], and size at capture. Total growth rates were examined using ANOVAs of total growth rates with terms for region, site[region], and size at capture. For more detail, see Appendix I.

3) *Do juvenile physical conditions (mass-length relationships) vary between regions or among local sites along the Oregon coast?*

Spatial patterns in physical conditions (mass-length relationships) were examined using an ANOVA of $\ln(\text{mass at capture})$ with terms for region, site[region], and $\ln(\text{length at capture})$. Mass at capture and length at capture were natural log transformed in order to linearize the data.

Blotted dry masses were plotted against SL and a power regression line was fit to the data (Least Sum-of-Squares), describing the mass-length relationship, of the form:

$$\text{Mass} = A*(\text{SL})^B$$

Condition factors, a proxy for physical conditions, were calculated as residuals from this power regression equation (Appendix V: Fig. D). Trade-offs between juvenile growth rates and juvenile physical conditions of fish were examined using ANOVAs of condition factors with terms for region, site[region], and juvenile growth rate (by mass or by length). For more detail, see Appendix I.

4) *Do faster growing larvae metamorphose at younger ages, as predicted by the Single Process Concept?*

ANOVAs of age at metamorphosis (i.e., larval duration) with terms for region, site[region], and larval growth rates (by length or by mass) were conducted to test whether faster growing larvae metamorphose at younger ages and experience shorter larval durations. Possible trade-offs between larval length growth rates and larval mass growth rates were investigated using an ANOVA of $\ln(\text{larval mass growth rate})$ with terms for $\ln(\text{larval length growth rate})$, region, and site[region]. Larval growth rates were natural log transformed in order to normalize variances. For more detail, see Appendix I.

5) *Do larval growth rates, size at metamorphosis, or larval duration (i.e., age at metamorphosis) predict juvenile growth rates?*

ANOVAs of juvenile growth rates (by length and by mass) with terms for region, site[region], and larval growth rate (by length or by mass) were conducted to test whether larval growth rates determine juvenile growth rates. ANOVAs of juvenile growth rates with terms for region, site[region], and size at metamorphosis (length or mass) were conducted to test whether size at metamorphosis determines juvenile growth rates. ANOVAs of juvenile growth rates with terms for region, site[region], and larval duration (i.e., age at metamorphosis) were conducted to test whether larval duration, or metamorphosis age, determines juvenile growth rates. For more detail, see Appendix I.

6) *Does growth-selective mortality occur during the early juvenile stage of young-of-year rockfish along the Oregon coast, as predicted by the Growth-Mortality Hypothesis?*

Values for juvenile growth rates were pooled into discrete juvenile duration classes with 10-day intervals of time since metamorphosis. For each site, variances and means were calculated for juvenile growth rates by length and by mass within each juvenile duration class. ANOVAs of variances of juvenile growth rates with terms for region, site[region], and juvenile duration class were conducted to test for changes in the variation of juvenile growth rates with increasing juvenile duration, which indicates the presence or absence of growth-selective mortality. ANOVAs of mean juvenile growth rates with terms for region, site[region], and juvenile duration class were conducted to test for changes in the averages of juvenile growth rates with increasing juvenile duration, which indicates the direction of growth-selective mortality. For more detail, see Appendix I.

RESULTS

Fish Identification

Pigmentation patterns, morphological characteristics, meristic fin ray counts, and known geographic distributions were consistent with four species in the genus *Sebastes*: *S. maliger* (quillback rockfish), *S. caurinus* (copper rockfish), *S. carnatus* (gopher rockfish) and *S. chrysomelas* (black-and-yellow rockfish) (Appendix V: Fig. B) (Matarese et al. 1989, Laidig and Adams 1991, Love et al. 2002). *S. carnatus* and *S. chrysomelas* are only known to occur south of Cape Blanco and were presumably not present in the central sites.

The ten fish (largest and smallest fish from each site) that underwent cytokine b site genetic analysis were identified to four different species: *S. maliger*, *S. caurinus*, and *S. carnatus* or *S. chrysomelas*. *S. carnatus* and *S. chrysomelas* are virtually indistinguishable genetically and were grouped together as a single species for DNA analyses (Larson 2002, T.E. Laidig and R.D. Vetter, personal communication). The largest fish from Nellie's Cove was identified as *S. caurinus*, and the largest fish from East Island Rock was identified as *S. carnatus* or *S. chrysomelas*. The other eight fish were identified as *S. maliger*, comprising 80% of the genetically analyzed sub-sample. *S. maliger* was the only species known to be present in collections from all five sites. Of the genetically analyzed fish, 100% (four out of four) from the central Oregon coast were *S. maliger*, compared to 67% (four out of six) from the southern Oregon coast. For more detail, see Appendix III.

Ages and Dates

Estimated total ages at capture for the collected young-of-year rockfish ranged from 60.7 days to 113.3 days, with a mean age at capture of 88.5 days (Appendix V: Table B). Estimated ages at metamorphosis, or larval durations, ranged from 32.7 days to 68.7 days, with a mean metamorphosis age or larval duration of 53.6 days. These metamorphosis ages correspond to the suspected larval durations of the collected species, typically between one and two months (A.J. Ammann, M.H. Carr, and T.E. Laidig, personal communication).

Estimated metamorphosis dates ranged from June 27th to August 23rd, with a mean metamorphosis date of July 22nd (Appendix V: Table B). These metamorphosis dates appear to correspond to published settlement dates for *S. maliger*, *S. caurinus*, *S. carnatus*, and *S. chrysomelas*, which are characterized by a very short pelagic juvenile stage and settlement immediately following metamorphosis (Love et al. 2002). *S. maliger* is reported to settle from July to November in Puget Sound (Yamanaka 2002). *S. caurinus* is reported to settle during late April and May off central California and during July and August in the Strait of Georgia (Love 2002). *S. carnatus* is reported to settle from January to July in central California (Larson 2002). *S. chrysomelas* and *S. carnatus* were reported to settle during June and July (Larson 2002). No settlement dates are provided for any of these species in Oregon specifically.

Estimated parturition dates ranged from May 3rd to June 23rd (Appendix V: Table B). The mean parturition date among all fish from the five sites and two regions was May 29th. These dates appear to correspond to published parturition dates for *S. maliger*, *S. caurinus*, *S. carnatus*, and *S. chrysomelas* (Love et al. 2002). *S. maliger* is reported to

parturate (i.e., release larvae) from April to July in northern and central California, and during April in Puget Sound (Yamanaka 2002). *S. caurinus* is reported to parturate during May and perhaps to July off Oregon (Love 2002). *S. carnatus* is reported to parturate from January to July in central California (Larson 2002). *S. chrysomelas* and *S. carnatus* were both reported to parturate from January to May off California (Larson 2002). No parturition dates are provided for *S. maliger*, *S. carnatus*, or *S. chrysomelas* in Oregon specifically. For more detail, see Appendix III.

Otolith Radial Measurements

Otolith radii differed among sites nested within regions ($p < 0.0001$) but not between regions ($p = 0.48$). Within the central Oregon coast, otolith radii from Depoe Bay fish were on average 0.0020 mm greater than otolith radii from Otter Crest fish ($p = 0.88$). Within the southern Oregon coast, otolith radii from Nellie's Cove fish were on average 0.14 mm greater than otolith radii from Orford Reef fish ($p < 0.0001$), and otolith radii from Orford Reef fish were on average 0.17 mm greater than otolith radii from East Island Rock fish ($p < 0.0001$). For more detail, see Appendix II.

Fish Size Back-calculations

There was a significant effect of otolith radius on length at capture ($p < 0.0001$) (Fig. 3). This relationship did not differ between regions ($p = 0.65$) or among sites nested within regions ($p = 0.23$). There was a marginally significant interaction between otolith

radius and region ($p=0.055$). Lengths at capture increased with otolith radius at a rate of 4.57 *mm^{-1} faster in the southern Oregon coast than in the central Oregon coast. However, this difference did not meet the p -value cut-off of $p=0.05$. A simple linear regression of length at capture versus otolith radius was used to describe the otolith-somatic growth relationship for all fish.

There was a significant effect of $\ln(\text{otolith radius})$ on $\ln(\text{mass at capture})$ ($p<0.0001$) (Fig. 3). This relationship did not differ between regions ($p=0.96$) or among sites nested within regions ($p=0.15$). There was no interaction between otolith radius and region ($p=0.24$). A simple linear regression of the natural log of mass at capture versus the natural log of otolith radius was used to describe the otolith-somatic growth relationship for all fish. For more detail, see Appendix II.

1) Do parturition dates, metamorphosis dates, or metamorphosis ages (i.e., larval durations) vary between regions or among local sites along the Oregon coast?

Parturition dates differed among sites nested within regions ($p<0.0001$) but not between regions ($p=0.62$) (Fig. 4). Within the central Oregon coast, fish larvae from Depoe Bay parturated on average 8.5 days later than fish from Otter Crest ($p<0.0001$). Within the southern Oregon coast, fish from East Island Rock parturated on average 13.3 days later than fish from Orford Reef ($p<0.0001$), and fish from Nellie's Cove parturated on average 8.1 days earlier than fish from Orford Reef ($p<0.0001$).

Metamorphosis dates differed among sites nested within regions ($p<0.0001$) but not between regions ($p=0.86$) (Fig. 4). Within the central Oregon coast, fish larvae from Depoe Bay metamorphosed on average 7.9 days later than fish from Otter Crest

($p < 0.0001$). Within the southern Oregon coast, fish from East Island Rock metamorphosed on average 14.0 days later than fish from Orford Reef ($p < 0.0001$), and fish from Nellie's Cove metamorphosed on average 9.1 days earlier than fish from Orford Reef ($p = 0.0002$).

Metamorphosis ages (larval durations) did not differ between regions ($p = 0.23$) or among sites nested within regions ($p = 0.96$) (Fig. 4). For more detail, see Appendix II.

2) *Do larval, juvenile, or total growth rates vary between regions or among local sites along the Oregon coast?*

Larval length growth rates did not differ between regions ($p = 0.23$) or among sites nested within regions ($p = 0.40$) (Fig. 5). There was no effect of length at metamorphosis on larval length growth rate ($p = 0.38$) and no interaction between length at metamorphosis and region ($p = 0.21$).

Larval mass growth rates did not differ between regions ($p = 0.25$) or among sites nested within regions ($p = 0.25$) (Fig. 5). There was a significant effect of mass at metamorphosis on larval mass growth rate ($p < 0.0001$) and a significant interaction between mass at metamorphosis and region ($p = 0.015$). Larval growth rates by mass were on average 0.00013 g/day faster for every 0.01-g increase in mass at metamorphosis. Larval growth rates by mass increased with mass at metamorphosis at a rate of 0.0016 day^{-1} faster on the southern Oregon coast compared to the central Oregon coast.

Juvenile length growth rates differed among sites nested within regions ($p = 0.041$) but did not differ between regions ($p = 0.26$) (Fig. 6). Within the central Oregon coast, juvenile growth rates by length were on average 0.021 mm/day faster in Otter Crest than

in Depoe Bay, for a given length at capture ($p=0.038$). Within the southern Oregon coast, juvenile growth rates by length were on average 0.042 mm/day faster in East Island Rock than in Orford Reef ($p=0.054$), and 0.033 mm/day faster in Orford Reef than in Nellie's Cove ($p=0.065$), for a given length at capture. There was a significant effect of length at capture on juvenile length growth rate ($p<0.0001$) but no interaction between length at capture and region ($p=0.71$). Juvenile growth rates by length were on average 0.020 mm/day faster for every 1.0-mm increase in length at capture.

Juvenile mass growth rates differed marginally among sites nested within regions ($p=0.068$) but did not differ between regions ($p=0.44$) (Fig. 6). Within the central Oregon coast, juvenile growth rates by mass were on average 0.00030 g/day faster in Otter Crest than in Depoe Bay, for a given mass at capture ($p=0.067$). Within the southern Oregon coast, juvenile growth rates by mass were on average 0.00048 g/day faster in East Island Rock than in Orford Reef ($p=0.098$), and 0.00051 g/day faster in Orford Reef than in Nellie's Cove ($p=0.054$), for a given mass at capture. There was a significant effect of mass at capture on juvenile mass growth rate ($p<0.0001$) but no interaction between mass at capture and region ($p=0.37$). Juvenile growth rates by mass were on average 0.00021 g/day faster for every 0.01-g increase in mass at capture.

Total length growth rates differed marginally between regions ($p=0.056$) and among sites nested within regions ($p<0.052$) (Fig. 7). Total growth rates by length were on average 0.011 mm/day faster on the southern Oregon coast compared to the central Oregon coast, for a given length at capture ($p<0.0001$). Within the central Oregon coast, total growth rates by length were on average 0.0055 mm/day faster in Otter Crest than in Depoe Bay, for a given length at capture ($p=0.051$). Within the southern Oregon coast,

total growth rates by length were on average 0.012 mm/day faster in East Island Rock than in Orford Reef ($p=0.052$), and 0.0088 mm/day faster in Orford Reef than in Nellie's Cove ($p=0.076$), for a given length at capture. There was a significant effect of length at capture on total length growth rate ($p<0.0001$) but no interaction between length at capture and region ($p=0.79$). Total growth rates by length were on average 0.0074 mm/day faster for every 1.0-mm increase in length at capture.

Total mass growth rates differed marginally between regions ($p=0.060$) but did not differ among sites nested within regions ($p=0.61$) (Fig. 7). Total growth rates by mass were on average 0.00006 g/day faster on the southern Oregon coast compared to the central Oregon coast, for a given mass at capture ($p=0.0014$). There was a significant effect of mass at capture on total mass growth rate ($p<0.0001$) but no interaction between mass at capture and region ($p=0.55$). Total growth rates by mass were on average 0.000094 g/day faster for every 0.01-g increase in mass at capture. For more detail, see Appendix II.

3) *Do juvenile physical conditions (mass-length relationships) vary between regions or among local sites along the Oregon coast?*

Juvenile physical conditions (mass-length relationships) differed among sites nested within regions ($p<0.0001$) but did not differ between regions ($p=0.67$) (Fig. 8). Within the central Oregon coast, the natural logs of mass (g) at capture were on average 0.079 greater in Depoe Bay than in Otter Crest, for a given natural log of length (mm) at capture ($p<0.0001$). Within the southern Oregon coast, the natural logs of mass (g) at capture were on average 0.037 greater in Nellie's Cove than in Orford Reef ($p=0.15$), and

0.037 greater in Orford Reef than in East Island Rock ($p=0.25$), for a given natural log of length (mm) at capture. There was a significant effect of $\ln(\text{length at capture})$ on $\ln(\text{mass at capture})$ ($p<0.0001$) but no interaction between $\ln(\text{length at capture})$ and region ($p=0.36$). The natural log of mass (g) at capture was on average 3.43 greater for every increase of 1.0 in the natural log of length (mm) at capture.

There was a marginally significant effect of juvenile length growth rate on condition factors ($p=0.058$) but no interaction between juvenile length growth rate and region ($p=0.22$) (Fig. 9). Condition factors decreased at an average rate of 0.0420g for every 1-mm/day increase in juvenile growth rates by length. Condition factors differed among sites nested within regions ($p=0.0002$) but not between regions ($p=0.93$). Within the central Oregon coast, condition factors were 0.0122g greater in Depoe Bay than in Otter Crest, for a given juvenile length growth rate ($p<0.0001$). Within the southern Oregon coast, condition factors were 0.00329g greater in Nellie's Cove than in Orford Reef ($p=0.36$), and 0.00103g greater in Orford Reef than in East Island Rock ($p=0.78$), for a given juvenile length growth rate.

There was no effect of juvenile mass growth rate on condition factors ($p=0.98$) and no interaction between juvenile mass growth rate and region ($p=0.40$) (Fig. 9). Condition factors differed among sites nested within regions ($p<0.0001$) but not between regions ($p=0.96$). Within the central Oregon coast, condition factors were 0.0136g greater in Depoe Bay than in Otter Crest, for a given juvenile mass growth rate ($p<0.0001$). Within the southern Oregon coast, condition factors were 0.00214g greater in Nellie's Cove than in Orford Reef ($p=0.58$), and 0.000867g greater in East Island Rock

than in Orford Reef ($p=0.84$), for a given juvenile mass growth rate. For more detail, see Appendix II.

4) *Do faster growing larvae metamorphose at younger ages, as predicted by the Single Process Concept?*

There was a significant effect of larval length growth rate on age at metamorphosis, or larval duration ($p<0.0001$) and a marginally significant interaction between larval length growth rate and region ($p=0.072$) (Fig. 10). Ages at metamorphosis (larval durations) were on average 2.12 days younger (shorter) for every 0.01-mm/day increase in larval length growth rates. Ages at metamorphosis (larval durations) decreased with larval length growth rates at a rate of 61.6 days²/mm faster in the central Oregon coast than in the southern Oregon coast. Ages at metamorphosis did not differ between regions ($p=0.21$) or among sites nested within regions ($p=0.76$).

There was a significant effect of larval mass growth rate on age at metamorphosis, or larval duration ($p<0.0001$) and a significant interaction between larval mass growth rate and region ($p=0.046$) (Fig. 10). Ages at metamorphosis (larval durations) were on average 2.11 days older (longer) for every 0.0001-g/day increase in larval mass growth rates. Ages at metamorphosis (larval durations) increased with larval mass growth rates at a rate of 10.0 days²/0.001g faster in the central Oregon coast than in the southern Oregon coast. Ages at metamorphosis differed marginally between regions ($p=0.087$) but not among sites nested within regions ($p=0.76$) (Fig. 10). Ages at metamorphosis (larval durations) were on average 1.9 days younger (shorter) in the southern Oregon coast than in the central Oregon coast, for a given larval mass growth rate ($p=0.046$).

There was a significant effect of $\ln(\text{larval length growth rate})$ on $\ln(\text{larval mass growth rate})$ ($p=0.0004$) but no interaction between $\ln(\text{larval length growth rate})$ and region ($p=0.31$) (Fig. 11). The natural log of larval mass growth rates (g/day) increased at a rate of 1.19 with every 1-unit increase in the natural log of larval length growth rates (mm/day). This relationship did not differ between regions ($p=0.25$) or among sites nested within regions ($p=0.49$). For more detail, see Appendix II.

5) *Do larval growth rates, size at metamorphosis, or larval duration (i.e., age at metamorphosis) predict juvenile growth rates?*

There was a significant effect of larval length growth rate on juvenile length growth rate ($p=0.0083$) but no interaction between larval length growth rate and region ($p=0.43$) (Fig. 12). Juvenile growth rates by length were on average 0.00975 mm/day slower for every 0.01-mm/day increase in larval growth rates by length. Juvenile growth rates differed among sites nested within regions ($p=0.027$) but not between regions ($p=0.94$). Within the central Oregon coast, juvenile growth rates by length were on average 0.015 mm/day faster in Otter Crest than in Depoe Bay, for a given larval length growth rate ($p=0.23$). Within the southern Oregon coast, juvenile growth rates by length were on average 0.025 mm/day faster in Nellie's Cove than in Orford Reef ($p=0.17$), and 0.054 mm/day faster in Orford Reef than in East Island Rock ($p=0.0054$), for a given larval length growth rate.

There was a marginally significant effect of larval mass growth rate on juvenile mass growth rate ($p=0.063$) but no interaction between larval mass growth rate and region ($p=0.92$) (Fig. 12). Juvenile growth rates by mass were on average 0.000191

g/day slower for every 0.0001-g/day increase in larval growth rates by mass. Juvenile mass growth rates differed among sites nested within regions ($p=0.0040$) but not between regions ($p=0.60$). Within the central Oregon coast, juvenile growth rates by mass were on average 0.000092 g/day faster in Depoe Bay than in Otter Crest, for a given larval mass growth rate ($p=0.75$). Within the southern Oregon coast, juvenile growth rates by mass were on average 0.00095 g/day faster in Nellie's Cove than in Orford Reef ($p=0.017$), and 0.0016 g/day faster in Orford Reef than in East Island Rock ($p=0.0003$), for a given larval mass growth rate.

There was a significant effect of length at metamorphosis on juvenile length growth rate ($p=0.0094$) but no interaction between length at metamorphosis and region ($p=0.37$) (Fig. 13). Juvenile growth rates by length were on average 0.0158 mm/day slower for every 1-mm increase in lengths at metamorphosis. Juvenile length growth rates differed among sites nested within regions ($p=0.0088$) but not between regions ($p=0.71$). Within the central Oregon coast, juvenile growth rates by length were on average 0.017 mm/day faster in Otter Crest than in Depoe Bay, for a given length at metamorphosis ($p=0.18$). Within the southern Oregon coast, juvenile growth rates by length were on average 0.029 mm/day faster in Nellie's Cove than in Orford Reef ($p=0.11$), and 0.064 mm/day faster in Orford Reef than in East Island Rock ($p=0.0017$), for a given length at metamorphosis.

There was no effect of mass at metamorphosis on juvenile mass growth rate ($p=0.27$) and no interaction between mass at metamorphosis and region ($p=0.74$) (Fig. 13). Juvenile mass growth rates differed among sites nested within regions ($p=0.0093$) but not between regions ($p=0.55$). Within the central Oregon coast, juvenile growth rates

by mass were on average 0.000093 g/day faster in Depoe Bay than in Otter Crest, for a given mass at metamorphosis ($p=0.75$). Within the southern Oregon coast, juvenile growth rates by mass were on average 0.00093 g/day faster in Nellie's Cove than in Orford Reef ($p=0.023$), and 0.0015 g/day faster in Orford Reef than in East Island Rock ($p=0.0009$), for a given mass at metamorphosis.

There was no effect of larval duration (age at metamorphosis) on juvenile length growth rate ($p=0.99$) and no interaction between larval duration and region ($p=0.56$) (Fig. 14). Juvenile length growth rates differed marginally among sites nested within regions ($p=0.072$) but not between regions ($p=0.81$). Within the central Oregon coast, juvenile growth rates by length were on average 0.017 mm/day faster in Otter Crest than in Depoe Bay, for a given larval duration (age at metamorphosis) ($p=0.21$). Within the southern Oregon coast, juvenile growth rates by length were on average 0.024 mm/day faster in Nellie's Cove than in Orford Reef ($p=0.22$), and 0.046 mm/day faster in Orford Reef than in East Island Rock ($p=0.019$), for a given larval duration.

There was no effect of larval duration (age at metamorphosis) on juvenile mass growth rate ($p=0.17$) and no interaction between larval duration and region ($p=0.86$) (Fig. 14). Juvenile mass growth rates differed among sites nested within regions ($p=0.016$) but not between regions ($p=0.70$). Within the central Oregon coast, juvenile growth rates by mass were on average 0.00012 g/day faster in Depoe Bay than in Otter Crest, for a given larval duration (age at metamorphosis) ($p=0.68$). Within the southern Oregon coast, juvenile growth rates by mass were on average 0.00087 g/day faster in Nellie's Cove than in Orford Reef ($p=0.030$), and 0.0013 g/day faster in Orford Reef than in East Island Rock ($p=0.0017$), for a given larval duration. For more detail, see Appendix II.

6) *Does growth-selective mortality occur during the early juvenile stage of young-of-year rockfish along the Oregon coast, as predicted by the Growth-Mortality Hypothesis?*

There was a significant effect of juvenile duration class on the variance of juvenile length growth rates ($p=0.012$) but no interaction between juvenile duration class and region ($p=0.90$) (Fig. 15). The variance of juvenile length growth rates decreased by 0.00431 for every 10-day increase in juvenile duration, after accounting for the effects of Region and Site[Region]. Variances of juvenile length growth rates did not differ between regions ($p=0.15$) or among sites nested within regions ($p=0.92$).

There was a significant effect of juvenile duration class on the variance of juvenile mass growth rates ($p=0.031$) and no interaction between juvenile duration class and region ($p=0.96$) (Fig. 15). The variance of juvenile mass growth rates decreased by 1.07×10^{-6} for every 10-day increase in juvenile duration, after accounting for the effects of Region and Site[Region]. Variances of juvenile mass growth rates did not differ between regions ($p=0.31$) or among sites nested within regions ($p=0.24$).

There was no effect of juvenile duration class on mean juvenile length growth rates ($p=0.25$) and no interaction between juvenile duration class and region ($p=0.47$) (Fig. 16). Mean juvenile length growth rates did not differ between regions ($p=0.96$) or among sites nested within regions ($p=0.61$).

There was no effect of juvenile duration class on mean juvenile mass growth rates ($p=0.45$) and no interaction between juvenile duration class and region ($p=0.58$) (Fig. 16). Mean juvenile mass growth rates did not differ between regions ($p=0.67$) or among sites nested within regions ($p=0.34$). For more detail, see Appendix II.

DISCUSSION

I examined spatial variation in the patterns of age and growth of young-of-year rockfish, *Sebastes spp.*, across two nested spatial scales – regional and local – along the Oregon coast (Fig. 1), spanning an important regional oceanographic discontinuity located at Cape Blanco (Parrish et al. 1981, Huyer 1983, Barth and Smith 1998, Barth et al. 2000, Freidenburg 2002). By examining otolith microstructural properties (Fig. 2), I was able to construct otolith-somatic growth relationships (Fig. 3) in order to back-calculate sizes at metamorphosis for fish. By counting daily otolith increments, I was able to estimate ages and dates at metamorphosis and at parturition, and to calculate average growth rates for the larval and juvenile stages.

Using a Nested ANOVA design, I investigated spatial patterns in parturition dates, metamorphosis dates, and metamorphosis ages (Question #1). I also investigated spatial patterns in larval, juvenile, and total growth rates (Question #2); as well as in juvenile physical conditions (mass-length relationships, or condition factors) (Question #3). Additionally, I tested a key assumption of the Single Process Concept (Cushing 1975, Houde 1987, Houde 1989) that larval growth rates control the timing of metamorphosis, and thus the larval duration (Question #4). I sought to identify linkages between the larval and juvenile stages by investigating the relationship between juvenile growth rates and larval growth and development (Question #5). Finally, I tested the Growth-Mortality Hypothesis during the juvenile stage, which predicts directional growth-selective mortality (Anderson 1988, Booth and Hixon 1999, Takasuka et al.

2003), by examining changes in the variances and means of juvenile growth rates across the juvenile duration (Question #6).

1) Do parturition dates, metamorphosis dates, or metamorphosis ages (i.e., larval durations) vary between regions or among local sites along the Oregon coast?

Differences in parturition dates among sites (Fig. 4) may result from distinct cohorts, released during discrete parturition events (Pasten et al. 2003) by different maternal populations (Burford 2001), at each site. This possibility implies that fish did not mix in the plankton as pelagic larvae and maintained “cohort cohesiveness” during their larval duration and through settlement (Jones et al. 1999, Swearer et al. 1999, Cowen et al. 2000, Swearer et al. 2002, Taylor and Hellberg 2003). Evidence of limited larval dispersal in rockfish along the Oregon coast supports this explanation (Miller and Shanks *In Press*).

Alternatively, differences in parturition dates may indicate systematic errors in daily otolith increment counts and thus local spatial biases in age and growth rate estimates (Geffen 1992). This conclusion relies upon the assumption that fish from all sites within each region parturated at approximately the same time (T.E. Laidig, personal communication). Differences among sites in otolith radii may have contributed to systematic errors in age estimates, based on the observation that larger otoliths exhibited more sub-daily increments than smaller otoliths. Suspected errors in growth rate estimates due to differences among sites in otolith radii and parturition dates corresponded with observed spatial variation in growth rates among sites in the southern region. However, local variation in growth rates between the central Oregon coast sites

contradicted patterns that would be expected from solely systematic errors in increment counts due to differences in parturition dates and otolith radii. Therefore, spatial patterns of age and growth likely reflect true ecological differences among sites. Estimated dates of parturition, ages of metamorphosis, and dates of settlement agreed well with those in the literature (Love et al. 2002), providing a tentative verification of age estimates from otolith daily increment counts.

Metamorphosis ages did not differ between regions or among sites within each region (Fig. 4), indicating spatially consistent timing of metamorphosis, or developmental rates. Variation in metamorphosis dates among sites (Fig. 4) is attributable to the combination of locally differing parturition dates and the lack of spatial structure in metamorphosis ages. For more detail, see Appendix III.

2) *Do larval, juvenile, or total growth rates vary between regions or among local sites along the Oregon coast?*

Spatial patterns in growth rates of young-of-year rockfish indicate that growth rates during the larval stage vary on a regional scale (Fig. 5), while growth rates during the juvenile stage vary predominantly on a local scale (Fig. 6). Small, consistent regional differences in growth rates during both larval and juvenile stages appeared to combine through an additive effect to result in substantial regional differences in total growth rates (Fig. 7). These results indicate that the spatial scale of control over young-of-year rockfish growth and development is largely stage-specific.

Regional factors such as coastal oceanography (Lasker 1978, Iles and Sinclair 1982, Fortier and Gagné 1990), water temperature (Love et al. 1991), or differences in

species composition (Love et al. 2002) may drive the growth dynamics of planktonic larval rockfish along the Oregon coast, as indicated by a significant regional pattern in larval mass growth rates (Fig. 5). An anomalous hypoxia event accompanied by intense persistent upwelling and cold water temperatures along the central Oregon coast in summer 2002 (Wheeler et al. 2003, Grantham et al. 2004) may explain the observation of slower larval mass growth rates in the central region than in the southern region (Fig. 5). Colder water temperatures tend to depress growth rates and have been demonstrated to be an important source of variation in the growth of juvenile rockfish (Love et al. 1991). Errors introduced by back-calculating lengths at metamorphosis, resulting from significant regional differences in otolith-somatic growth relationships (Appendix V: Fig. E) (Secor and Dean 1989), may have concealed a similar regional pattern in larval length growth rates (Fig. 5).

In contrast, during the demersal juvenile stage of young-of-year rockfish, site-to-site variation on a local spatial scale outweighed regional factors for determining juvenile growth rates (Fig. 6). Local, site-specific features that appear to vary greatly on small spatial scales are possibly regulating growth during the juvenile stage, after metamorphosis and settlement. For instance, settlement habitat (Love et al. 1991, Levin et al. 1997, Tupper and Boutilier 1997), species composition of recruits (Carr 1989, T.H. Young, personal observation), cohort density (Bystroem and Garcia-Berthou 1999), wave and current exposure (Clark 1997, Graham et al. 1997), predation intensity (Connell 1998, Connell 2002), local productivity (Leichter and Witman 1997, Genovese and Witman 1999), and food availability (Love et al. 1991, Booth and Hixon 1999) may vary

on small spatial scales and either directly influence growth or interact with other important local factors.

The early life history stage of young-of-year rockfish appears to determine the spatial scale of variation in growth rates along the Oregon coast. I propose that the dispersal larval stage of rockfish may be heavily influenced by large-scale, regional oceanographic features that are relatively homogeneous on scales of tens of kilometers (Sunye 1999). Conversely, the demersal or benthic juvenile and adult stages may be primarily controlled by locally heterogeneous ecological factors, which operate on scales of hundreds of meters and may vary tremendously from site to site (Love et al. 1991).

The emergent spatial scale of variation in the demographics of marine organisms may be similar to the spatial scale of dispersion in the particular life history stage of interest and should also reflect the spatial scale of homogeneity for influential environmental factors. Therefore, the manifested spatial scale of demographic variation for a life history stage may be coupled to the scale of dispersion and to the scale of variability in relevant environmental conditions and resources. Shifts in spatial scale of demographic variation (e.g., from regional to local) between life history stages (e.g., from larval to juvenile) may thus result from order of magnitude changes in the degree of dispersion or in the spatial heterogeneity of a crucial environmental factor. The difference in spatial scale of growth between larval and juvenile stages underscores the complexity of the early life history of marine fishes and other marine organisms with biphasic life cycles (Menge and Sutherland 1987, Roughgarden et al. 1988, Caley et al. 1996), and emphasizes the importance of this ontogenetic and ecological transition period

(metamorphosis and settlement) (Kaufman et al. 1992, McCormick and Makey 1997).

For more detail, see Appendix III.

3) *Do juvenile physical conditions (mass-length relationships) vary between regions or among local sites along the Oregon coast?*

Significant local variation in juvenile physical conditions (mass-length relationships) existed among sites within the central region (Fig. 8). However, these site-to-site differences were confounded with a time lag of three weeks between fish collections along the central Oregon coast, underscoring the need to investigate demographic parameters across temporal scales as well as spatial scales (Sanford and Menge 2001, Hakala et al. 2003). Juvenile condition factors were negatively correlated with juvenile growth rates by length, but were not correlated with juvenile growth rates by mass (Fig. 9). This trade-off between juvenile length growth rates and condition factors indicates that fish sacrificed their linear growth in order to acquire more mass per unit of length. For more detail, see Appendix III.

4) *Do faster growing larvae metamorphose at younger ages, as predicted by the Single Process Concept?*

I found an inverse relationship between larval length growth rates and ages at metamorphosis (Fig. 10), which argues for the control of developmental rates and larval durations by linear growth rate in young-of-year rockfish, as posited by the Single Process Concept (Cushing 1975, Houde 1987, Houde 1989). Furthermore, the magnitude

of this effect (i.e., the slope of the relationship) differed between regions (Fig. 10), indicating either the influence of differences in species compositions or possible control of regional environmental factors upon this ontogenetic process. If the larval stage experiences disproportionately higher mortality rates than the juvenile stage, then these results present a hypothetical mechanism by which variation in rockfish recruitment may be regulated by the linear growth rates of rockfish larvae (Cushing and Horwood 1994, Bergenius et al. 2002), as mediated through timing of metamorphosis and settlement (Shima and Findlay 2002).

I observed a direct, positive relationship between larval mass growth rates and ages at metamorphosis (Fig. 10), which may indicate an ability of larval rockfish to delay metamorphosis after attaining an ontogenetic “threshold” length (Fuiman 2002) by compromising linear growth for mass growth (Pasten et al. 2003). This explanation would entail a trade-off between larval length growth rates and larval mass growth rates in fish that delay metamorphosis. However, a positive relationship between larval mass growth rates and larval length growth rates (Fig. 11) did not support this mechanism of delayed development by compromising linear growth for mass growth as a plausible explanation. Nonetheless, by exhibiting flexibility over the timing of development, rockfish larvae may be able to extend their larval duration while waiting for appropriate settlement habitat or other critical environmental cues to trigger metamorphosis (Youson 1988). This finding suggests that the timing, or age, of metamorphosis is controlled by a combination of exogenous factors, such as the presence of a suitable bottom habitat (Montgomery et al. 2001, Parmentier et al. 2004), and endogenous factors, such as a

postponable threshold length that may hormonally trigger juvenile transformation (Pasten et al. 2003). For more detail, see Appendix III.

5) *Do larval growth rates, size at metamorphosis, or larval duration (i.e., age at metamorphosis) predict juvenile growth rates?*

Larval growth rates and lengths at metamorphosis exhibited inverse relationships with juvenile growth rates (Fig. 12 and 13), demonstrating a significant trade-off between larval growth and juvenile growth. Larval durations, however, did not exhibit an effect on juvenile growth rates (Fig. 14). The trade-off between larval growth and juvenile growth may result from dramatic ontogenetic shifts in diet, habitat requirements, and physiological tolerances during metamorphosis (Love et al. 2002, McCormick and Makey 1997). Pelagic productivity may favor faster growth in planktonic rockfish larvae (Lasker 1978, Love et al. 2002), but varies inversely on regional spatial scales with benthic productivity or kelp forest biomass (Broitman and Kinlan *In Review*), which may promote faster growth in demersal juvenile rockfishes (Love et al. 1991, Love et al. 2002). Consequently, oceanographic conditions that enhance larval growth rates may hinder juvenile growth rates, suggesting that individual young-of-year rockfish may be in-phase with their ideal conditions and resources during the planktonic larval stage, but out-of-phase with their ideal environment during the demersal juvenile stage, or vice versa. For more detail, see Appendix III.

6) *Does growth-selective mortality occur during the early juvenile stage of young-of-year rockfish along the Oregon coast, as predicted by the Growth-Mortality Hypothesis?*

By examining changes in variances and means of juvenile growth rates through the juvenile duration, I found no evidence of directional growth-selective mortality, thereby disproving the Growth-Mortality Hypothesis (Anderson 1988, Booth and Hixon 1999, Takasuka et al. 2003) during the early juvenile stage for young-of-year rockfish. Variances of juvenile growth rates decreased (Fig. 15) while mean juvenile growth rates remained unchanged (Fig. 16) with increasing juvenile duration, indicating the possibility of stabilizing growth-selective mortality. Alternatively, this pattern may result from growth depensation during the larval stage, metamorphosis, and settlement (Koebele 1985, Ochi 1986), followed by compensatory growth throughout the demersal juvenile stage (Jones 2002, Ali et al. 2003).

An additional explanation may be an artifact whereby growth rates for older juveniles are less variable because they are integrated over a wide range of multiple conditions that the juvenile fish have experienced throughout a longer juvenile duration (M.S. Webster, personal communication). In contrast, younger juveniles depend on a short period of either good or bad conditions, and their growth rates tend to be highly variable among individual fish since fewer condition types were experienced by each fish over its shorter juvenile duration. This artifact implies that the environmental conditions which promote fast or slow growth in juvenile rockfish vary temporally on a scale that is captured by the juvenile duration of the collected fish, which ranged from days to approximately a month. Therefore, the temporal scale of variation in growth rates is likely on the order of days to weeks, emphasizing the potential importance of intra-

seasonal variability for marine fish demographics (Dahlgren and Eggleston 2001). For more detail, see Appendix III.

Recommendations for Future Research

This study highlights the importance of using a spatially nested sampling design for investigating spatial patterns in demographics of marine organisms (Caselle and Warner 1996). Future research should focus on testing the hypothesis that regional factors control larval demographics while local factors control juvenile demographics. Experiments and studies should be directed towards identifying the independent and interactive effects of habitat, biological interactions, and oceanographic conditions on the population dynamics of larval and juvenile rockfish. Unraveling the relative contributions of these processes operating on multiple spatial scales will assist efforts to predict the consequences of anthropogenic disturbances such as climate change (Scavia et al. 2002, Walther et al. 2002), overfishing (Dayton et al. 2002), and habitat destruction (Watling and Norse 1998) for the early life history stages of rockfish. Additionally, a test of the Recruitment-Limitation Hypothesis (Hjort 1914, Lasker 1978, Houde 1987) in rockfish would permit a greater understanding of the importance of growth and recruitment during the larval and juvenile stages for structuring year-class strength, for ensuring cohort persistence, and for replenishing adult populations and fisheries stocks.

Further work is needed to investigate temporal variability in growth rates, metamorphosis ages, and selective mortality of the early life history stages of *Sebastes spp.* across similar nested spatial scales. A complementary study of temporal and spatial

patterns in settlement and recruitment for young-of-year rockfish would permit an in-depth assessment of the ecological ramifications of growth and development for cohort persistence and population dynamics. The adoption of a long-term, large-scale approach to examining these demographic parameters would allow correlative explorations of the effects of varying oceanographic conditions (PISCO 2002, A.J. Ammann, M.H. Carr, J.E. Caselle, and C. Syms, personal communication) and habitat features, such as macroalgal dynamics (Mann 1973, Carr 1994a), on the fitness and recruitment of young-of-year rockfish (Carr 1991, Love et al. 1991, Love et al. 2002). For instance, past research has identified the importance of episodic and stochastic events, such as storms (Harger and Landenberger 1971, Cabello-Pasini et al. 2002), El Niños (Victor et al. 2001, Gluyas Millan et al. 2002, Peterson and Keister 2002), and disease outbreaks (Scheibling et al. 1999, Green and Bruckner 2000), for influencing growth and population dynamics in marine organisms.

Ultimately, an improved understanding of spatial and temporal variability in the early life history demographics of rockfish, and their causes and consequences, may assist the planning of necessary conservation efforts. Management strategies that may benefit from superior knowledge of the dynamics of young-of-year rockfish growth and recruitment include the design and placement of marine reserves to enhance fishery yields, protect biodiversity, or facilitate recovery of depleted stocks (Warner et al. 2000, Botsford et al. 2003, Lubchenco et al. 2003), and the establishment of sustainable fishing quotas (Rutherford 2002).

FIGURES

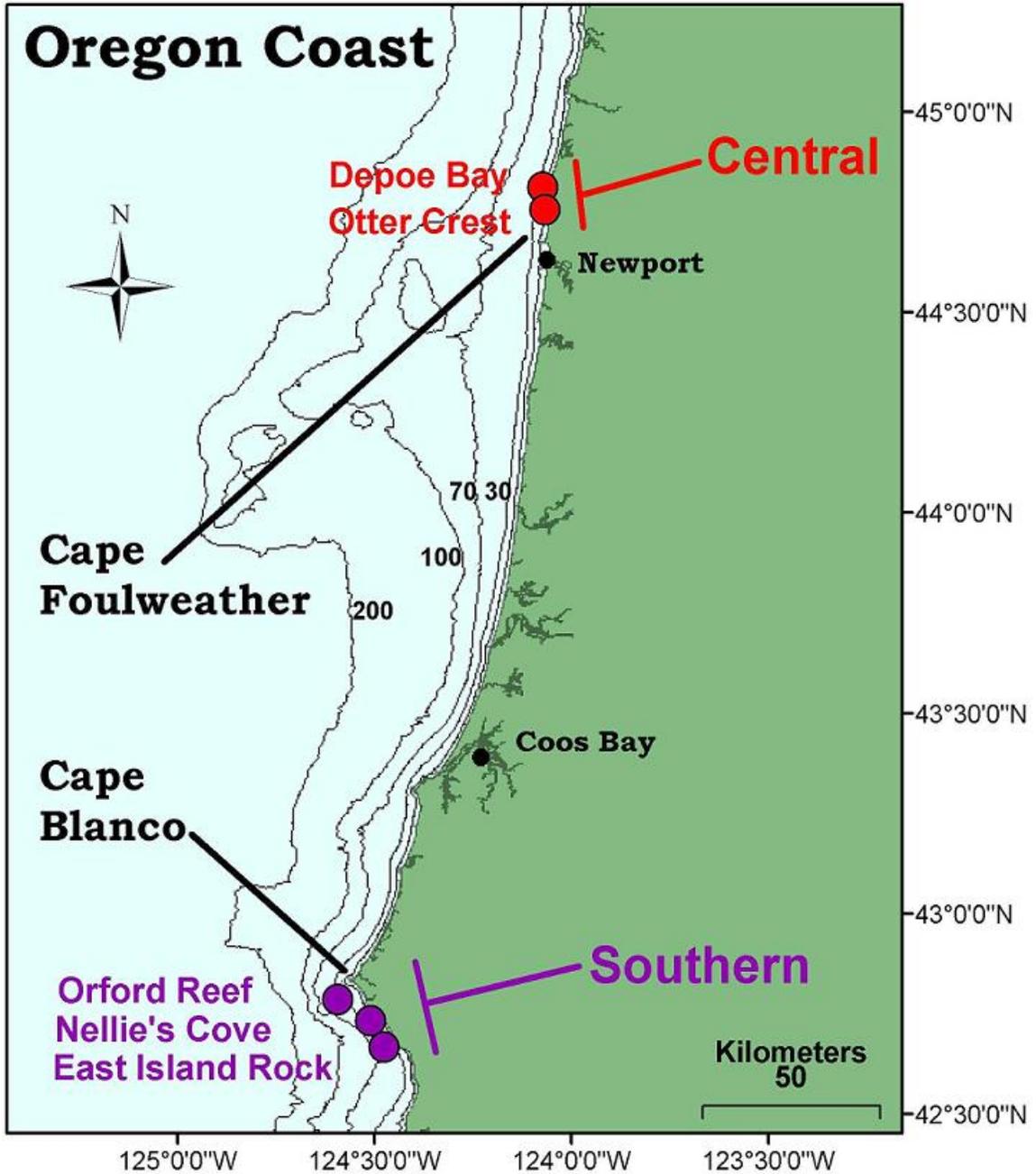


Figure 1. Fish collection sites and regions along the Oregon coast, showing nested sampling scheme. The southern region consists of three local sites south of Cape Blanco, including Orford Reef, Nellie's Cove, and East Island Rock. The central region consists of two local sites near Cape Foulweather, including Depoe Bay and Otter Crest.

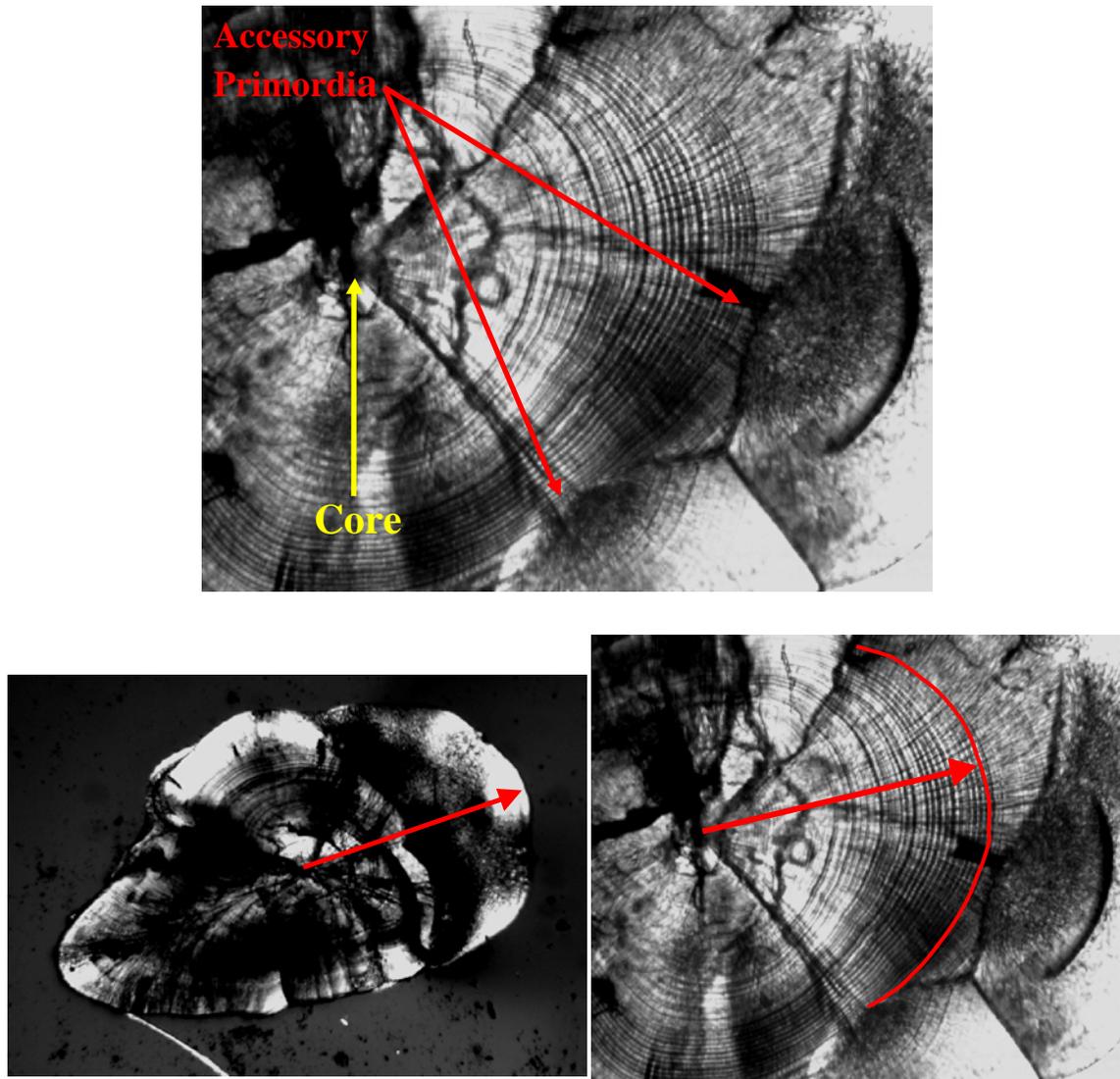


Figure 2. Polished sections of rockfish otoliths, showing important microstructural features and otolith radial measurements. Top: two accessory primordia and daily growth increments radiating from a central nucleus, or primordium (100x magnification). Bottom left: otolith post-rostral radius (40x magnification), measured from the nucleus to the post-rostrum. Bottom right: otolith radius to the first accessory primordium (100x magnification), measured along a posterior transect from the nucleus to the increment marking formation of the first accessory primordium.

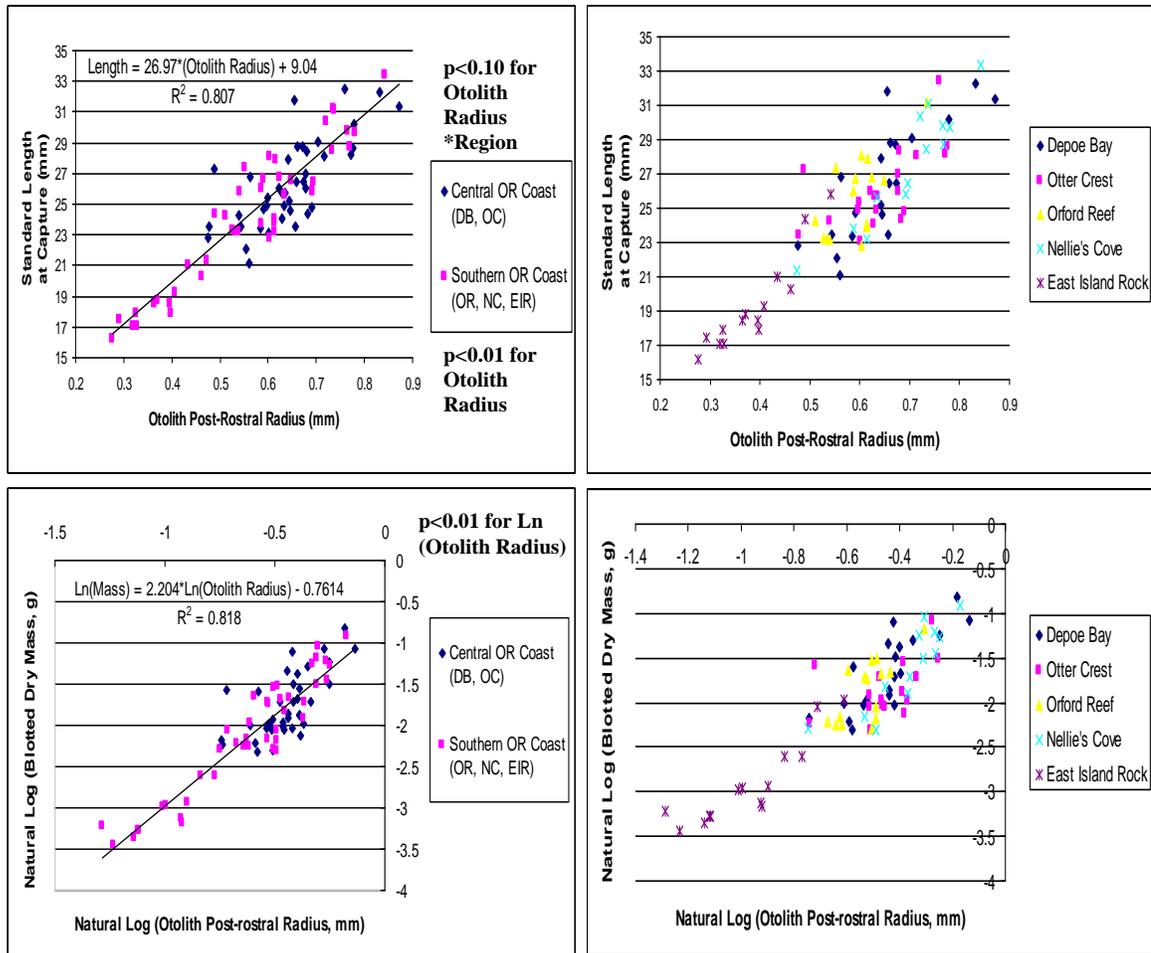


Figure 3. Otolith-somatic growth relationships. Scatter plots of size at capture versus otolith radius, coded by region (left) and site(right). Top: standard length at capture versus otolith post-rostral radius. Bottom: natural log of blotted dry mass at capture versus the natural log of otolith post-rostral radius.

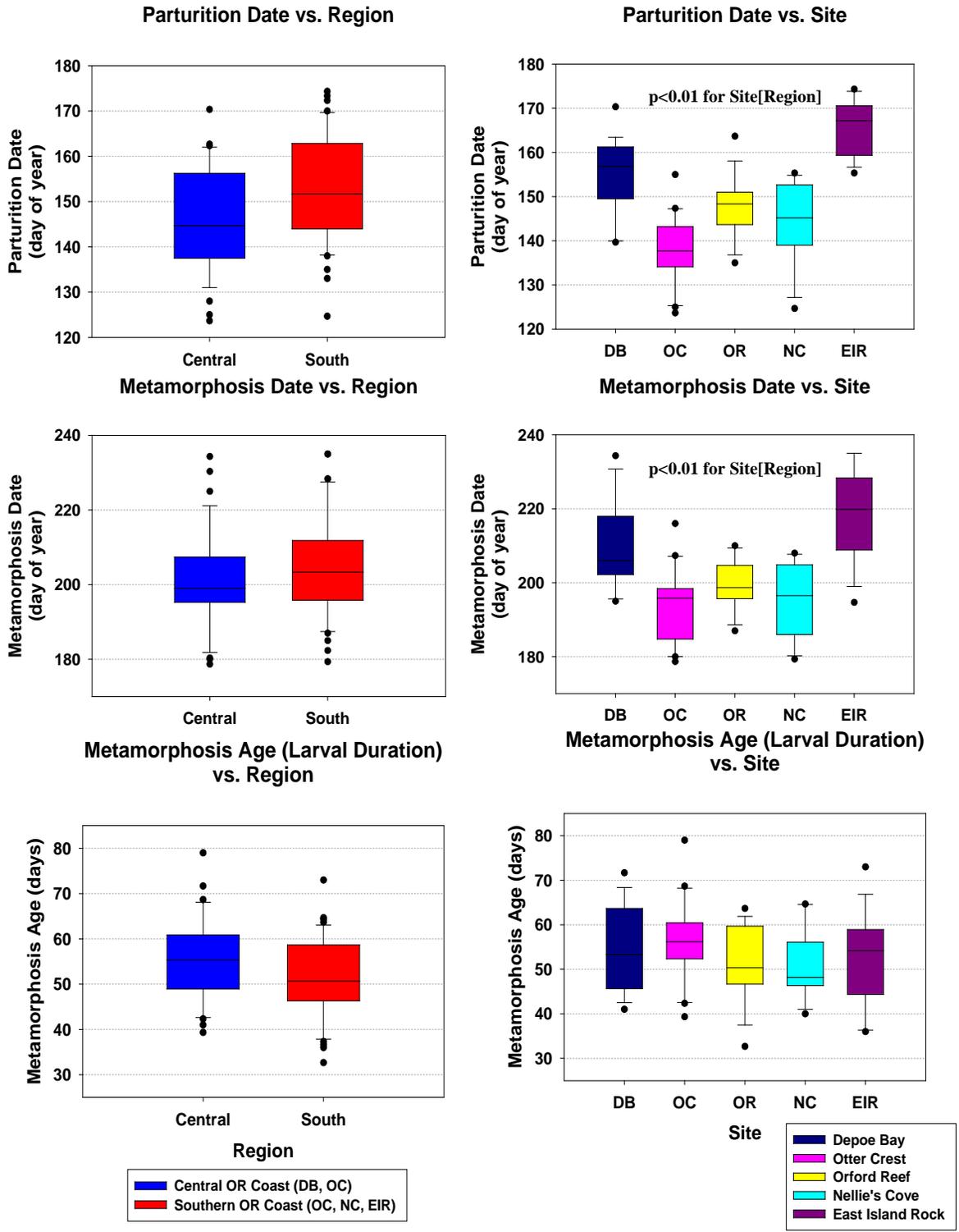


Figure 4. Spatial patterns of dates and ages. Box plots of dates and ages versus region (left) and site (right). Top: parturition dates. Middle: metamorphosis dates. Bottom: metamorphosis ages.

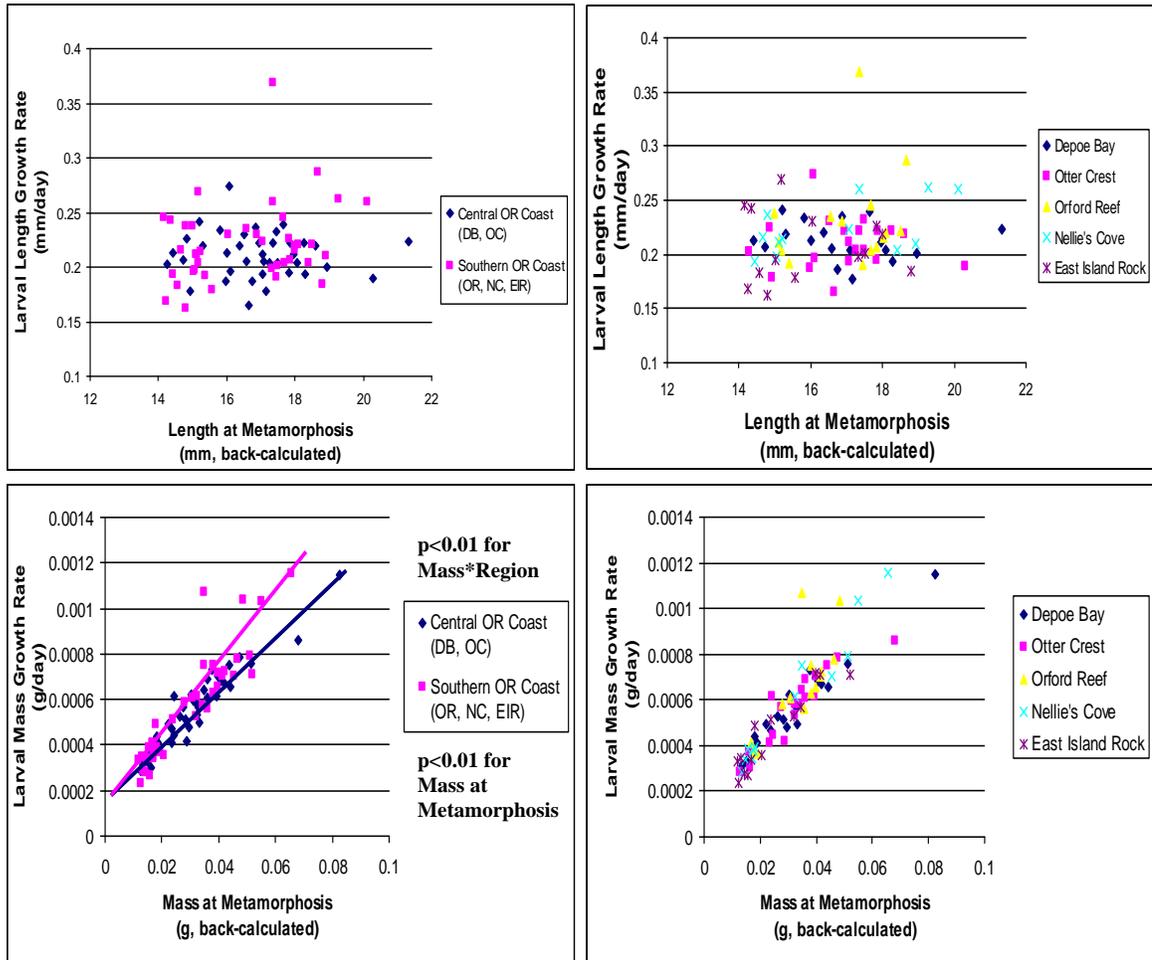


Figure 5. Spatial patterns of larval growth rates. Scatter plots of larval growth rate versus size at metamorphosis, coded by region (left) and site (right). Top: larval length growth rate versus length at metamorphosis. Bottom: larval mass growth rate versus mass at metamorphosis.

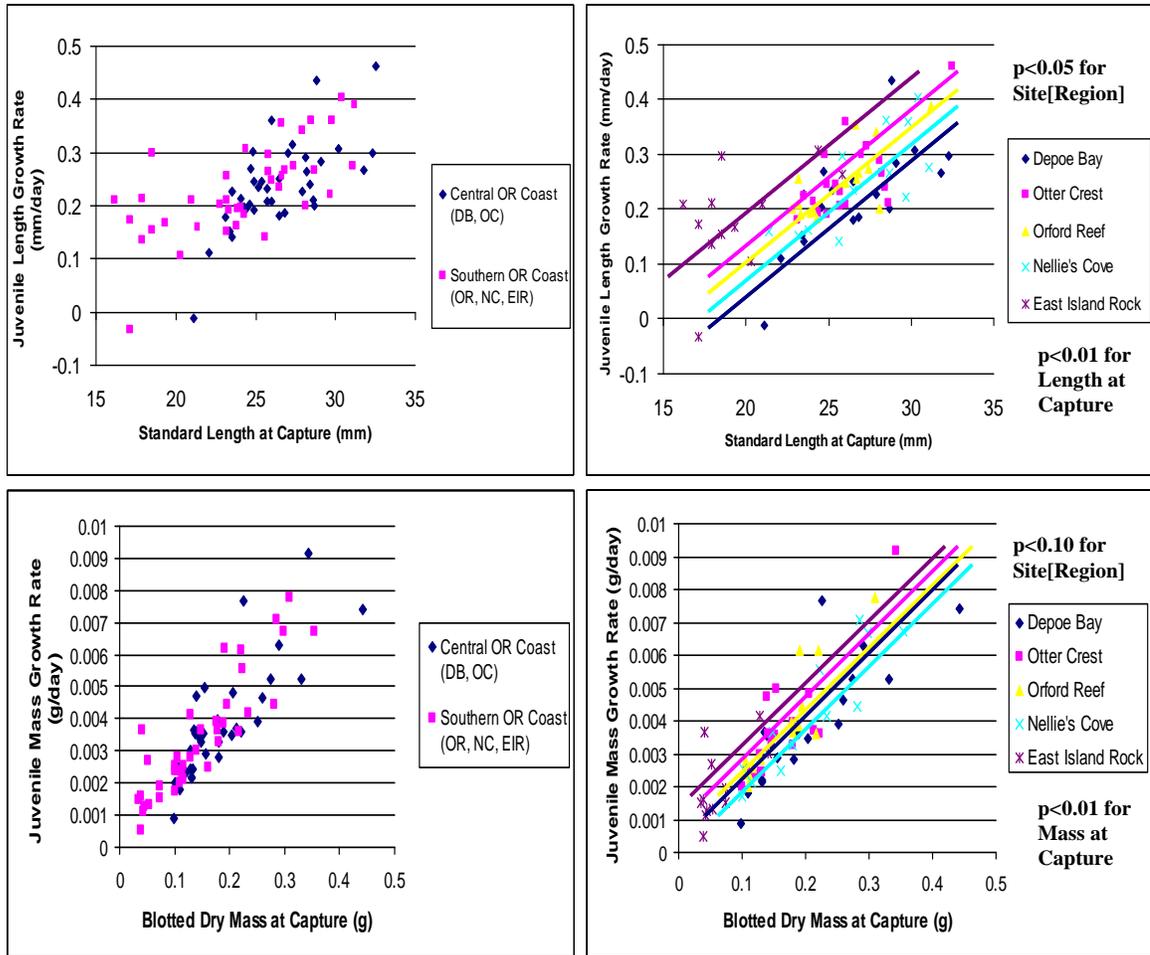


Figure 6. Spatial patterns of juvenile growth rates. Scatter plots of juvenile growth rate versus size at capture, coded by region (left) and site (right). Top: juvenile length growth rate versus length at capture. Bottom: juvenile mass growth rate versus mass at capture.

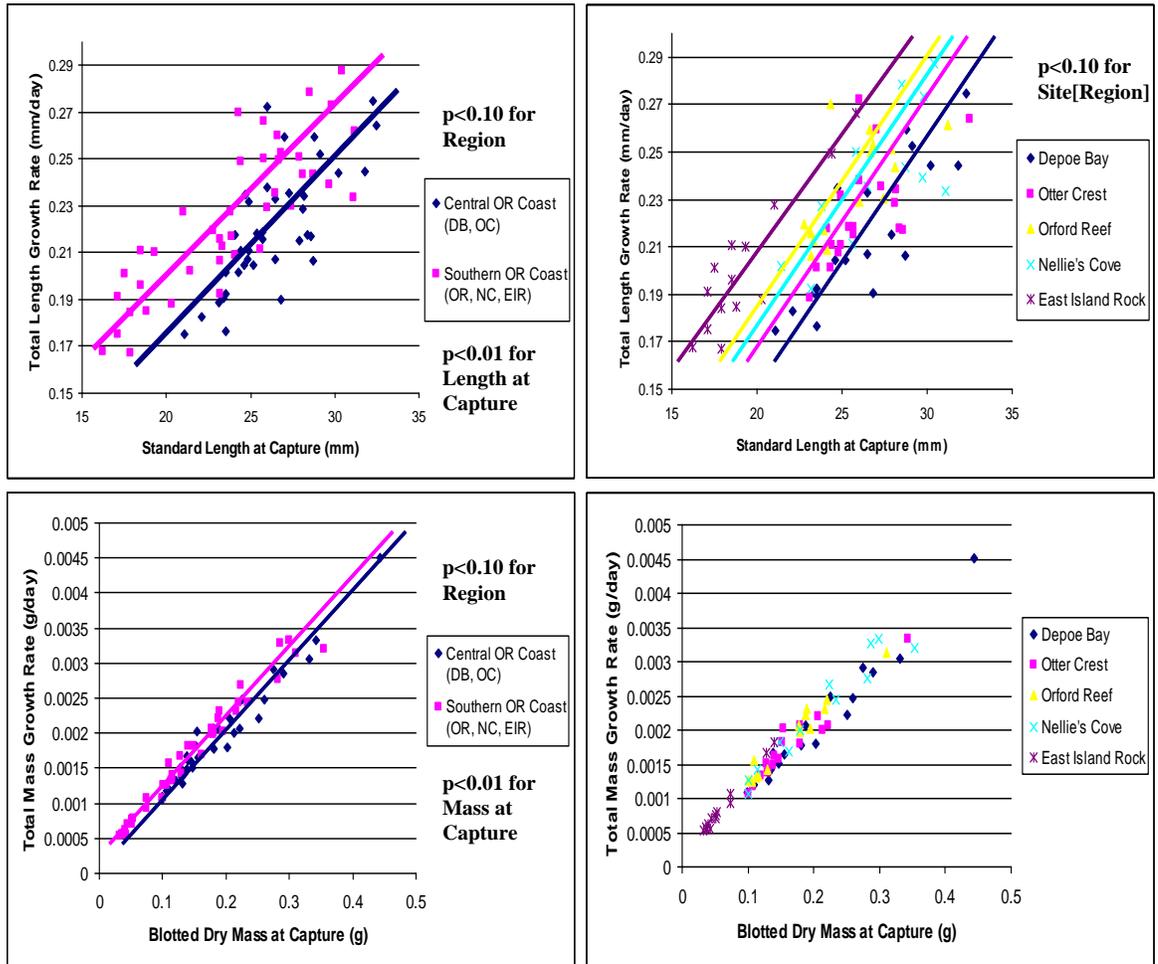


Figure 7. Spatial patterns of total growth rates. Scatter plots of total growth rate versus size at capture, coded by region (left) and site (right). Top: total length growth rate versus length at capture. Bottom: total mass growth rate versus mass at capture.

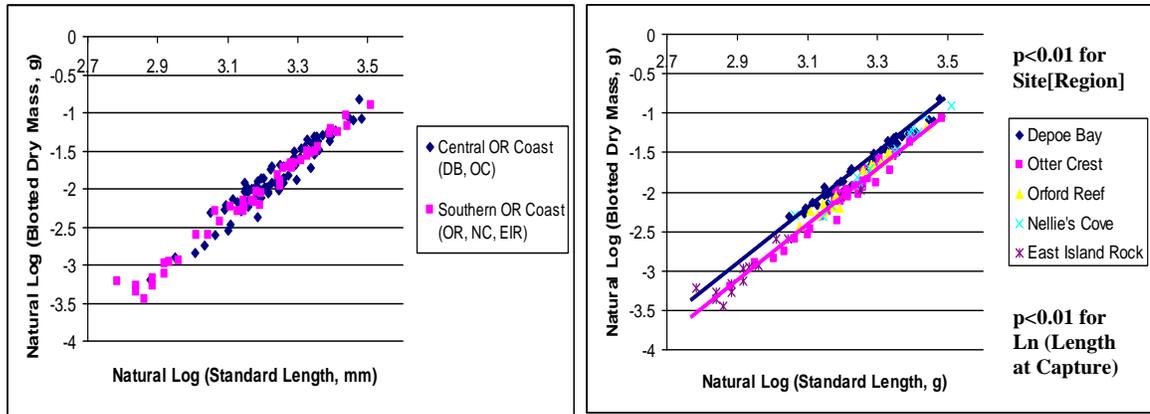


Figure 8. Spatial patterns of juvenile mass-length relationships. Scatter plots of natural log of blotted dry mass versus natural log of standard length at capture, coded by region (left) and site (right).

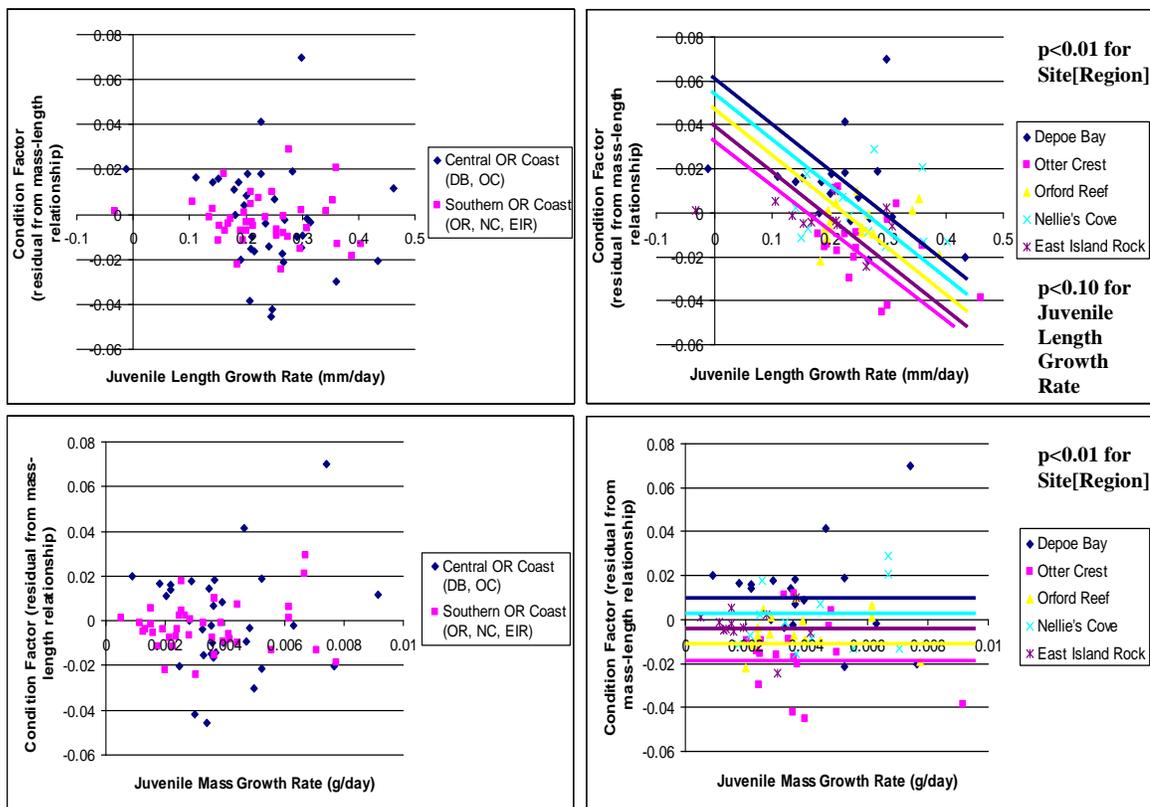


Figure 9. Spatial patterns of juvenile condition factors. Scatter plots of residuals from mass-length relationship, coded by region (left) and site (right). Top: condition factor versus juvenile length growth rate. Bottom: condition factor versus juvenile mass growth rate.

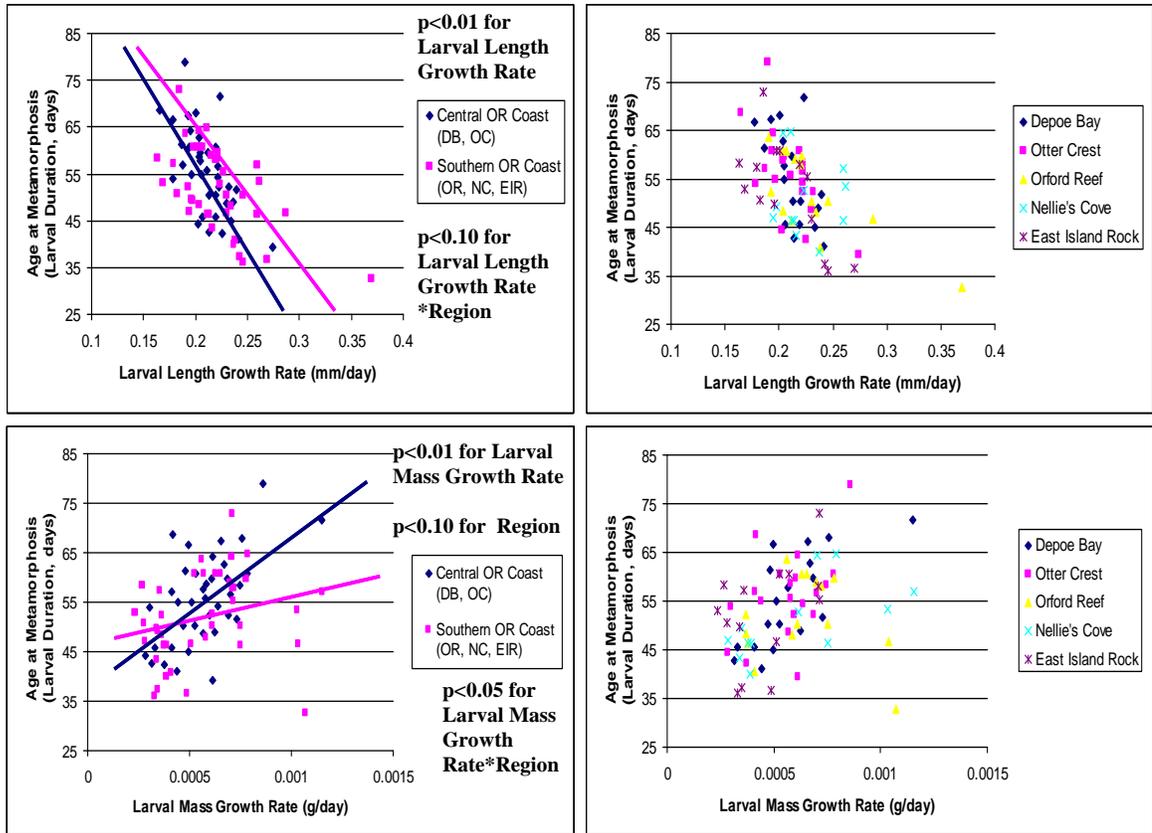


Figure 10. Effect of larval growth rate on larval duration (age at metamorphosis). Top: age at metamorphosis versus larval length growth rate, coded by region (left) and site (right). Bottom: age at metamorphosis versus larval mass growth rate.

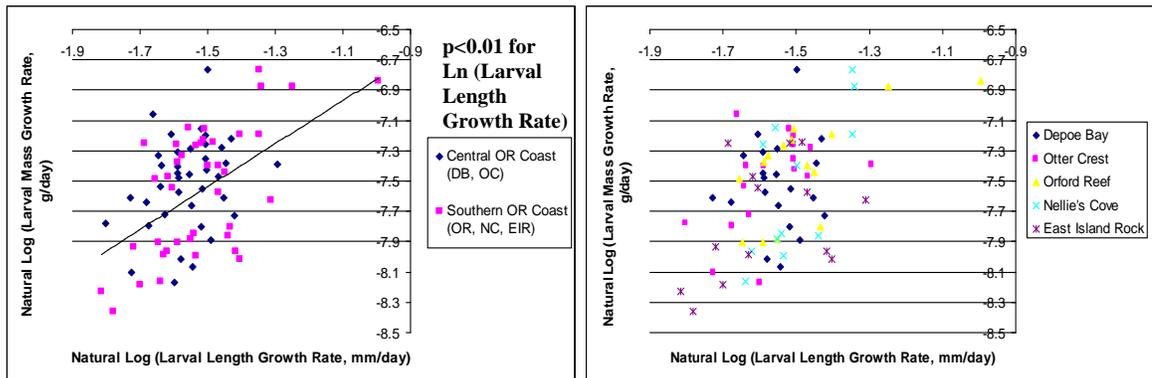


Figure 11. Relationship between larval mass growth rate and larval length growth rate. Scatter plot of natural log of larval mass growth rate versus natural log of larval length growth rate, coded by region (left) and site (right).

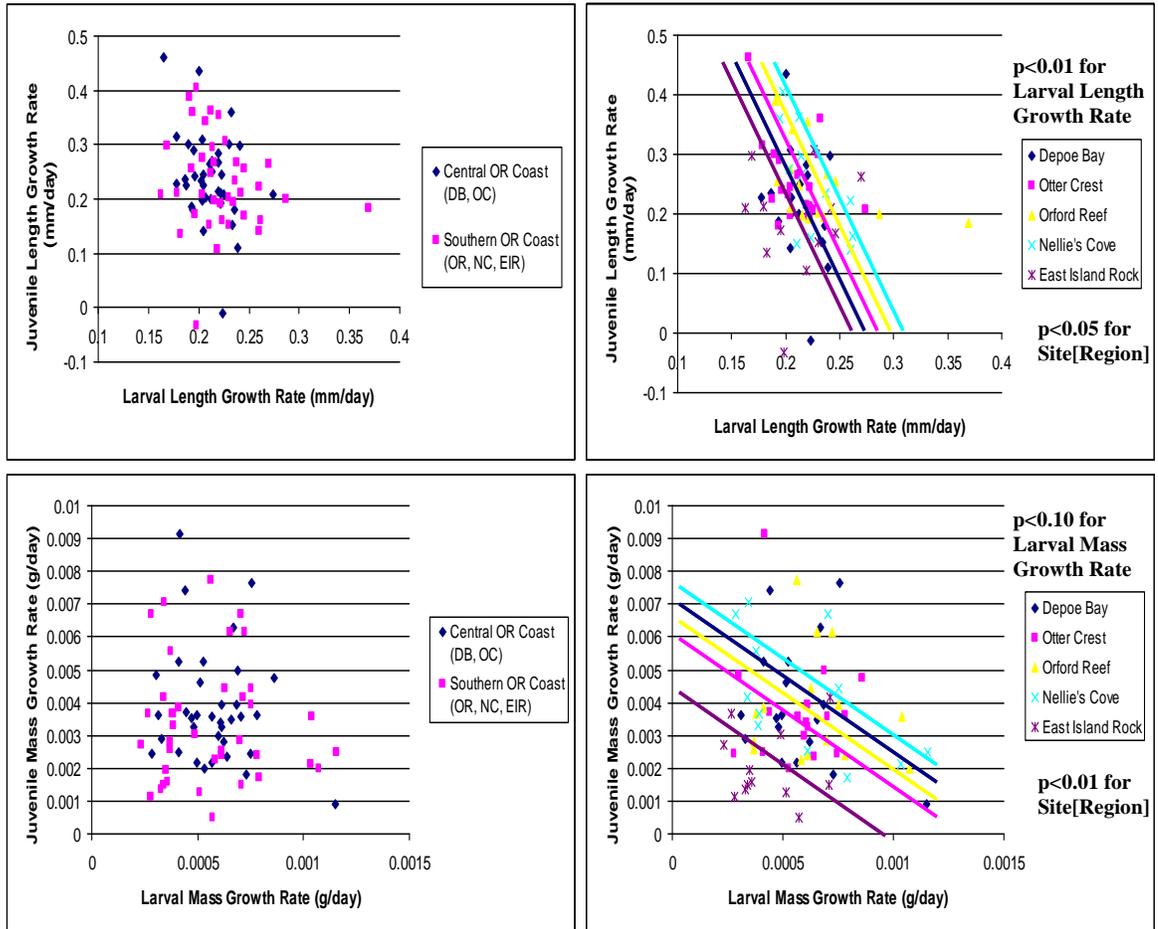


Figure 12. Effect of larval growth rate on juvenile growth rate. Top: juvenile length growth rate versus larval length growth rate, coded by region (left) and site (right). Bottom: juvenile mass growth rate versus larval mass growth rate.

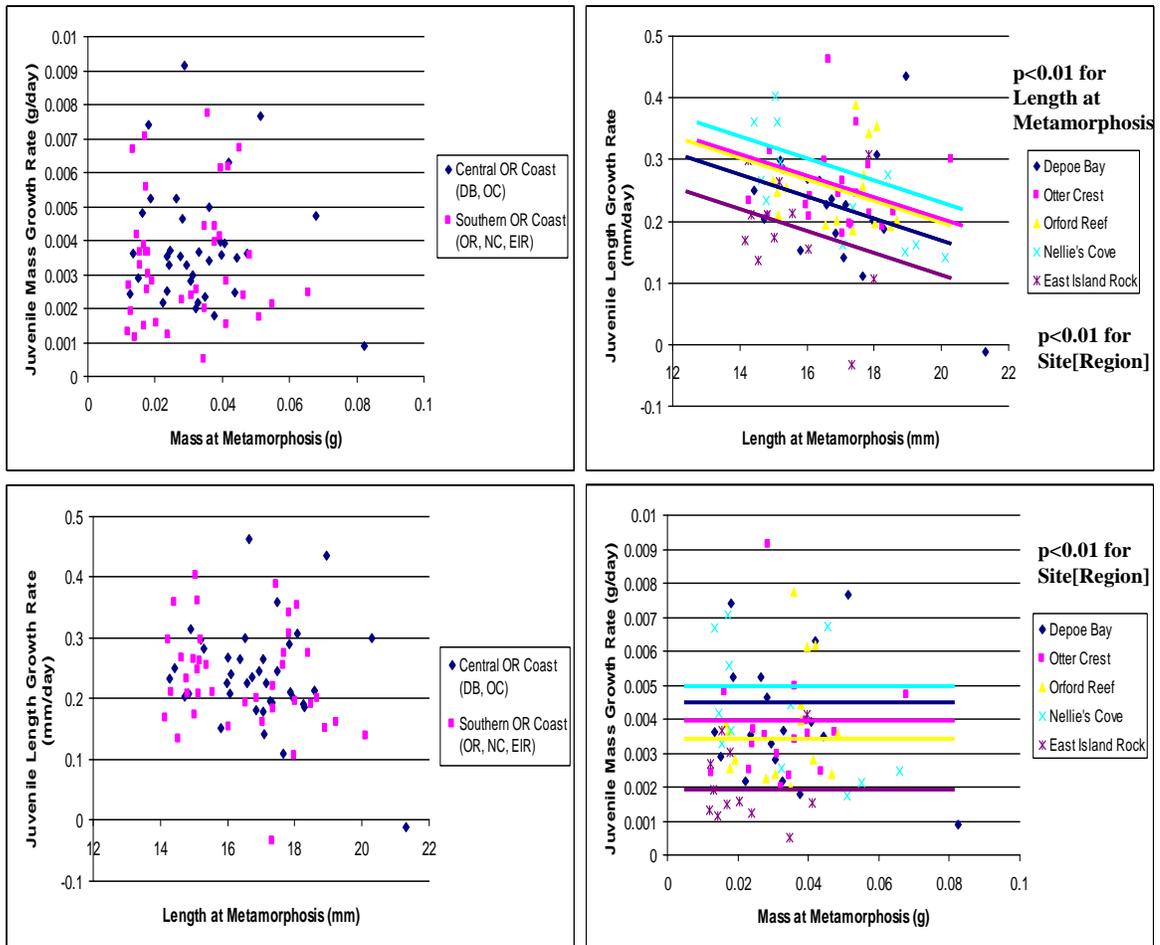


Figure 13. Effect of size at metamorphosis on juvenile growth rate. Top: juvenile length growth rate versus length at metamorphosis, coded by region (left) and site (right). Bottom: juvenile mass growth rate versus mass at metamorphosis.

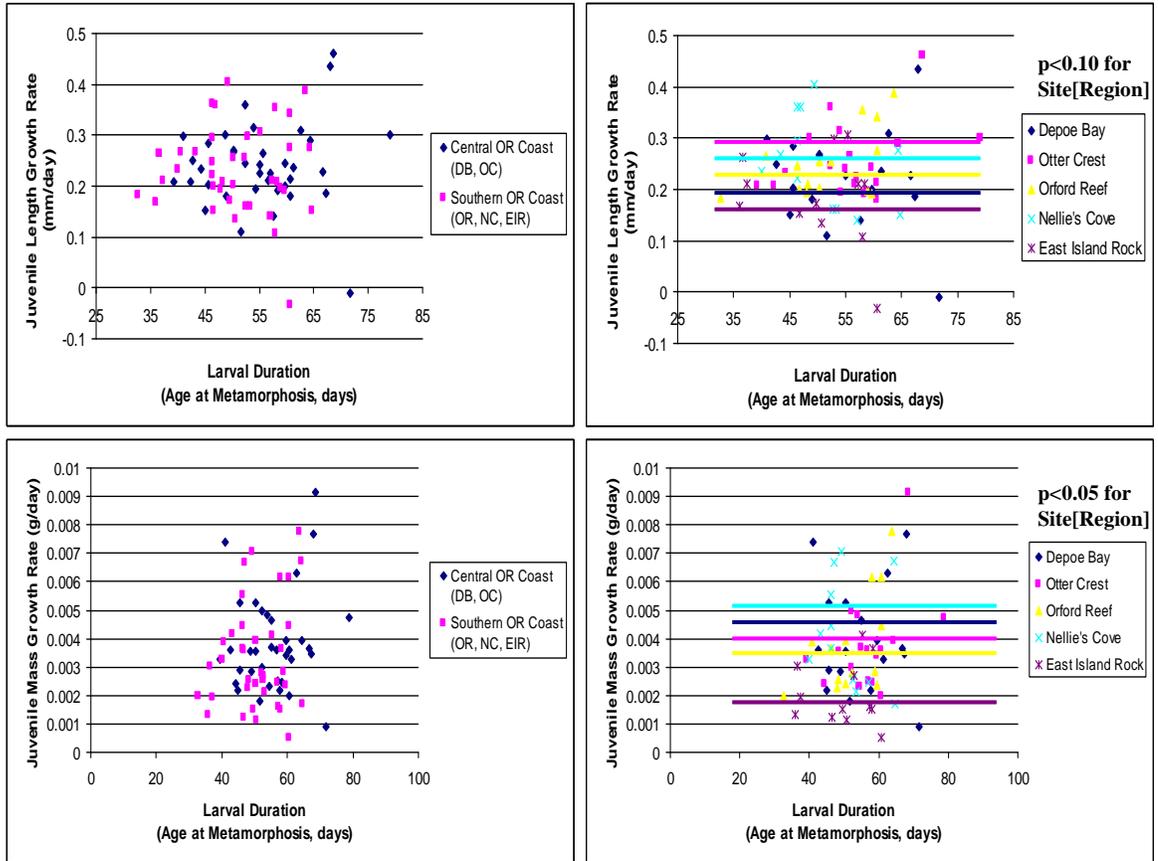


Figure 14. Effect of larval duration (age at metamorphosis) on juvenile growth rate. Top: juvenile length growth rate versus larval duration, coded by region (left) and site (right). Bottom: juvenile mass growth rate versus larval duration.

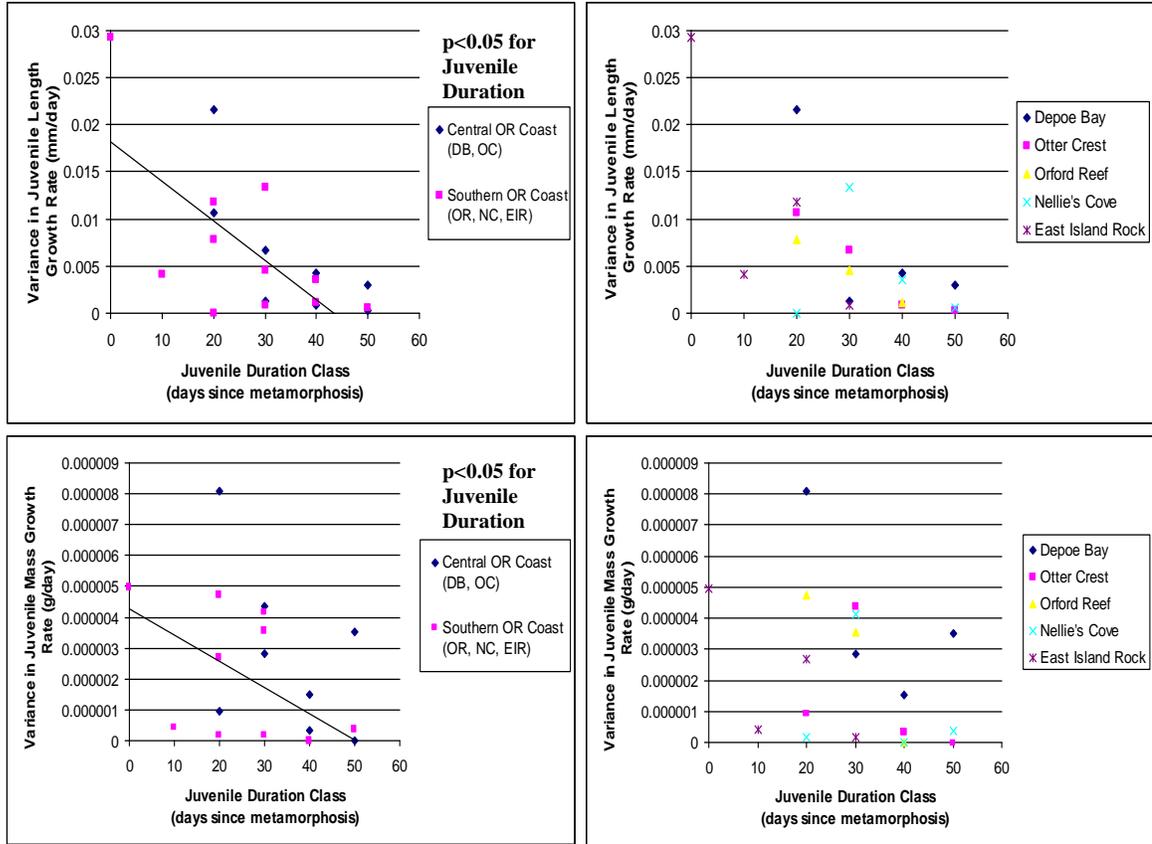


Figure 15. Effect of juvenile duration on variance in juvenile growth rates. Top: variance in juvenile length growth rate versus juvenile duration class, coded by region (left) and site (right). Bottom: variance in juvenile mass growth rate versus juvenile duration class.

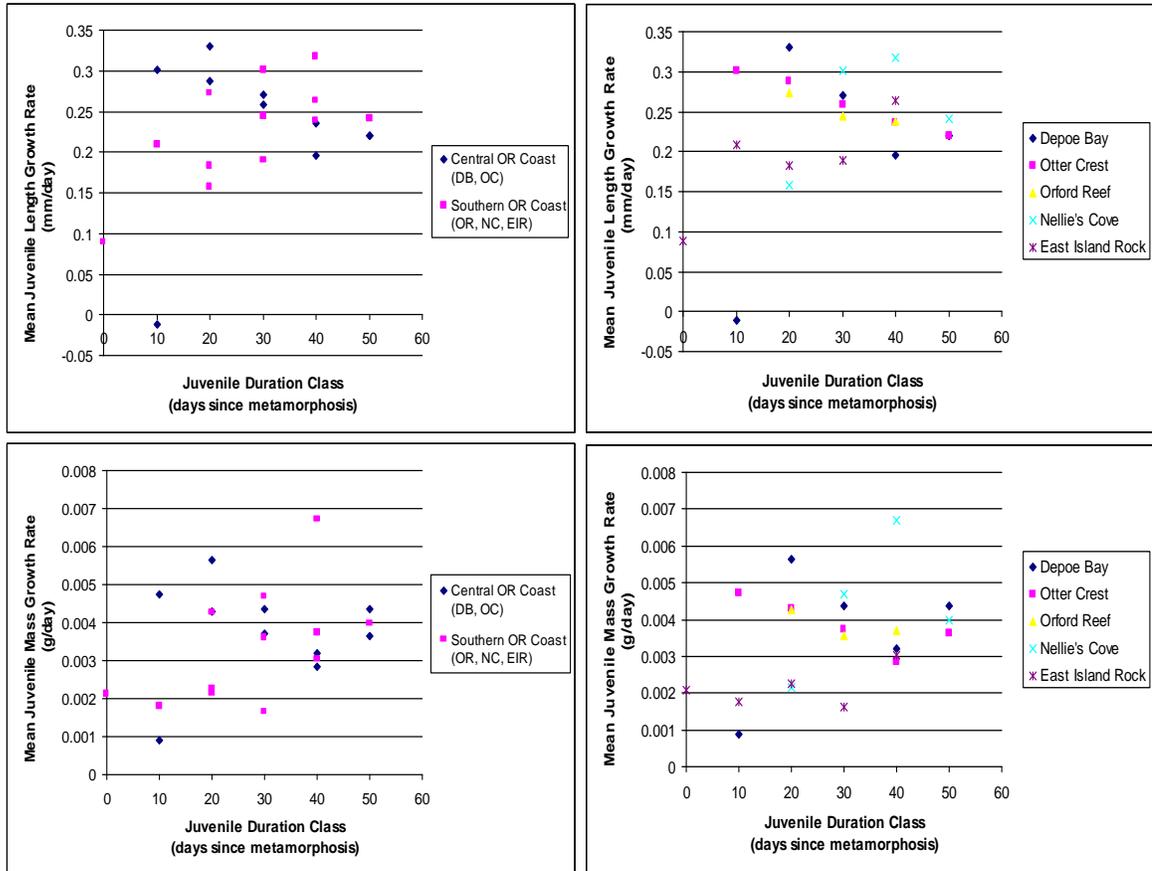


Figure 16. Effect of juvenile duration on mean juvenile growth rate. Top: mean juvenile length growth rate versus juvenile duration class, coded by region (left) and site (right). Bottom: mean juvenile mass growth rate versus juvenile duration class.

BIBLIOGRAPHY

- Abbott, I.A., and G.J. Hollenberg. 1976. *Marine Algae of California*. Stanford University Press. Stanford, CA.
- Alhossaini, M., Q. Liu, and T.J. Pitcher. 1989. Otolith microstructure indicating growth and mortality among plaice, *Pleuronectes platessa* L., juvenile otoliths. *Journal of Fish Biology* **35**(Supplement A): 81-90.
- Ali, M., A. Nicieza, and R.J. Wootton. 2003. Compensatory growth in fishes: a response to growth depression. *Fish and Fisheries* **4**(2): 147-190.
- Ammann, A.J. 2004. SMURFs: standard monitoring units for the recruitment of temperate reef fishes. *Journal of Experimental Marine Biology and Ecology* **299**: 135-154.
- Anderson, J.T. 1988. A review of size dependent survival during pre-recruit stages of fishes in relation to recruitment. *Journal of Northwest Atlantic Fisheries Science* **8**: 55-66.
- Anderson, T.W., and M.H. Carr. 1998. BINCKE: a highly efficient net for collecting reef fishes. *Environmental Biology of Fishes* **51**: 111-115.
- Anderson, T.W., and B.D. Sabado. 1999. Effects of kinship on growth of a live-bearing reef fish. *Marine Biology* **133**: 115-121.
- Bailey, K.M., and E.D. Houde. 1989. Predation on eggs and larvae of marine fishes and the recruitment problem. *Advances in Marine Biology* **25**: 1-83.
- Barth, J.A., S.D. Pierce, and R.L. Smith. 2000. A separating coastal upwelling jet at Cape Blanco, Oregon and its connection to the California Current System. *Deep-Sea Research* **47**: 783-810.
- Barth, J.A., and R.L. Smith. 1998. Separation of a coastal upwelling jet at Cape Blanco, Oregon, USA. *South African Journal of Marine Science* **19**: 5-14.
- Bergenius, M.A.J., M.G. Meekan, D.R. Robertson, and M.I. McCormick. 2002. Larval growth predicts the recruitment success of a coral reef fish. *Oecologia* **131**: 521-525.
- Berkeley, S.A., C. Chapman, and S.M. Sogard. 2004. Maternal age as a determinant of larval growth and survival in a marine fish, *Sebastes melanops*. *Ecology* **85**(5): 1258-1264.

- Beyer, J.E. 1989. Recruitment stability and survival-simple size-specific theory with examples from the early life dynamics of marine fish. *Dana* **7**: 45-147.
- Booth, D.J.. 1995. Juvenile groups in a coral-reef damselfish: density-dependent effects on individual fitness and population demography. *Ecology* **76**(1): 91-106.
- Booth, D.J., and M.A. Hixon. 1999. Food ration and condition affect early survival of the coral reef damselfish, *Stegastes partitus*. *Oecologia* **121**: 364-368.
- Botsford, L.W., F. Micheli, and A. Hastings. 2003. Principles for the design of marine reserves. *Ecological Applications* **13**(1) Supplement: S25-S31.
- Broitman, B.R., and B.P. Kinlan. *In Review*. Spatial scales of primary production in coastal upwelling ecosystems. Submitted to *Limnology and Oceanography*.
- Buchheim, J.R., and M.A. Hixon. 1992. Competition for shelter holes in the coral-reef fish *Acanthemblemaria spinosa* Metzelaar. *Journal of Experimental Marine Biology and Ecology* **164**: 45-54.
- Buonaccorsi, B.P., C.A. Kimbrell, E.A. Lynn, and R.D. Vetter. 2002. Population structure of copper rockfish (*Sebastes caurinus*) reflects post-glacial colonization and contemporary patterns of larval dispersal. *Canadian Journal of Fisheries and Aquatic Sciences* **59**: 1374-1384.
- Burford, M.O. 2001. *Population structure and year-class formation in blue rockfish using microsatellite loci*. M.S. Thesis. San Francisco State University. San Francisco, CA.
- Butler, J.L. 1992. Collection and preservation of material for otolith analysis. Pages 13-17. In, D.K. Stevenson, and S.E. Campana (editors). *Otolith Microstructure Examination and Analysis*. Canada Department of Fisheries and Oceans. Canadian Special Publication of Fisheries and Aquatic Sciences **117**.
- Bystroem, P. and E. Garcia-Berthou. 1999. Density dependent growth and size specific competitive interactions in young fish. *Oikos* **86**(2): 217-232.
- Cabello-Pasini, A., C. Lara-Turrent, and R.C. Zimmerman. 2002. Effect of storms on photosynthesis, carbohydrate content and survival of eelgrass populations from a coastal lagoon and the adjacent open ocean. *Aquatic Botany* **74**(2): 149-164.
- Caley, M.J., M.H. Carr, M.A. Hixon, T.P. Hughes, G.P. Jones, and B.A. Menge. 1996. Recruitment and the local dynamics of open marine populations. *Annual Review of Ecology and Systematics* **27**: 477-500.

- Campana, S.E. 1984. Microstructural growth patterns in the otoliths of larval and juvenile starry flounder, *Platichthys stellatus*. *Canadian Journal of Zoology* **62**: 1507-1512.
- Campana, S.E. 1992. Measurement and interpretation of the microstructure of fish otoliths. Pages 59-71. In, D.K. Stevenson, and S.E. Campana (editors). *Otolith Microstructure Examination and Analysis*. Canada Department of Fisheries and Oceans. Canadian Special Publication of Fisheries and Aquatic Sciences **117**.
- Campana, S.E., and C.M. Jones. 1992. Analysis of otolith microstructure data. Pages 73-100. In, D.K. Stevenson, and S.E. Campana (editors). *Otolith Microstructure Examination and Analysis*. Canada Department of Fisheries and Oceans. Canadian Special Publication of Fisheries and Aquatic Sciences **117**.
- Campana, S.E., and J.D. Neilson. 1985. Microstructure of fish otoliths. *Canadian Journal of Fisheries and Aquatic Sciences* **42**: 1014-1032.
- Carr, M.H. 1989. Effects of macroalgal assemblages on the recruitment of temperate zone reef fishes. *Journal of Experimental Marine Biology and Ecology* **126**: 59-76.
- Carr, M.H. 1991. Habitat selection and recruitment of an assemblage of temperate zone reef fishes. *Journal of Experimental Marine Biology and Ecology* **146**: 59-76.
- Carr, M.H. 1994a. Effects of macroalgal dynamics on recruitment of a temperate reef fish. *Ecology* **75**(5): 1320-1333.
- Carr, M.H. 1994b. Predicting recruitment of temperate reef fishes in response to changes in macrophyte density caused by disturbance. Pages 255-269. In, D.J. Stouder, K.L. Fresh, and R.J. Feller (editors). *Theory and Application in Fish Feeding Ecology*. The Belle W. Baruch Library in Marine Science, Number 18. University of South Carolina Press. Columbia, South Carolina.
- Caselle, J.E., and R.R. Warner. 1996. Variability in recruitment of coral reef fishes: the importance of habitat at two spatial scales. *Ecology* **77**(8): 2488-2504.
- Clark, B.M. 1997. Variation in surf-zone fish community structure across a wave-exposure gradient. *Estuarine Coastal and Shelf Science* **44**(6): 659-674.
- Connell, S.D. 1998. Effects of predators on growth, mortality and abundance of a juvenile reef-fish: evidence from manipulations of predator and prey abundance. *Marine Ecology Progress Series* **169**: 251-261.
- Connell, S.D. 2002. Effects of a predator and prey on a foraging reef fish: implications for understanding density-dependent growth. *Journal of Fish Biology* **60**(6): 1551-1561.

- Cowan, Jr., J.H., E.D. Houde, and K.A. Rose. 1996. Size-dependent vulnerability of marine fish larvae to predation: an individual-based numerical experiment. *ICES Journal of Marine Science* **53**: 23-37.
- Cowan, Jr., J.H., and R.F. Shaw. 2002. Recruitment. Pages 88-111. In, L.A. Fuiman, and R.G. Werner (editors). *Fishery Science: The Unique Contributions of Early Life History Stages*. Blackwell Science. Oxford, UK.
- Cowen, R.K. 1991. Variation in the planktonic larval duration of the temperate wrasse *Semicossyphus pulcher*. *Marine Ecology Progress Series* **69**: 9-15.
- Cowen, R.K., K.M.M. Lwiza, S. Sponaugle, C.B. Paris, and D.B. Olson. 2000. Connectivity of marine populations: open or closed? *Science* **287**(5454): 857-859.
- Cushing, D.H. 1975. *Marine Ecology and Fisheries*. Cambridge University Press. London, UK.
- Cushing, D.H., and J.W. Horwood. 1994. The growth and death of fish larvae. *Journal of Plankton Research* **16**: 291-300.
- Dahlgren, C.P., and D.B. Eggleston. 2001. Spatio-temporal variability in abundance, size and microhabitat associations of early juvenile Nassau grouper *Epinephelus striatus* in an off-reef nursery system. *Marine Ecology Progress Series* **217**: 145-156.
- Dayton, P.K. 1985. Ecology of kelp communities. *Annual Review of Ecology and Systematics* **16**: 215-245.
- Dayton, P.K., M.J. Tegner, P.B. Edwards, and K.L. Riser. 1999. Temporal and spatial scales of kelp demography: the role of oceanographic climate. *Ecological Monographs* **69**(2): 219-250.
- Dayton, P.K., Thrush, S., and F.C. Coleman. 2002. *Ecological Effects of Fishing in Marine Ecosystems of the United States*. Pew Oceans Commission. Arlington, VA.
- Doherty, P., and T. Fowler. 1994. An empirical test of recruitment limitation in a coral reef fish. *Science* **263**(5149): 935-939.
- Doherty, P., and D. Williams. 1988. The replenishment of coral reef fish populations. *Oceanography and Marine Biology. An Annual Review* **26**: 487-551.
- Fortier, L., and J.A. Gagné. 1990. Larval herring (*Clupea harengus*) dispersion, growth, and survival in the St. Lawrence Estuary: match/mismatch or

- membership/vagrancy? *Canadian Journal of Fisheries and Aquatic Sciences* **47**: 1898-1912.
- Freidenburg, T.L. 2002. *The Effects of Oceanographic Processes on Rocky Intertidal Communities*. Ph.D. Thesis. Oregon State University. Corvallis, OR.
- Fuiman, L.A. 1989. Vulnerability of Atlantic herring larvae to predation by yearling herring. *Marine Ecology Progress Series* **51**: 291-299.
- Fuiman, L.A. 1994. The interplay of ontogeny and scaling in the interactions of fish larvae and their predators. *Journal of Fish Biology* **45**(Supplement A): 55-79.
- Fuiman, L.A. 2002. Special considerations of fish eggs and larvae. Pages 1-32. In, L.A. Fuiman, and R.G. Werner (editors). *Fishery Science: The Unique Contributions of Early Life History Stages*. Blackwell Science. Oxford, UK.
- Fuiman, L.A., and B.C. Delbos. 1998. Developmental changes in visual sensitivity of red drum, *Sciaenops ocellatus*. *Copeia* **1998**: 936-943.
- Fuiman, L.A., and P.W. Webb. 1988. Ontogeny of routine swimming activity and performance in zebra danios (*Teleostei: Cyprinidae*). *Animal Behaviour* **36**: 250-261.
- Gaines, S.D., and J. Roughgarden. 1987. Fish in offshore kelp forests affect recruitment to intertidal barnacle populations. *Science* **235**(4787): 479-481.
- Gartner, Jr., J.V. 1991. Life histories of three species of lanternfishes (Pisces: Myctophidae) from the eastern Gulf of Mexico. I. Morphological and microstructural analysis of sagittal otoliths. *Marine Biology* **111**: 11-20.
- Geffen, A.J. 1992. Validation of otolith increment deposition rate. Pages 101-113. In, D.K. Stevenson, and S.E. Campana (editors). *Otolith Microstructure Examination and Analysis*. Canada Department of Fisheries and Oceans. Canadian Special Publication of Fisheries and Aquatic Sciences **117**.
- Genovese, S.J., and J.D. Witman. 1999. Interactive effects of flow speed and particle concentration on growth rates of an active suspension feeder. *Limnology and Oceanography* **44**(4): 1120-1131.
- Gluyas Millan, M.G., C. Quinonez Velazquez, and J. Talavera Maya. 2002. Effect of El Niño 1997-98 on the snail *Astraea undosa* (Wood) population along the Baja California western coast. *Journal of Shellfish Research* **21**(2): 831-834.
- Graham, M.H., C. Harrold, S. Lisin, K. Light, J.M. Watanabe, and M.S. Foster. 1997. Population dynamics of giant kelp *Macrocystis pyrifera* along a wave exposure gradient. *Marine Ecology Progress Series* **148**: 269-279.

- Grantham, B.A., F. Chan, K.J. Nielsen, D.S. Fox, J.A. Barth, A. Huyer, J. Lubchenco, and B.A. Menge. 2004. Upwelling-driven nearshore hypoxia signals ecosystem and oceanographic changes in the northeast Pacific. *Nature* **429**(6993): 749-754.
- Green, E.P., and A.W. Bruckner. 2000. The significance of coral disease epizootiology for coral reef conservation. *Biological Conservation* **96**(3): 347-361.
- Hakala, T., M. Viitasalo, H. Rita, E. Aro, J. Flinkman, and I. Vuorinen. 2003. Temporal and spatial variation in the growth rates of Baltic herring (*Clupea harengus membras* L.) larvae during summer. *Marine Biology* **142**: 25-33.
- Hare, J.A., and R.K. Cowen. 1994. Ontogeny and otolith microstructure of bluefish, *Pomatomus saltatrix* (Pisces: Pomatomidae). *Marine Biology* **118**: 541-550.
- Hare, J.A., and R.K. Cowen. 1997. Size, growth, development, and survival of the planktonic larvae *Pomatomus saltatrix* (Pisces: Pomatomidae). *Ecology* **78**(8): 2415-2431.
- Harger, J.R.E., and D.E. Landenberger. 1971. The effect of storms as a density dependent mortality factor on populations of sea mussels. *Veliger* **14**(2): 195-201.
- Hjort, J. 1914. Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. *Rapports et Procès-verbaux des Réunions, Conseil International pour l'Exploration de la Mer* **20**: 1-228.
- Hoelzer, G.A. 1987. The effect of early experience on aggression in two territorial scorpaenid fishes. *Environmental Biology of Fishes* **19**: 183-194.
- Hoelzer, G.A. 1988. Juvenile movement patterns in a territorial scorpaenid fish before and during settlement. *Marine Ecology Progress Series* **45**: 193-195.
- Houde, E.D. 1987. Fish early life dynamics and recruitment variability. *American Fisheries Society, Symposium* **2**: 17-29.
- Houde, E.D. 1989. Subtleties and episodes in the early life of fishes. *Journal of Fish Biology* **35**(Supplement A): 29-38.
- Houde, E.D. 1994. Differences between marine and freshwater fish larvae: implications for recruitment. *ICES Journal of Marine Science* **51**: 91-97.
- Houde, E.D. 1997. Patterns and trends in larval-stage growth and mortality of teleost fish. *Journal of Fish Biology* **51**(Supplement A): 52-83.

- Houde, E.D. 2002. Mortality. Pages 64-87. In, L.A. Fuiman, and R.G. Werner (editors). *Fishery Science: The Unique Contributions of Early Life History Stages*. Blackwell Science. Oxford, UK.
- Huyer, A. 1983. Coastal upwelling in the California Current System. *Progress in Oceanography* **12**: 259-284.
- Iles, T.D., and M. Sinclair. 1982. Atlantic herring: stock discreteness and abundance. *Science* **215**(4533): 627-633.
- Jones, C.M. 1986. Determining age of larval fish with the otolith increment technique. *Fishery Bulletin* **84**: 91-104.
- Jones, C.M. 1992. Development and application of the otolith increment technique. Pages 1-11. In, D.K. Stevenson, and S.E. Campana (editors). *Otolith Microstructure Examination and Analysis*. Canada Department of Fisheries and Oceans. Canadian Special Publication of Fisheries and Aquatic Sciences **117**.
- Jones, G.P. 1988. Experimental evaluation of the effects of habitat structure and competitive interactions on the juveniles of two coral reef fishes. *Journal of Experimental Marine Biology* **123**: 115-126.
- Jones, G.P., M.J. Milicich, M.J. Emslie, and C. Lunow. 1999. Self-recruitment in a coral reef fish population. *Nature* **402**(6763): 802-804.
- Jones, C.M. 2002. Age and growth. Pages 33-63. In, L.A. Fuiman, and R.G. Werner (editors). *Fishery Science: The Unique Contributions of Early Life History Stages*. Blackwell Science. Oxford, UK.
- Karakiri, M., R. Berghahn, and H. von Westernhagen. 1989. Growth differences in 0-group plaice *Pleuronectes platessa* as revealed by otolith microstructure analysis. *Marine Ecology Progress Series* **55**: 15-22.
- Kaufman, L., J. Ebersole, J. Beets, and C.C. McIvor. 1992. A key phase in the recruitment dynamics of coral reef fishes: post-settlement transition. *Environmental Biology of Fishes* **34**: 109-118.
- Koebele, B.P. 1985. Growth and the size hierarchy effect: an experimental assessment of three proposed mechanisms; activity differences, disproportional food acquisition, physiological stress. *Environmental Biology of Fishes* **12**(3): 181-188.
- Kramer, S.H. 1991. Growth, mortality, and movements of juvenile California halibut *Paralichthys californicus* in shallow coastal and bay habitats of San Diego County, California. *Fishery Bulletin* **89**: 195-207.

- Laidig, T.E., S. Ralston, and J.R. Bence. 1991. Dynamics of growth in the early life history of shortbelly rockfish *Sebastes jordani*. *Fishery Bulletin* **89**: 611-621.
- Laidig, T.E., and K.M. Sakuma. 1998. Description of pelagic larval and juvenile grass rockfish, *Sebastes rastrelliger* (family Scorpaenidae), with an examination of age and growth. *Fishery Bulletin* **96**: 788-796.
- Laidig, T.E., K.M. Sakuma, and M.M. Nishimoto. 1996. Description of pelagic larval and juvenile stripetail rockfish, *Sebastes saxicola* (family Scorpaenidae), with an examination of larval growth. *Fishery Bulletin* **94**: 289-299.
- Larson, R. 2002. *Sebastes carnatus*, *Sebastes chrysomelas*. Pages 140-143. In, M.S. Love, M. Yoklavich, and L. Thorsteinson. *The Rockfishes of the Northeast Pacific*. University of California Press. Berkeley and Los Angeles, CA.
- Lasker, R. 1978. The relationship between oceanographic conditions and larval anchovy food in the California Current: identification of factors contributing to recruitment failure. *Rapports et Procès-verbaux des Réunions, Conseil International pour l'Exploration de la Mer* **173**: 212-230.
- Leggett, W.C., and E. DeBlois. 1994. Recruitment in marine fishes: is it regulated by starvation and predation in the egg and larval stages? *Netherlands Journal of Sea Research* **32**: 119-134.
- Leichter, J.J., and J.D. Witman. 1997. Water flow over subtidal rock walls: relation to distributions and growth rates of sessile suspension feeders in the Gulf of Maine. Water flow and growth rates. *Journal of Experimental Marine Biology and Ecology* **209**: 293-307.
- Levin, P., R. Petrik, and J. Malone. 1997. Interactive effects of habitat selection, food supply and predation on recruitment of an estuarine fish. *Oecologia* **112**: 55-63.
- Linkowski, T.B. 1991. Otolith microstructure and growth pattern during the early life history of lanternfishes (family Myctophidae). *Canadian Journal of Zoology* **69**: 1777-1792.
- Love, M.S. 2002. *Sebastes caurinus*. Pages 144-147. In, M.S. Love, M. Yoklavich, and L. Thorsteinson. *The Rockfishes of the Northeast Pacific*. University of California Press. Berkeley and Los Angeles, CA.
- Love, M.S., M.H. Carr, and L.J. Haldorson. 1991. The ecology of substrate-associated juveniles of the genus *Sebastes*. *Environmental Biology of Fishes* **30**: 225-243.
- Love, M.S., M. Yoklavich, and L. Thorsteinson. 2002. *The Rockfishes of the Northeast Pacific*. University of California Press. Berkeley and Los Angeles, CA.

- Lubchenco, J., S.R. Palumbi, S.D. Gaines, and S. Andelman. 2003. Plugging a hole in the ocean: the emerging science of marine reserves. *Ecological Applications* **13**(1) Supplement: S3-S7.
- Magnuson, J.J. 1962. An analysis of aggressive behavior, growth, and competition for food and space in medaka (*Oryzias latipes*). *Canadian Journal of Zoology* **40**: 313-363.
- Mann, K.H. 1973. Seaweeds: their productivity and strategy for growth. *Science* **182**(4116): 975-981.
- Matarese, A.C., A.W. Kendall, Jr., D.M. Blood, and B.M. Vinter. 1989. *Laboratory Guide to Early Life History Stages of Northeast Pacific Fishes*. U.S. Department of Commerce. NOAA Technical Report NMFS **80**.
- McCormick, M.I. 1998. Condition and growth of reef fish at settlement: Is it important? *Australian Journal of Ecology* **23**: 258-264.
- McCormick, M.I. 1999. Delayed metamorphosis of a tropical reef fish (*Acanthurus triostegus*): a field experiment. *Marine Ecology Progress Series* **176**: 25-38.
- McCormick, M.I., and L.J. Makey. 1997. Post-settlement transition in coral reef fishes: overlooked complexity in niche shifts. *Marine Ecology Progress Series* **153**: 247-257.
- McCormick, M.I., and B.W. Molony. 1992. Effects of feeding history on the growth characteristics of a reef fish at settlement. *Marine Biology* **114**: 165-173.
- McCormick, M.I., and B.W. Molony. 1995. Influence of water temperature during the larval stage on size, age and body condition of a tropical reef fish at settlement. *Marine Ecology Progress Series* **118**: 59-68.
- Menge, B.A., and J.P. Sutherland. 1987. Community regulation – variation in disturbance, competition, and predation in relation to environmental-stress and recruitment. *American Naturalist* **30**: 730-757.
- Metcalf, N.B., F.A. Huntingford, and J.E. Thorpe. 1987. The influence of predation risk on the feeding motivation and foraging strategy of juvenile Atlantic salmon. *Animal Behaviour* **35**: 901-911.
- Miller, J.A., and A.L. Shanks. *In Press*. Limited larval dispersal in a temperate marine fish: implications for population structure and marine reserve design. *Canadian Journal of Fisheries and Aquatic Sciences*.

- Miller, T.J., L.B. Crowder, J.A. Rice, and E.A. Marschall. 1988. Larval size and recruitment mechanisms in fishes: toward a conceptual framework. *Canadian Journal of Fisheries and Aquatic Sciences* **45**: 1657-1670.
- Montgomery, J.C., N. Tolimieri, O.S. Haine. 2001. Active habitat selection by pre-settlement reef fishes. *Fish and Fisheries* **2**(3): 261-277.
- Moreland, S.L., and C.A. Reilly. 1991. Key to the juvenile rockfishes of central California. In, Laidig, T.E., and P.B. Adams (editors). *Methods Used to Identify Pelagic Juvenile Rockfish (Genus Sebastes) Along the Coast of Central California*. U.S. Department of Commerce. NOAA Technical Memorandum NMFS-SWFSC-166.
- Murray, S.N., R.F. Ambrose, J.A. Bohnsack, L.W. Botsford, M.H. Carr, G.E. Davis, P.K. Dayton, D. Gotshall, D.R. Gunderson, M.A. Hixon, J. Lubchenco, M. Mangel, A. MacCall, D.A. McArdle, J.C. Ogden, J. Roughgarden, R.M. Starr, M.J. Tegner, M.M. Yoklavich. 1999. No-take reserve networks: protection for fishery populations and marine ecosystems. *Fisheries* **24**(11): 11-25.
- Myers, R.A., and N.G. Cadigan. 1993. Density-dependent juvenile mortality in marine demersal fish. *Canadian Journal of Fisheries and Aquatic Sciences* **50**: 1576-1590.
- Neilson, J.D. 1992. Sources of error in otolith microstructure examination. Pages 115-126. In, D.K. Stevenson, and S.E. Campana (editors). *Otolith Microstructure Examination and Analysis*. Canada Department of Fisheries and Oceans. Canadian Special Publication of Fisheries and Aquatic Sciences **117**.
- Nelson, P.A. 2001. Behavioral ecology of young-of-the-year kelp rockfish, *Sebastes atrovirens* Jordan and Gilbert (Pisces: Scorpaenidae). *Journal of Experimental Marine Biology and Ecology* **256**: 33-50.
- Ochi, H. 1986. Growth of the anemonefish *Amphiprion clarkii* in temperate waters, with special reference to the influence of settling time on the growth of 0-year olds. *Marine Biology* **92**: 223-229.
- Parmentier, E., D. Lecchini, F. Lagardere, and P. Vandewalle. 2004. Ontogenic and ecological control of metamorphosis onset in a carapid fish, *Carapus homei*: experimental evidence from vertebra and otolith comparisons. *Journal of Experimental Zoology* **301A**: 617-628.
- Parrish, R.H., C.S. Nelson, and A. Bakun. 1981. Transport mechanisms and reproductive success of fishes in the California Current. *Biological Oceanography* **1**: 175-203.

- Pasten, G.P., S. Katayama, and M. Omori. 2003. Timing of parturition, planktonic duration, and settlement patterns of the black rockfish, *Sebastes inermis*. *Environmental Biology of Fishes* **68**(3): 229-239.
- Peterson, W.T., and J.E. Keister. 2002. The effect of a large cape on distribution patterns of coastal and oceanic copepods off Oregon and northern California during the 1998-1999 El Niño - La Niña. *Progress in Oceanography* **53**(Special Issue): 389-411.
- Pfister, C.A. 1997. Demographic consequences of within-year variation in recruitment. *Marine Ecology Progress Series* **153**: 229-238.
- PFMC (Pacific Fishery Management Council). 2000. *Status of the Pacific Coast Groundfish Fishery through 2000 and Acceptable Biological Catches for 2001*. Pacific Fishery Management Council. Portland, OR.
- PFMC (Pacific Fishery Management Council). 2002. *Status of the Pacific Coast Groundfish Fishery through 2001 and Acceptable Biological Catches for 2002*. Pacific Fishery Management Council. Portland, OR.
- PFMC (Pacific Fishery Management Council). 2003. *Status of the Pacific Coast Groundfish Fishery through 2003, Stock Assessment and Fishery Evaluation*. Pacific Fishery Management Council. Portland, OR.
- PFMC (Pacific Fishery Management Council). 2004a. *Pacific Coast Groundfish Fishery Management Plan for the California, Oregon, and Washington Groundfish Fishery, as Amended through Amendment 17*. Pacific Fishery Management Council. Portland, OR.
- PFMC (Pacific Fishery Management Council). 2004b. *Status of the Pacific Coast Groundfish Fishery through 2004, Stock Assessment and Fishery Evaluation*. Pacific Fishery Management Council. Portland, OR.
- PISCO. 2002. *Coastal Connections, Volume One*. Partnership for Interdisciplinary Studies of Coastal Oceans. Available Online at URL <http://www.piscoweb.org/outreach/pubs/PCC3.html>
- Plaza, G., S. Katayama, and M. Omori. 2001. Otolith microstructure of the black rockfish, *Sebastes inermis*. *Marine Biology* **139**: 797-805.
- Ralston, S. 1998. The status of federally managed rockfish on the U.S. west coast. Pages 6-16. In, M. Yoklavich (editor). *Marine Harvest Refugia for West Coast Rockfish: A Workshop*. NOAA Technical Memorandum NMFS-SWFSC-255.
- Ralston, S., E.B. Brothers, D.A. Roberts, and K.M. Sakuma. 1996. Accuracy of age estimates for larval *Sebastes jordani*. *Fishery Bulletin* **94**: 89-97.

- Ramsey, F.L., and D.W. Schafer. 1997. *The Statistical Sleuth: A Course in Methods of Data Analysis*. Duxbury Press. Belmont, CA.
- Ricker, W.E. 1969. Effects of size-selective mortality and sampling bias on estimates of growth, mortality, production, and yield. *Journal of the Fisheries Research Board of Canada* **26**: 479-541.
- Roberts, C.M. 1997. Connectivity and management of Caribbean coral reefs. *Science* **278**(5342): 1454-1457.
- Roughgarden, J., S. Gaines, and H. Possingham. 1988. Recruitment dynamics in complex life cycles. *Science* **241**(4872): 1460-1466.
- Rutherford, E.S. 2002. Fishery management. Pages 206-221. *In*, L.A. Fuiman, and R.G. Werner (editors). *Fishery Science: The Unique Contributions of Early Life History Stages*. Blackwell Science. Oxford, UK.
- Sakuma, K.M., and T.E. Laidig. 1995. Description of larval and pelagic juvenile chilipepper, *Sebastes goodei* (family Scorpaenidae), with an examination of larval growth. *Fishery Bulletin* **93**: 721-731.
- Sale, P.F. 1990. Recruitment of marine species: Is the bandwagon rolling in the right direction? *Trends in Ecology and Evolution* **5**(1): 25-27.
- Sanford, E., and B.A. Menge. 2001. Spatial and temporal variation in barnacle growth in a coastal upwelling system. *Marine Ecology Progress Series* **209**: 143-157.
- Scavia, D., J.C. Field, D.V. Boesch, R.W. Buddemeir, V. Burkett, D.R. Cayan, M. Fogarty, M.A. Harwell, R.W. Howarth, C. Mason, D.J. Reed, T.C. Royer, A.H. Sallenger, and J.G. Titus. 2002. Climate change impacts on U.S. coastal and marine ecosystems. *Estuaries* **25**(2): 149-164.
- Scheibling, R.E., A.W. Hennigar, and T. Balch. 1999. Destructive grazing, epiphytism, and disease: the dynamics of sea urchin - kelp interactions in Nova Scotia. *Canadian Journal of Fisheries and Aquatic Sciences* **56**: 2300-2314.
- Searcy, S.P., and S. Sponaugle. 2001. Selective mortality during the larval-juvenile transition in two coral reef fishes. *Ecology* **82**(9): 2452-2470.
- Secor, D.H., and J.M. Dean. 1989. Somatic growth effects on the otolith – fish size relationship in young pond-reared striped bass, *Morone saxatilis*. *Canadian Journal of Fisheries and Aquatic Sciences* **46**: 113-121.
- Secor, D.H., J.M. Dean, and E.H. Laban. 1992. Otolith removal and preparation for microstructural examination. Pages 19-57. *In*, D.K. Stevenson, and S.E.

- Campana (editors). *Otolith Microstructure Examination and Analysis*. Canada Department of Fisheries and Oceans. Canadian Special Publication of Fisheries and Aquatic Sciences **117**.
- Segar, D.A. 1998. *Introduction to Ocean Sciences*. Wadsworth Publishing Company. Belmont, CA.
- Service, R.F. 2004. New dead zone off Oregon coast hints at sea change in currents. *Science* **305**: 1099.
- Shima, J.S., and A.M. Findlay. 2002. Pelagic larval growth rate impacts benthic settlement and survival of a temperate reef fish. *Marine Ecology Progress Series* **235**: 303-309.
- Sponaugle, S., and R.K. Cowen. 1994. Larval durations and recruitment patterns of two Caribbean gobies (Gobiidae): contrasting early life histories in a demersal spawner. *Marine Biology* **120**: 133-143.
- Sokal, R.R., and F.J. Rohlf. 1995. *Biometry: The Principles and Practice of Statistics in Biological Research*. W.H. Freeman and Company. New York, NY.
- Sogard, S.M. 1991. Interpretation of otolith microstructure in juvenile winter flounder (*Pseudopleuronectes americanus*): ontogenetic development, daily increment validation, and somatic growth relationships. *Canadian Journal of Fisheries and Aquatic Sciences* **48**: 1862-1871.
- Sogard, S.M. 1997. Size-selective mortality in the juvenile stage of teleost fishes: a review. *Bulletin of Marine Science* **60**(3): 1129-1157.
- Steneck, R.S., M.H. Graham, B.J. Bourque, D. Corbett, J.M. Erlandson, J.A. Estes, and M.J. Tegner. 2002. Kelp forest ecosystems: biodiversity, stability, resilience and future. *Environmental Conservation* **29**(4): 436-459.
- Stephens, Jr., J.S., R.J. Larson, and D.J. Pondella, II. *In Press*. Rocky reefs and kelp beds. Chapter 9. *In*, L.G. Allen, M. Horn, and D.J. Pondella, II, (editors). *The Ecology of California Marine Fishes*. University of California Press. Berkeley and Los Angeles, CA.
- Sunye, P.S. 1999. *Effects of regional climate changes on the sardine fishery Sardinella brasiliensis off South-East coast of Brazil (1964-1993)*. Universite de Bretagne Occidentale. IUEM. Brest, France.
- Swearer, S.E., J.E. Caselle, D.W. Lea, and R.R. Warner. 1999. Larval retention and recruitment in an island population of a coral-reef fish. *Nature* **402**(6763): 799-802.

- Swearer, S.E., J.S. Shima, M.E. Hellberg, S.R. Thorrold, G.P. Jones, D.R. Robertson, S.G. Morgan, K.A. Selkoe, G.M. Ruiz, and R.W. Warner. 2002. Evidence of self-recruitment in demersal marine populations. *Bulletin of Marine Science* **70**(1) Supplement: 251-271.
- Takasuka, A., I. Aoki, and I. Mitani. 2003. Evidence of growth-selective predation on larval Japanese anchovy *Engraulis japonicus* in Sagami Bay. *Marine Ecology Progress Series* **252**: 223-238.
- Taylor, M.S., and M.E. Hellberg. 2003. Genetic evidence for local retention of pelagic larvae in a Caribbean reef fish. *Science* **299**(5603): 107-109.
- Toole, C.L., D.F. Markle, and P.M. Harris. 1993. Relationships between otolith microstructure, microchemistry, and early life history events in Dover sole, *Microstomus pacificus*. *Fishery Bulletin* **91**: 732-753.
- Tupper, M., and R.G. Boutilier. 1997. Effects of habitat on settlement, growth, predation risk and survival of a temperate reef fish. *Marine Ecology Progress Series* **151**: 225-236.
- Victor, B.C. 1986. Delayed metamorphosis with reduced larval growth in a coral reef fish (*Thalassoma bifasciatum*). *Canadian Journal of Fisheries and Aquatic Sciences* **43**: 1208-1213.
- Victor, B.C., G.M. Wellington, D.R. Robertson, and B.I. Ruttenberg. 2001. The effect of the El Niño-Southern Oscillation event on the distribution of reef-associated labrid fishes in the eastern Pacific Ocean. *Bulletin of Marine Science* **69**(1): 279-288.
- Walther, G.R., E. Post, P. Convey, A. Menzel, C. Parmesan, J.C.T. Beebee, J.M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. *Nature* **416**(6879): 389-395.
- Warner, R.R., S.E. Swearer, and J.E. Caselle. 2000. Larval accumulation and retention: implications for the design of marine reserves and essential fish habitat. *Bulletin of Marine Science* **66**(3): 821-830.
- Watling, L., and E.A. Norse. 1998. Disturbance of the seabed by mobile fishing gear: a comparison to forest clearcutting. *Conservation Biology* **12**(6): 1180-1197.
- Webster, M.S. 2004. Density dependence via intercohort competition in a coral-reef fish. *Ecology* **85**(4): 986-994.
- Webster, M.S., and M.A. Hixon. 2000. Mechanisms and individual consequences of intraspecific competition in a coral-reef fish. *Marine Ecology Progress Series* **196**: 187-194.

- Wieters, E.A., D.M. Kaplan, S.A. Navarrete, A. Sotomayor, J. Largier, K.J. Nielsen, and F. Véliz. 2003. Alongshore and temporal variability in chlorophyll *a* concentration in Chilean nearshore waters. *Marine Ecology Progress Series* **249**: 93-105.
- Wheeler, P.A., A. Huyer, and J. Fleischbein. Cold halocline, increased nutrients and higher productivity off Oregon in 2002. *Geophysical Research Letters* **30**: 8021.
- Williams, P.J., J.A. Brown, V. Gotceitas, and P. Pepin. 1996. Developmental changes in escape response performance of marine larval fish. *Canadian Journal of Fisheries and Aquatic Sciences* **53**: 1246-1253.
- Yamanaka, L. 2002. *Sebastes maliger*. Pages 201-203. In, M.S. Love, M. Yoklavich, and L. Thorsteinson. *The Rockfishes of the Northeast Pacific*. University of California Press. Berkeley and Los Angeles, CA.
- Yoklavich, M.M., and G.W. Boehlert. 1987. Daily growth increments in otoliths of juvenile black rockfish, *Sebastes melanops*: An evaluation of autoradiography as a new method of validation. *Fishery Bulletin* **85**: 826-832.
- Youson, J.H. 1988. First metamorphosis. Pages 135-196. In, W.S. Hoar, and D.J. Randall (editors). *Fish Physiology. Volume II: The Physiology of Developing Fish. Part B: Viviparity and Posthatching*. Academic Press. San Diego, CA.
- Zar, J.H. 1999. *Biostatistical Analysis*. Prentice Hall. Upper Saddle River, NJ.
- Zaunreiter, M., H. Junger, and K. Kotrschal. 1991. Retinal morphology of cyprinid fishes: a quantitative histological study of ontogenetic changes and interspecific variation. *Vision Research* **31**: 383-394.

APPENDICES

APPENDIX I: DETAILED DATA ANALYSES

P-values

P-values from ANOVA terms of $p < 0.01$ were interpreted as convincing evidence of a significant effect (Ramsey and Schafer 1997). P-values of $0.01 < p < 0.05$ were interpreted as moderate evidence of a significant effect. P-values of $0.05 < p < 0.10$ were interpreted as suggestive, but inconclusive, evidence of a significant effect. P-values of $p > 0.10$ were interpreted as no evidence of a significant effect.

Fish Size Back-calculations

Fish sizes were back-calculated to the age of metamorphosis by modeling the otolith-somatic growth relationship with a Multifactorial Nested ANOVA of fish size on otolith radius, region, and site within region (Sokal and Rohlf 1995, Zar 1999). An appropriate regression equation was then fit to the relationship between fish size and otolith radius after eliminating non-significant terms at a p-value cut-off of 0.05 (Campana and Jones 1992). Measurements of otolith radii to the first accessory primordia were used as proxies for otolith radii at metamorphosis (Laidig et al. 1991). These values were inputted to the regression equation describing the otolith-somatic growth relationship in order to back-calculate predicted fish sizes at metamorphosis.

A Multifactorial Nested ANOVA of SL at capture with terms for Region, Site[Region], Otolith Post-rostral Radius, and Otolith Post-rostral Radius*Region was conducted in JMP 4.0 (Sokal and Rohlf 1995, Zar 1999). Region was considered a fixed effect, while Site[Region] was considered a random effect. Non-significant terms of Region, Site[Region], and Otolith Post-rostral Radius*Region were eliminated from the ANOVA model at a p-value cut-off of 0.05. A simple linear regression of SL at Capture versus Average Otolith Post-rostral Radius was fitted to the data in Microsoft Excel, describing the otolith-somatic growth relationship with the equation:

$$\text{Standard Length} = 26.97 * (\text{Otolith Radius}) + 9.04$$

Average post-rostral otolith radii to the first accessory primordium were inserted as explanatory variables (Otolith Radius) in the regression equation to back-calculate lengths of fish at the age of formation of the first accessory primordium (Campana and Jones 1992). This age was taken to be the age of metamorphosis (Laidig et al. 1991). Standard lengths at capture were used as the lengths at metamorphosis for two fish with no accessory primordia visible in their otoliths.

The procedure described above for fish size back-calculations was repeated after substituting blotted dry masses for SL, using a natural log transformation on mass and otolith radius in order to linearize the data. Terms of Region, Site[Region], and $\text{Ln}(\text{Otolith Post-rostral Radius}) * \text{Region}$ were also non-significant at $p > 0.05$ and were eliminated from the ANOVA model. A simple linear regression of $\text{Ln}(\text{Blotted Dry Mass})$

at Capture) versus Ln(Average Otolith Post-rostral Radius) was fitted to the data in Microsoft Excel, describing the otolith-somatic growth relationship with the equation:

$$\text{Ln(Blotted Dry Mass)} = 2.204 * \text{Ln(Otolith Radius)} - 0.761$$

Average post-rostral otolith radii to the first accessory primordium were inserted as explanatory variables into the regression equation and used to back-calculate masses at metamorphosis. Blotted dry masses at capture were used as the masses at metamorphosis for two fish with no accessory primordia visible in their otoliths.

6) *Do parturition dates, metamorphosis dates, or metamorphosis ages (i.e., larval durations) vary between regions or among local sites along the Oregon coast?*

An ANOVA of estimated parturition date with terms for region and site[region] was conducted to validate age estimates from otolith increment counts, with the assumption that all juvenile rockfish collected from each region along the Oregon coast parturated at approximately the same time. Spatial differences in estimated parturition dates among sites within each region may indicate that otolith increments are not formed with a consistent temporal periodicity (e.g., daily) (Geffen 1992), or that there may be a systematic error in otolith increment counts (T.E. Laidig, personal communication). For instance, Depoe Bay fish were collected 22 days later than Otter Crest fish and should on average be estimated at 22 days older than fish from Otter Crest, if fish from the two sites parturated at the same time and exhibit daily otolith increment formation. Alternatively, spatial patterns in parturition dates may suggest that populations of collected fish from different sites or regions were produced by distinct parturition events, originated from different maternal populations, or comprised dissimilar species compositions.

An ANOVA of estimated metamorphosis date with terms for region and site[region] was conducted to test for spatial patterns in timing of metamorphosis. Spatial differences in metamorphosis dates may indicate the importance of regional or local environmental effects, such as oceanographic conditions, on the timing of metamorphosis and subsequent settlement.

An ANOVA of estimated metamorphosis age (larval duration) with terms for region and site[region] was conducted to test for spatial patterns in age of metamorphosis. Spatial differences in metamorphosis ages may indicate a systematic spatial bias in otolith increment counting errors. Alternatively, spatial patterns in metamorphosis ages may be attributable to differences in larval growth and development rates among sites or regions. Spatial patterns in estimated metamorphosis ages may also result from spatial differences in the accuracy of the first accessory primordium as a marker for metamorphosis. Such differences would indicate the potential importance of environmental factors (i.e., exogenous cues) rather than ontogeny (i.e., endogenous, physiological cues) for triggering the formation of the first accessory primordium, and an uncoupling of otolith and somatic development.

7) *Do larval, juvenile, or total growth rates vary between regions or among local sites along the Oregon coast?*

Spatial patterns of larval growth rates by length were examined using an ANOVA of Larval Length Growth Rate with terms for Region, Site[Region], and Length at Metamorphosis. Juvenile growth rates by length were examined using an ANOVA of Juvenile Length Growth Rate with terms for Region, Site[Region], and Length at Capture. Total growth rates by length were examined using an ANOVA of Total Length Growth Rate with terms for Region, Site[Region], and Length at Capture.

Spatial patterns of larval growth rates by mass were examined using an ANOVA of Larval Mass Growth Rate with terms for Region, Site[Region], and Mass at Metamorphosis. Juvenile growth rates by mass were examined using an ANOVA of Juvenile Mass Growth Rate with terms for Region, Site[Region], and Mass at Capture. Total growth rates by mass were examined using an ANOVA of Total Mass Growth Rate with terms for Region, Site[Region], and Mass at Capture.

8) *Do juvenile physical conditions (mass-length relationships) vary between regions or among local sites along the Oregon coast?*

Spatial patterns in physical conditions (mass-length relationships) were examined using an ANOVA of Ln(Mass at Capture) with terms for Region, Site[Region], and Ln(Length at Capture). Mass at Capture and Length at Capture were natural log transformed in order to linearize the data. This analysis tested whether mass-length relationships differed between regions or among sites.

Trade-offs between juvenile growth rates and physical conditions, or mass-length relationships, of fish were examined using an ANOVA of Condition Factors with terms for Region, Site[Region], and Juvenile Length Growth Rate. An identical ANOVA was also conducted after substituting Juvenile Mass Growth Rate as the covariate. Condition factors were calculated as the residuals from the best-fit power regression equation describing the mass-length relationship. Fish blotted dry masses were plotted against SL in Excel and a power regression line was fitted to the data (Least Sum-of-Squares) to derive an equation to describe the mass-length relationship, of the form:

$$\text{Mass} = A * (\text{SL})^B$$

The mass-length power regression equation was used to calculate predicted mass from the measured SL for each fish. The residuals from the mass-length regression line were calculated as the difference between the actual measured mass and the predicted mass for each fish. The residuals from the mass-length regression, or condition factors, were used as a proxy for the physical condition of the fish.

9) *Do faster growing larvae metamorphose at younger ages, as predicted by the Single Process Concept?*

ANOVAs of Age at Metamorphosis (i.e., Larval Duration) with terms for Region, Site[Region], and Larval Growth Rate were conducted to test whether faster growing

larvae metamorphose at younger ages and experience shorter larval durations, as predicted by the Single Process Concept. Both Larval Length Growth Rate and Larval Mass Growth Rate were used as covariates in two separate ANOVAs. A significant positive slope (i.e., a significant positive effect of Larval Growth Rate on Age at Metamorphosis) would indicate that faster growing rockfish larvae metamorphose at younger ages and experience shorter larval durations than slower growing larvae.

Possible trade-offs between larval length growth rates and larval mass growth rates were investigated using an ANOVA of Ln(Larval Mass Growth Rate) with terms for Ln(Larval Length Growth Rate), Region, and Site[Region]. A significant negative correlation between the natural log of larval length growth rates and the natural log of larval mass growth rates would indicate a trade-off between these two forms of growth in larval rockfish. Larval growth rates were natural log transformed in order to meet assumptions of normally distributed variances (i.e., to normalize variances).

10) Do larval growth rates, size at metamorphosis, or larval duration (i.e., age at metamorphosis) predict juvenile growth rates?

ANOVAs of Juvenile Growth Rate with terms for Region, Site[Region], and Larval Growth Rate were conducted to test whether larval growth rates determine juvenile growth rates. Length and Mass Growth Rates were analyzed in two separate ANOVAs.

ANOVAs of Juvenile Growth Rate with terms for Region, Site[Region], and Size at Metamorphosis were conducted to test whether size at metamorphosis determines juvenile growth rates. Juvenile Mass Growth Rate was analyzed with Mass at Metamorphosis as an explanatory variable, and Juvenile Length Growth Rate was analyzed with Length at Metamorphosis as an explanatory variable, in two separate ANOVAs.

ANOVAs of Juvenile Growth Rates with terms for Region, Site[Region], and Larval Duration (i.e., Age at Metamorphosis) were conducted to test whether larval duration, or metamorphosis age, determines juvenile growth rates. Juvenile Length and Mass Growth Rates were analyzed in two separate ANOVAs.

6) Does growth-selective mortality occur during the early juvenile stage of young-of-year rockfish along the Oregon coast, as predicted by the Growth-Mortality Hypothesis?

Values for juvenile growth rates were pooled into discrete juvenile duration classes with 10-day intervals of time since metamorphosis (0-10 days, 10-20 days, 20-30 days, 30-40 days, 40-50 days, and 50-60 days). Juvenile duration was calculated as estimated age at capture minus estimated age at metamorphosis (Juvenile Duration = Age at Capture – Age at Metamorphosis). For each site, variances and means were calculated in Excel for juvenile growth rates by length and by mass within each juvenile duration class. ANOVAs of Variances of Juvenile Growth Rates with terms for Region, Site[Region], and Juvenile Duration Class were conducted to test for changes in the

variation of juvenile growth rates with increasing juvenile duration, which would indicate the presence or absence of growth-selective mortality. ANOVAs of Means of Juvenile Growth Rates with terms for Region, Site[Region], and Juvenile Duration Class were conducted to test for changes in the averages of juvenile growth rates with increasing juvenile duration, which would indicate the overall direction of growth-selective mortality.

If variances of juvenile growth rates decrease as juvenile duration increases, then one can infer, although not deduce, that growth-selective mortality may be occurring. Changes in the means of juvenile growth rates as juvenile duration increases indicate the direction of any growth-selective mortality. An increase in mean growth rates as juvenile duration increases would indicate mortality that selects against slower growing fish, while a decrease in mean growth rates would indicate mortality that selects against faster growing fish. No change in mean growth rates and decreasing variances indicates possible stabilizing selection, or mortality that selects against the fastest and slowest growing individuals with average individuals exhibiting higher survivorship.

Tables and Figures

Tables were assembled in Microsoft Word. The map of sites and regions along the Oregon coast was compiled using ARCView GIS Software. All scatter plots were constructed in Microsoft Excel. Regression lines were included in scatterplots for all terms with $p < 0.10$, with the exception of otolith-somatic growth relationships, in which regression lines were only drawn for terms with $p < 0.05$. Simple linear regression lines were fit to the data in Excel using a Least Sum-of-Squares method. Multiple linear regression lines were fit to the data by eye and hand drawn in Microsoft Word, based on parameter estimates for significant terms from ANOVAs. Box plots were constructed using SigmaPlot. The line within each box marks the median of the data, the lower and upper boundaries of the boxes indicate the 25th and 75th percentiles, respectively, and the whiskers below and above the boxes depict the 10th and 90th percentiles, respectively. Outliers are shown as points below and above the box plot whiskers, outside the 10th and 90th percentiles. P-values were depicted in figures for all terms with $p < 0.10$.

APPENDIX II: DETAILED STATISTICAL RESULTS

Otolith Radial Measurements

There was no evidence of an effect of Region on Otolith Post-rostral Radius (Nested ANOVA, $p=0.48$ with 1 d.f.). There was convincing evidence of an effect of Site[Region] on Otolith Post-rostral Radius ($p<0.0001$ with 3 d.f.). Within the central Oregon coast, otolith radii from Depoe Bay fish were on average 0.0020 mm greater than otolith radii from Otter Crest fish ($p=0.88$). Within the southern Oregon coast, otolith radii from Nellie's Cove fish were on average 0.14 mm greater than otolith radii from Orford Reef fish ($p<0.0001$), and otolith radii from Orford Reef fish were on average 0.17 mm greater than otolith radii from East Island Rock fish ($p<0.0001$).

Fish Size Back-calculations

There was convincing evidence of an effect of Otolith Post-rostral Radius on Standard Length at Capture, indicating a significant otolith-somatic growth relationship (Nested ANOVA, $p<0.0001$ with 1 d.f., Figure 3). There was no evidence of an effect of Region or Site[Region] on SL at Capture ($p=0.65$ with 1 d.f. for Region, $p=0.23$ with 3 d.f. for Site[Region], Figure 3). There was suggestive, but inconclusive, evidence of an interaction between Otolith Post-rostral Radius and Region ($p=0.055$ with 1 d.f.). Standard lengths at capture increased with otolith post-rostral radius at a rate of 4.57 *mm^{-1} faster in the southern Oregon coast than in the central Oregon coast, but this difference was non-significant ($p>0.05$). A simple linear regression of SL at Capture vs. Otolith Post-Rostral Radius adequately described the otolith-somatic growth relationship for fish from all sites and both regions. A best-fit linear regression of SL at Capture vs. Otolith Post-rostral Radius described 80.7% of variation in the data (Least Sum-of-Squares, Figure 3), with the regression equation:

$$\text{Standard Length} = 26.97 * (\text{Otolith Radius}) + 9.04$$

This regression equation was used to back-calculate lengths at metamorphosis for all fish by inputting values for otolith post-rostral radii to the first accessory primordium.

There was convincing evidence of an effect of Ln(Otolith Post-rostral Radius) on Ln(Blotted Dry Mass at Capture), indicating a significant otolith-somatic growth relationship (Nested ANOVA, $p<0.0001$ with 1 d.f., Figure 3). There was no evidence of an effect of Region or Site[Region] on Ln(Blotted Dry Mass at Capture) ($p=0.96$ with 1 d.f. for Region, $p=0.15$ with 3 d.f. for Site[Region], Figure 3). There was no evidence of an interaction between Otolith Post-rostral Radius and Region ($p=0.24$ with 1 d.f.). A simple linear regression of the natural log of Blotted Dry Mass at Capture vs. the natural log of Otolith Post-Rostral Radius adequately described the otolith-somatic growth relationship for fish from all sites and both regions. A best-fit linear regression of Ln(Blotted Dry Mass at Capture) vs. Ln(Otolith Post-rostral Radius) described 81.8% of variation in the data (Least Sum-of-Squares, Figure 3), with the regression equation:

$$\text{Ln(Blotted Dry Mass)} = 2.204 * \text{Ln(Otolith Radius)} - 0.761$$

This regression equation was used to back-calculate masses at metamorphosis for all fish by inputting values for otolith post-rostral radii to the first accessory primordium.

6) *Do parturition dates, metamorphosis dates, or metamorphosis ages (i.e., larval durations) vary between regions or among local sites along the Oregon coast?*

There was no evidence of an effect of Region on Estimated Parturition Date (Nested ANOVA, $p=0.62$ with 1 d.f., Figure 4). There was convincing evidence of an effect of Site[Region] on Estimated Parturition Date ($p<0.0001$ with 3 d.f., Figure 4). Within the central Oregon coast, fish larvae from Depoe Bay parturated (i.e., were released or extruded) on average 8.5 days later than fish from Otter Crest ($p<0.0001$). Within the southern Oregon coast, fish from East Island Rock parturated on average 13.3 days later than fish from Orford Reef ($p<0.0001$), and fish from Nellie's Cove parturated on average 8.1 days earlier than fish from Orford Reef ($p<0.0001$).

There was no evidence of an effect of Region on Estimated Metamorphosis Date (Nested ANOVA, $p=0.86$ with 1 d.f., Figure 4). There was convincing evidence of an effect of Site[Region] on Estimated Metamorphosis Date ($p<0.0001$ with 3 d.f., Figure 4). Within the central Oregon coast, fish larvae from Depoe Bay metamorphosed on average 7.9 days later than fish from Otter Crest ($p<0.0001$). Within the southern Oregon coast, fish from East Island Rock metamorphosed on average 14.0 days later than fish from Orford Reef ($p<0.0001$), and fish from Nellie's Cove metamorphosed on average 9.1 days earlier than fish from Orford Reef ($p=0.0002$).

There was no evidence of an effect of Region or Site[Region] on Metamorphosis Age (Larval Duration) (Nested ANOVA, $p=0.23$ with 1 d.f. for Region, and $p=0.96$ with 3 d.f. for Site[Region], Figure 4).

7) *Do larval, juvenile, or total growth rates vary between regions or among local sites along the Oregon coast?*

There was no evidence of an effect of Region or Site[Region] on Larval Length Growth Rate (Nested ANOVA, $p=0.23$ with 1 d.f. for Region, $p=0.40$ with 3 d.f. for Site[Region], Figure 5). There was no evidence of an effect of Length at Metamorphosis on Larval Length Growth Rate ($p=0.38$ with 1 d.f., Figure 5). There was no evidence of an interaction between Length at Metamorphosis and Region ($p=0.21$ with 1 d.f.).

There was no evidence of an effect of Region or Site[Region] on Larval Mass Growth Rate (Nested ANOVA, $p=0.25$ with 1 d.f. for Region, and $p=0.25$ with 3 d.f. for Site[Region], Figure 5). There was convincing evidence of an effect of Mass at Metamorphosis on Larval Mass Growth Rate ($p<0.0001$ with 1 d.f., Figure 5). Larval growth rates by mass were on average 0.00013 g/day faster for every 0.01-g increase in mass at metamorphosis, after accounting for the effects of Region and Site[Region]. There was moderate evidence of an interaction between Mass at Metamorphosis and Region ($p=0.015$ with 1 d.f.). Larval growth rates by mass increased with mass at metamorphosis at a rate of 0.0016 *day⁻¹ faster on the southern Oregon coast compared to the central Oregon coast.

There was no evidence of an effect of Region on Juvenile Length Growth Rate (Nested ANOVA, $p=0.26$ with 1 d.f., Figure 6). There was moderate evidence of an effect of Site[Region] on Juvenile Length Growth Rate ($p=0.041$ with 3 d.f., Figure 6). Within the central Oregon coast, juvenile growth rates by length were on average 0.021 mm/day faster in Otter Crest than in Depoe Bay, for a given length at capture ($p=0.038$). Within the southern Oregon coast, juvenile growth rates by length were on average 0.042 mm/day faster in East Island Rock than in Orford Reef ($p=0.054$), and 0.033 mm/day faster in Orford Reef than in Nellie's Cove ($p=0.065$), for a given length at capture. There was convincing evidence of an effect of Length at Capture on Juvenile Length Growth Rate ($p<0.0001$ with 1 d.f., Figure 6). Juvenile growth rates by length were on average 0.020 mm/day faster for every 1.0-mm increase in length at capture, after accounting for the effects of Region and Site[Region]. There was no evidence of an interaction between Length at Capture and Region ($p=0.71$ with 1 d.f.).

There was no evidence of an effect of Region on Juvenile Mass Growth Rate (Nested ANOVA, $p=0.44$ with 1 d.f., Figure 6). There was suggestive, but inconclusive, evidence of an effect of Site[Region] on Juvenile Mass Growth Rate ($p=0.068$ with 3 d.f. for Site[Region], Figure 6). Within the central Oregon coast, juvenile growth rates by mass were on average 0.00030 g/day faster in Otter Crest than in Depoe Bay, for a given mass at capture ($p=0.067$). Within the southern Oregon coast, juvenile growth rates by mass were on average 0.00048 g/day faster in East Island Rock than in Orford Reef ($p=0.098$), and 0.00051 g/day faster in Orford Reef than in Nellie's Cove ($p=0.054$), for a given mass at capture. There was convincing evidence of an effect of Mass at Capture on Juvenile Mass Growth Rate ($p<0.0001$ with 1 d.f., Figure 6). Juvenile growth rates by mass were on average 0.00021 g/day faster for every 0.01-g increase in mass at capture, after accounting for the effects of Region and Site[Region]. There was no evidence of an interaction between Mass at Capture and Region ($p=0.37$ with 1 d.f.).

There was suggestive, but inconclusive, evidence of an effect of Region on Total Length Growth Rate (Nested ANOVA, $p=0.056$ with 1 d.f., Figure 7). Total growth rates by length were on average 0.011 mm/day faster on the southern Oregon coast compared to the central Oregon coast, for a given length at capture ($p<0.0001$). There was suggestive, but inconclusive, evidence of an effect of Site[Region] on Total Length Growth Rate ($p=0.052$ with 3 d.f., Figure 7). Within the central Oregon coast, total growth rates by length were on average 0.0055 mm/day faster in Otter Crest than in Depoe Bay, for a given length at capture ($p=0.051$). Within the southern Oregon coast, total growth rates by length were on average 0.012 mm/day faster in East Island Rock than in Orford Reef ($p=0.052$), and 0.0088 mm/day faster in Orford Reef than in Nellie's Cove ($p=0.076$), for a given length at capture. There was convincing evidence of an effect of Length at Capture on Total Length Growth Rate ($p<0.0001$ with 1 d.f., Figure 7). Total growth rates by length were on average 0.0074 mm/day faster for every 1.0-mm increase in length at capture, after accounting for the effects of Region and Site[Region]. There was no evidence of an interaction between Length at Capture and Region ($p=0.79$ with 1 d.f.).

There was suggestive, but inconclusive, evidence of an effect of Region on Total Mass Growth Rate (Nested ANOVA, $p=0.060$ with 1 d.f., Figure 7). Total growth rates by mass were on average 0.00006 g/day faster on the southern Oregon coast compared to the central Oregon coast, for a given mass at capture ($p=0.0014$). There was no evidence

of an effect of Site[Region] on Total Mass Growth Rate ($p=0.61$ with 3 d.f., Figure 7). There was convincing evidence of an effect of Mass at Capture on Total Mass Growth Rate ($p<0.0001$ with 1 d.f., Figure 7). Total growth rates by mass were on average 0.000094 g/day faster for every 0.01-g increase in mass at capture, after accounting for the effects of Region and Site[Region]. There was no evidence of an interaction between Mass at Capture and Region ($p=0.55$ with 1 d.f.).

8) *Do juvenile physical conditions (mass-length relationships) vary between regions or among local sites along the Oregon coast?*

There was no evidence of an effect of Region on Ln(Mass at Capture) (Nested ANOVA, $p=0.67$ with 1 d.f., Figure 8). There was convincing evidence of an effect of Site[Region] on Ln(Mass at Capture) ($p<0.0001$ with 3 d.f., Figure 8). Within the central Oregon coast, the natural logs of mass (g) at capture were on average 0.079 greater in Depoe Bay than in Otter Crest, for a given natural log of length (mm) at capture ($p<0.0001$). Within the southern Oregon coast, the natural logs of mass (g) at capture were on average 0.037 greater in Nellie's Cove than in Orford Reef ($p=0.15$), and 0.037 greater in Orford Reef than in East Island Rock ($p=0.25$), for a given natural log of length (mm) at capture. There was convincing evidence of an effect of Ln(Length at Capture) on Ln(Mass at Capture) ($p<0.0001$ with 1 d.f., Figure 8). The natural log of mass (g) at capture was on average 3.43 greater for every increase of 1.0 in the natural log of length (mm) at capture, after accounting for the effects of Region and Site[Region]. There was no evidence of an interaction between Ln(Length at Capture) and Region ($p=0.36$ with 1 d.f.).

The power regression equation for the mass-length relationship of all fish was described by the following equation ($R^2 = 0.9604$, Appendix V: Figure D):

$$\text{Mass} = (1.1587 \times 10^{-6}) * (\text{SL})^{3.6495}$$

Condition factors were calculated as the residuals of masses from this equation.

There was suggestive, but inconclusive evidence of an effect of Juvenile Length Growth Rate on Condition Factors (Nested ANOVA, $p=0.058$ with 1 d.f., Figure 9). Condition factors decreased at an average rate of 0.0420g for every 1-mm/day increase in juvenile growth rates by length, after accounting for the effects of Region and Site[Region]. There was no evidence of an effect of Region on Condition Factors ($p=0.93$ with 1 d.f.). There was convincing evidence of an effect of Site[Region] on Conditions Factors ($p=0.0002$ with 3 d.f., Figure 9). Within the central Oregon coast, condition factors were 0.0122g greater in Depoe Bay than in Otter Crest, for a given juvenile length growth rate ($p<0.0001$). Within the southern Oregon coast, condition factors were 0.00329g greater in Nellie's Cove than in Orford Reef ($p=0.36$), and 0.00103g greater in Orford Reef than in East Island Rock ($p=0.78$), for a given juvenile length growth rate. There was no evidence of an interaction between Juvenile Length Growth Rate and Region ($p=0.22$ with 1 d.f.).

There was no evidence of an effect of Juvenile Mass Growth Rate on Condition Factors (Nested ANOVA, $p=0.98$ with 1 d.f., Figure 9). There was no evidence of an effect of Region on Condition Factors ($p=0.96$ with 1 d.f.). There was convincing evidence of an effect of Site[Region] on Conditions Factors ($p<0.0001$ with 3 d.f., Figure

9). Within the central Oregon coast, condition factors were 0.0136g greater in Depoe Bay than in Otter Crest, for a given juvenile mass growth rate ($p < 0.0001$). Within the southern Oregon coast, condition factors were 0.00214g greater in Nellie's Cove than in Orford Reef ($p = 0.58$), and 0.000867g greater in East Island Rock than in Orford Reef ($p = 0.84$), for a given juvenile mass growth rate. There was no evidence of an interaction between Juvenile Mass Growth Rate and Region ($p = 0.40$ with 1 d.f.).

9) *Do faster growing larvae metamorphose at younger ages, as predicted by the Single Process Concept?*

There was convincing evidence of an effect of Larval Length Growth Rate on Age at Metamorphosis, or Larval Duration (Nested ANOVA, $p < 0.0001$ with 1 d.f., Figure 10). Ages at metamorphosis (larval durations) were on average 2.12 days younger (shorter) for every 0.01-mm/day increase in larval length growth rates, after accounting for the effects of Region and Site[Region]. There was no evidence of an effect of Region or Site[Region] on Age at Metamorphosis ($p = 0.21$ with 1 d.f. for Region, and $p = 0.76$ with 3 d.f. for Site[Region], Figure 10). There was suggestive, but inconclusive, evidence of an interaction between Larval Length Growth Rate and Region ($p = 0.072$ with 1 d.f.). Ages at metamorphosis (larval durations) decreased with larval length growth rates at a rate of 61.6 days²/mm faster in the central Oregon coast than in the southern Oregon coast.

There was convincing evidence of an effect of Larval Mass Growth Rate on Age at Metamorphosis, or Larval Duration (Nested ANOVA, $p < 0.0001$ with 1 d.f., Figure 10). Ages at metamorphosis (larval durations) were on average 2.11 days older (longer) for every 0.0001-g/day increase in larval mass growth rates, after accounting for the effects of Region and Site[Region]. There was suggestive, but inconclusive, evidence of an effect of Region on Age at Metamorphosis ($p = 0.87$ with 1 d.f., Figure 10). Ages at metamorphosis (larval durations) were on average 1.9 days younger (shorter) in the southern Oregon coast than in the central Oregon coast, for a given larval mass growth rate ($p = 0.046$). There was no evidence of an effect of Site[Region] on Age at Metamorphosis ($p = 0.76$ with 3 d.f., Figure 10). There was moderate evidence of an interaction between Larval Mass Growth Rate and Region ($p = 0.046$ with 1 d.f.). Ages at metamorphosis (larval durations) increased with larval mass growth rates at a rate of 10.0 days²/0.001g faster in the central Oregon coast than in the southern Oregon coast.

There was convincing evidence of an effect of Ln(Larval Length Growth Rate) on Ln(Larval Mass Growth Rate) (Nested ANOVA, $p = 0.0004$ with 1 d.f., Figure 11). The natural log of larval mass growth rates (g/day) increased at a rate of 1.19 with every 1-unit increase in the natural log of larval length growth rates (mm/day). There was no evidence of an effect of Region or Site[Region] on this relationship ($p = 0.25$ with 1 d.f. for Region, and $p = 0.49$ with 3 d.f. for Site[Region]). There was no evidence of an interaction between Ln(Larval Length Growth Rate) and Region ($p = 0.31$ with 1 d.f.).

10) Do larval growth rates, size at metamorphosis, or larval duration (i.e., age at metamorphosis) predict juvenile growth rates?

There was convincing evidence of an effect of Larval Length Growth Rate on Juvenile Length Growth Rate (Nested ANOVA, $p=0.0083$ with 1 d.f., Figure 12). Juvenile growth rates by length were on average 0.00975 mm/day slower for every 0.01-mm/day increase in larval growth rates by length, after accounting for the effects of Region and Site[Region]. There was no evidence of an effect of Region on Juvenile Length Growth Rate ($p=0.94$ with 1 d.f., Figure 12). There was moderate evidence of an effect of Site[Region] on Juvenile Length Growth Rate ($p=0.027$ with 3 d.f., Figure 12). Within the central Oregon coast, juvenile growth rates by length were on average 0.015 mm/day faster in Otter Crest than in Depoe Bay, for a given larval length growth rate ($p=0.23$). Within the southern Oregon coast, juvenile growth rates by length were on average 0.025 mm/day faster in Nellie's Cove than in Orford Reef ($p=0.17$), and 0.054 mm/day faster in Orford Reef than in East Island Rock ($p=0.0054$), for a given larval length growth rate. There was no evidence of an interaction between Larval Length Growth Rate and Region ($p=0.43$ with 1 d.f.).

There was suggestive, but inconclusive, evidence of an effect of Larval Mass Growth Rate on Juvenile Mass Growth Rate (Nested ANOVA, $p=0.063$ with 1 d.f., Figure 12). Juvenile growth rates by mass were on average 0.000191 g/day slower for every 0.0001-g/day increase in larval growth rates by mass, after accounting for the effects of Region and Site[Region]. There was no evidence of an effect of Region on Juvenile Mass Growth Rate ($p=0.60$ with 1 d.f., Figure 12). There was convincing evidence of an effect of Site[Region] on Juvenile Mass Growth Rate ($p=0.0040$ with 3 d.f., Figure 12). Within the central Oregon coast, juvenile growth rates by mass were on average 0.000092 g/day faster in Depoe Bay than in Otter Crest, for a given larval mass growth rate ($p=0.75$). Within the southern Oregon coast, juvenile growth rates by mass were on average 0.00095 g/day faster in Nellie's Cove than in Orford Reef ($p=0.017$), and 0.0016 g/day faster in Orford Reef than in East Island Rock ($p=0.0003$), for a given larval mass growth rate. There was no evidence of an interaction between Larval Mass Growth Rate and Region ($p=0.92$ with 1 d.f.).

There was convincing evidence of an effect of Length at Metamorphosis on Juvenile Length Growth Rate (Nested ANOVA, $p=0.0094$ with 1 d.f., Figure 13). Juvenile growth rates by length were on average 0.0158 mm/day slower for every 1-mm increase in lengths at metamorphosis, after accounting for the effects of Region and Site[Region]. There was no evidence of an effect of Region on Juvenile Length Growth Rate ($p=0.71$ with 1 d.f., Figure 13). There was convincing evidence of an effect of Site[Region] on Juvenile Length Growth Rate ($p=0.0088$ with 3 d.f., Figure 13). Within the central Oregon coast, juvenile growth rates by length were on average 0.017 mm/day faster in Otter Crest than in Depoe Bay, for a given length at metamorphosis ($p=0.18$). Within the southern Oregon coast, juvenile growth rates by length were on average 0.029 mm/day faster in Nellie's Cove than in Orford Reef ($p=0.11$), and 0.064 mm/day faster in Orford Reef than in East Island Rock ($p=0.0017$), for a given length at metamorphosis. There was no evidence of an interaction between Length at Metamorphosis and Region ($p=0.37$ with 1 d.f.).

There was no evidence of an effect of Mass at Metamorphosis on Juvenile Mass Growth Rate (Nested ANOVA, $p=0.27$ with 1 d.f., Figure 13). There was no evidence of an effect of Region on Juvenile Mass Growth Rate ($p=0.55$ with 1 d.f., Figure 13). There was convincing evidence of an effect of Site[Region] on Juvenile Mass Growth Rate ($p=0.0093$ with 3 d.f., Figure 13). Within the central Oregon coast, juvenile growth rates by mass were on average 0.000093 g/day faster in Depoe Bay than in Otter Crest, for a given mass at metamorphosis ($p=0.75$). Within the southern Oregon coast, juvenile growth rates by mass were on average 0.00093 g/day faster in Nellie's Cove than in Orford Reef ($p=0.023$), and 0.0015 g/day faster in Orford Reef than in East Island Rock ($p=0.0009$), for a given mass at metamorphosis. There was no evidence of an interaction between Mass at Metamorphosis and Region ($p=0.74$ with 1 d.f.).

There was no evidence of an effect of Larval Duration (Age at Metamorphosis) on Juvenile Length Growth Rate (Nested ANOVA, $p=0.99$ with 1 d.f., Figure 14). There was no evidence of an effect of Region on Juvenile Length Growth Rate ($p=0.81$ with 1 d.f., Figure 14). There was suggestive, but inconclusive, evidence of an effect of Site[Region] on Juvenile Length Growth Rate ($p=0.072$ with 3 d.f., Figure 14). Within the central Oregon coast, juvenile growth rates by length were on average 0.017 mm/day faster in Otter Crest than in Depoe Bay, for a given larval duration (age at metamorphosis) ($p=0.21$). Within the southern Oregon coast, juvenile growth rates by length were on average 0.024 mm/day faster in Nellie's Cove than in Orford Reef ($p=0.22$), and 0.046 mm/day faster in Orford Reef than in East Island Rock ($p=0.019$), for a given larval duration (age at metamorphosis). There was no evidence of an interaction between Larval Duration (Age at Metamorphosis) and Region ($p=0.56$ with 1 d.f.).

There was no evidence of an effect of Larval Duration (Age at Metamorphosis) on Juvenile Mass Growth Rate (Nested ANOVA, $p=0.17$ with 1 d.f., Figure 14). There was no evidence of an effect of Region on Juvenile Mass Growth Rate ($p=0.70$ with 1 d.f., Figure 14). There was moderate evidence of an effect of Site[Region] on Juvenile Mass Growth Rate ($p=0.016$ with 3 d.f., Figure 14). Within the central Oregon coast, juvenile growth rates by mass were on average 0.00012 g/day faster in Depoe Bay than in Otter Crest, for a given larval duration (age at metamorphosis) ($p=0.68$). Within the southern Oregon coast, juvenile growth rates by mass were on average 0.00087 g/day faster in Nellie's Cove than in Orford Reef ($p=0.030$), and 0.0013 g/day faster in Orford Reef than in East Island Rock ($p=0.0017$), for a given larval duration (age at metamorphosis). There was no evidence of an interaction between Larval Duration (Age at Metamorphosis) and Region ($p=0.86$ with 1 d.f.).

6) *Does growth-selective mortality occur during the early juvenile stage of young-of-year rockfish along the Oregon coast, as predicted by the Growth-Mortality Hypothesis?*

There was moderate evidence of an effect of Juvenile Duration Class on Variance of Juvenile Length Growth Rates (Nested ANOVA, $p=0.012$ with 1 d.f., Figure 15). The variance of juvenile length growth rates decreased by 0.00431 for every 10-day increase in juvenile duration, after accounting for the effects of Region and Site[Region]. There was no evidence of an effect of Region or Site[Region] on Variance of Juvenile Length

Growth Rates ($p=0.15$ with 1 d.f. for Region, and $p=0.92$ with 3 d.f. for Site[Region]). There was no evidence of an interaction between Juvenile Duration Class and Region ($p=0.90$ with 1 d.f.).

There was moderate evidence of an effect of Juvenile Duration Class on Variance of Juvenile Mass Growth Rates (Nested ANOVA, $p=0.031$ with 1 d.f., Figure 15). The variance of juvenile mass growth rates decreased by 1.07×10^{-6} for every 10-day increase in juvenile duration, after accounting for the effects of Region and Site[Region]. There was no evidence of an effect of Region or Site[Region] on Variance of Juvenile Mass Growth Rates ($p=0.31$ with 1 d.f. for Region, and $p=0.24$ with 3 d.f. for Site[Region]). There was no evidence of an interaction between Juvenile Duration Class and Region ($p=0.96$ with 1 d.f.).

There was no evidence of an effect of Juvenile Duration Class on Mean of Juvenile Length Growth Rates (Nested ANOVA, $p=0.25$ with 1 d.f., Figure 16). There was no evidence of an effect of Region or Site[Region] on Mean of Juvenile Length Growth Rates ($p=0.96$ with 1 d.f. for Region, and $p=0.61$ with 3 d.f. for Site[Region]). There was no evidence of an interaction between Juvenile Duration Class and Region ($p=0.47$ with 1 d.f.).

There was no evidence of an effect of Juvenile Duration Class on Mean of Juvenile Mass Growth Rates (Nested ANOVA, $p=0.45$ with 1 d.f., Figure 16). There was no evidence of an effect of Region or Site[Region] on Mean of Juvenile Mass Growth Rates ($p=0.67$ with 1 d.f. for Region, and $p=0.34$ with 3 d.f. for Site[Region]). There was no evidence of an interaction between Juvenile Duration Class and Region ($p=0.58$ with 1 d.f.).

APPENDIX III: DETAILED COMMENTS ON RESULTS

Fish Identification

Four species in the Genus *Sebastes* were identified as candidates for all juvenile young-of-year rockfish collected: *Sebastes maliger* (quillback rockfish), *S. caurinus* (copper rockfish), *S. carnatus* (gopher rockfish), and *S. chrysomelas* (black-and-yellow rockfish) (Appendix V: Fig. B). *S. carnatus* and *S. chrysomelas* cannot be distinguished genetically with reasonable confidence (Larson 2002) and therefore these two species were grouped together for the purpose of genetic species identification (R.D. Vetter and T.E. Laidig, personal communication). 80% of fish identified genetically to species were *S. maliger*, 10% were *S. caurinus*, and 10% were *S. carnatus* or *S. chrysomelas*. 100% (four out of four) of central Oregon coast fish identified genetically to species were *S. maliger*. Only 67% (four out of six) of southern Oregon coast fish identified genetically to species were *S. maliger*; 11.5% (one out of six) were *S. caurinus*, and 11.5% were *S. carnatus* or *S. chrysomelas*. Within the southern Oregon coast, 100% of fish analyzed from Orford Reef were *S. maliger*; 50% of fish analyzed from Nellie's Cove were *S. maliger* and 50% were *S. caurinus*; 50% of fish analyzed from East Island Rock were *S. maliger* and 50% were *S. carnatus* or *S. chrysomelas*.

Differences in species composition between regions and among sites may be attributable to spatial variation in settlement habitat, such as macroalgal (e.g., kelp) assemblages (Carr 1989, Carr 1991), or to oceanographic conditions that influence settlement patterns, such as upwelling and downwelling (A.J. Ammann, personal communication). The potential implications of different species compositions for spatial patterns of growth are examined in the discussion for physical conditions (Question #3).

S. maliger is genetically very similar to *S. caurinus*, with evidence of possible hybridization between the two (Love 2002, Yamanaka 2002). Likewise, *S. carnatus* and *S. chrysomelas* are practically identical genetically and may represent environmentally induced color morphs of a single species, as the two exhibit distinct pigmentation and occupy different depth ranges (Larson 2002). These four species are virtually indistinguishable as larvae and early juveniles (T.E. Laidig and A.J. Ammann, personal communication) and constitute a species group sharing common morphological, behavioral, and ecological characteristics (Love et al. 2002). Therefore, similar factors and processes likely influence patterns of growth and development in the early life history stages of these four species. *S. maliger*, *S. caurinus*, *S. carnatus*, and *S. chrysomelas* are all characterized by a relatively short pelagic larval duration of typically less than two months (A.J. Ammann, M.H. Carr, and T.E. Laidig, personal communication), a very short or absent pelagic juvenile stage with settlement occurring during or immediately following metamorphosis (Love et al. 2002), and settlement to nearshore rocky reefs, eelgrass beds, or kelp canopies (Larson 2002, Love 2002, Yamanaka 2002, Ammann 2004). Settlement of these species appears to occur preferentially during periods of downwelling or wind relaxation (A.J. Ammann, personal communication, T.H. Young, personal observation), suggesting that pelagic larvae and

juveniles reside in shallow surface waters and that upwelling inhibits settlement to nearshore habitats while downwelling enhances settlement (Roughgarden et al. 1988). This group of species has also been observed to recruit as juveniles to *Macrocystis* kelp canopies in California at higher densities during El Niño years than during Normal years, and at the lowest densities during La Niña years (PISCO 2002, M.H. Carr, J.E. Caselle, and C. Syms, personal communication), hypothetically as a consequence of suppressed coastal upwelling during El Niños and intensified upwelling during La Niñas (Segar 1998). The adults and older juveniles of these species are solitary and benthic or demersal, are common in the shallow nearshore environment where they prefer rocky reef habitats of high relief and/or kelp cover, and feed predominantly on crustaceans and small fish (Larson 2002, Love 2002, Yamanaka 2002).

Ages and Dates

Estimated parturition dates and metamorphosis dates for the collected fish agreed with parturition dates and settlement dates documented in the literature (Laidig 2002, Larson 2002, Yamanaka 2002), suggesting that otolith increment counts reflect true fish ages and that the first accessory primordium may be an accurate indicator of metamorphosis age. However, the published ranges of parturition and settlement dates are sufficiently broad to preclude a validation of daily otolith increment formation and metamorphosis timing to a high level of confidence. Nonetheless, there is no reason to believe that the young-of-year rockfish of the four species collected do not exhibit daily otolith increments in the same manner as most fish (Campana and Neilson 1985, Jones 1986), including other species of the Genus *Sebastes* whose ages have been validated (Yoklavich and Boehlert 1987, Laidig et al. 1991, Sakuma and Laidig 1995, Laidig et al. 1996, Ralston et al. 1996, Plaza et al. 2001).

The most likely source of error in estimating ages and growth rates from otolith increment counts is the presence of irregular sub-daily increments within the underlying, regular daily increment pattern, leading to possible overestimation of ages and underestimation of growth rates (Campana 1992). The inclusion of sub-daily increments in otolith counts may have caused a systematic bias in estimates of ages and growth rates, despite randomized, blind otolith examination methods. The proportion of sub-daily increments deposited appeared to vary with fish age and otolith size, with the number of sub-daily increments increasing along the otolith radius from nucleus to edge. Therefore, larger otoliths, from larger fish, tended to exhibit proportionally more sub-daily increments than smaller otoliths, with an associated increase in the risk of overestimating ages and underestimating growth rates, especially during the juvenile stage. This may have been an important confounding factor and source of systematic error in estimates of ages and growth rates, due to spatial differences in sizes at capture and otolith radii among sites (Fig. 3).

Although the formation of the first accessory primordium has been found to occur simultaneously with metamorphosis in shortbelly rockfish, *Sebastes jordani* (Laidig et al. 1991), and in black rockfish of Japan, *S. inermis* (Plaza et al. 2001), it is not known how consistent is this coupling of otolith and somatic development across the Genus *Sebastes*. However, first accessory primordia have also been shown to form during the initiation of

juvenile transformation in numerous other genera of fish (Campana 1984, Campana and Neilson 1985, Alhossaini et al. 1989, Karakiri et al. 1989, Gartner 1991, Kramer 1991, Linkowski 1991, Sogard 1991, Toole et al. 1993, Hare and Cowen 1994), indicating a potentially great degree of taxonomic breadth to the ontogenetic significance of this otolith character.

While the rate of deposition of otolith increments has not been experimentally evaluated in any of the four species of *Sebastes* studied here, the daily periodicity of otolith increment formation has been confirmed for the early life history stages in other species of the Genus *Sebastes* (Love et al. 2002). The daily formation of otolith increments was validated in laboratory-reared juveniles of *S. melanops* and *S. auriculatus* using fluorescent oxytetracycline injections and autoradiography methods (Yoklavich and Boehlert 1987, T.E. Laidig, personal communication). Similarly, otolith increment counts were accurate estimates of actual ages in larval *S. jordani* (Ralston et al. 1996). Comparisons of growth rates estimated from otolith increment counts with growth rates calculated from changes in length of the same cohort of fish over a known period of time were used to validate daily increment formation in juvenile *S. jordani* (Laidig et al. 1991). Back-calculated parturition size estimates from otolith-somatic growth relationships were compared with empirical (i.e., observed) values to confirm the daily periodicity of otolith increments in larval *S. saxicola* and *S. goodei* (Sakuma and Laidig 1995, Laidig et al. 1996).

Otolith Radial Measurements

Otolith radii did not differ between regions, but did differ between sites within each region. Within the central Oregon coast, otoliths were larger in fish from Depoe Bay than in fish from Otter Crest, although this difference was not significant. Within the southern Oregon coast, otoliths were largest in fish from Nellie's Cove and smallest in fish from East Island, with intermediate otolith sizes in Orford Reef fish. I observed that larger otoliths, usually from larger fish, exhibited more sub-daily increments than smaller otoliths. The majority of these additional increments were located distally from the first accessory primordium, or within the juvenile, post-metamorphosis portion of the otolith. Given the greater possibility of including sub-daily increments into otolith counts for otoliths with increasing radii, I expect ages to be overestimated and growth rates to be underestimated in fish with larger otoliths. These errors may considerably affect the estimated juvenile durations of fish and probably do not appreciably affect the estimated larval durations of fish. Thus, total ages, juvenile growth rates, and total growth rates will likely be most heavily impacted by variation in otolith radii. Fish with the smallest otoliths or shortest juvenile durations probably yielded the most accurate age and growth rate estimations.

Consequently, juvenile growth rates, total growth rates, and total age at capture estimations are probably most accurate in fish from East Island Rock, with the smallest otoliths. Age estimates for Orford Reef and Nellie's Cove fish are expected to overestimate the true values of this parameter, while growth rate estimates for these sites are expected to underestimate true growth rates. These errors may be more pronounced in fish from Nellie's Cove than in fish from Orford Reef. Since otoliths from both Depoe

Bay and Otter Crest, of the central Oregon coast, were larger than otoliths from East Island Rock, age estimates for these central sites may also overestimate true ages, and growth rate estimates may underestimate their true values, relative to fish from East Island Rock. These error predictions are examined further along with a discussion of spatial patterns in parturition dates, metamorphosis dates, and metamorphosis ages (Question #1).

Fish Size Back-calculations

There was no evidence to suggest a significant difference in the otolith-somatic growth relationships between regions or among sites within each region (Fig. 3). However, there was inconclusive evidence to suggest a difference in the slope of the otolith-somatic growth relationship for lengths between regions (Appendix V: Fig. E), although this difference was not considered statistically significant. A simple linear regression equation was used to back-calculate sizes at metamorphosis for each of length and mass, with the same equation applied across regions and sites (Fig. 3).

Estimated sizes at metamorphosis and larval growth rates from collected young-of-year rockfish roughly corresponded with published sizes at metamorphosis (i.e., juvenile transformation) and growth rates for the early life history stages of other species in the Genus *Sebastes* (Love et al. 2002). Back-calculated lengths at metamorphosis for the collected fish ranged between 14.1 mm and 21.3 mm, with a median length at metamorphosis of 16.9 mm (and a mean of 16.7 mm). Published sizes at metamorphosis for most juvenile rockfish are approximately 20 mm, with some rockfish species metamorphosing as large as 30 mm (Love et al. 2002).

The use of a single linear regression equation to back-calculate lengths at metamorphosis for both southern and central Oregon coast fish may have introduced additional error into the analyses of spatial patterns in growth rates. Disregarding a potentially important difference in the slopes of otolith-somatic growth relationships between regions would lead to errors in estimating the differences of growth rates between the two regions (Appendix V: Fig. E). The magnitude of error in estimated lengths at metamorphosis would be particularly large for larger fish and otolith sizes at metamorphosis (predicted by otolith radii to the first accessory primordium). The larger the otolith radii to the first accessory primordium, the more pronounced are differences between the predicted values of size at metamorphosis from two otolith-somatic growth relationships with separate slopes for each region, and the predicted values of size at metamorphosis from a single regression equation, used to back-calculate sizes for both regions (Appendix V: Fig. E).

The slope of the otolith-somatic growth relationship for lengths was shown to be steeper for southern Oregon coast fish than for the central coast ($p < 0.10$), but with the same intercept (Appendix V: Fig. E). Therefore, back-calculated lengths at metamorphosis using one otolith-somatic growth relationship for both regions (a simple linear regression equation) underestimated actual lengths at metamorphosis for southern Oregon coast fish, and overestimated actual lengths at metamorphosis for central Oregon coast fish, with this error being more pronounced for larger fish at time of metamorphosis. The calculated juvenile growth rates overestimated true juvenile growth

rates for southern Oregon coast fish, and underestimated true juvenile growth rates for central Oregon coast fish, relative to growth rate calculations using a separate otolith-somatic growth relationship for each region. The opposite is true for larval growth rates by length, which were underestimated in the southern region and overestimated in the central region.

Regional differences in the slope of otolith-somatic growth relationships may have resulted from differences in somatic growth rates or in species composition between southern and central regions. Secor and Dean (1989) found that faster growing fish exhibited steeper otolith-somatic growth relationships compared to slower growing fish, providing a mechanism by which otolith-somatic growth relationships may become spatially uncoupled. Therefore, the observation of a steeper otolith-somatic growth relationship for southern Oregon coast fish than for central Oregon coast fish (Appendix V: Fig. E) may be attributable to faster growth rates in the southern region compared to the central region (Fig. 5 and 7).

1) Do parturition dates, metamorphosis dates, or metamorphosis ages (i.e., larval durations) vary between regions or among local sites along the Oregon coast?

Estimated parturition dates and metamorphosis dates differed significantly among sites within each region, but not between the regions themselves (Fig. 4). In the central Oregon coast, fish from Depoe Bay parturated and metamorphosed later than fish from Otter Crest. In the southern Oregon coast, fish from East Island Rock parturated and metamorphosed later than fish from Orford Reef, and fish from Nellie's Cove parturated and metamorphosed earlier than fish from Orford Reef. Metamorphosis ages, or larval durations, did not differ between regions or among sites within each region along the Oregon coast (Fig. 4).

The observed differences in estimated parturition dates among sites within each region (Fig. 4) may indicate systematic, site-based errors in otolith increment counts, causing spatial biases in estimated ages and growth rates. This conclusion depends on the assumption of no significant difference in actual parturition dates among sites within each region (T.E. Laidig, personal communication). Within the central Oregon coast, the estimated ages at capture for Depoe Bay fish were younger than would be expected with the assumption that Depoe Bay fish and Otter Crest fish parturated on the same date (conversely, estimated ages at capture for Otter Crest fish were older than would be expected). Within the southern Oregon coast, the estimated ages at capture for East Island Rock fish were younger than would be expected, and the estimated ages at capture for Nellie's Cove fish were older than would be expected, given the assumption of equal parturition dates with Orford Reef fish.

Since there were no significant differences in estimated metamorphosis ages (larval durations) among sites or between regions (Fig. 4), differences in estimated parturition dates among sites (i.e., deviations in ages at capture from expected values) may be attributed to varying degrees of accuracy in estimates of juvenile durations. This interpretation of the data is dependent on the assumption of equal actual larval durations among sites and between regions, and therefore no systematic, spatial error in estimates of larval durations. This conclusion is also supported by the observation that the larval

pre-metamorphosis segments of otoliths, proximal to the nucleus, were consistently easier to read and daily otolith increments became more difficult to read distal from the nucleus and the first accessory primordium, in the juvenile segments.

Juvenile durations were estimated from otolith increment counts between the first accessory primordium and the otolith edge and were equivalent to the age at metamorphosis subtracted from the age at capture. This juvenile region of the otoliths typically contained many sub-daily increments and very faint increments in the most distal portions of the otolith, near the edge. Daily increments were very difficult to discern in the juvenile stage, increasing the possibility of inaccurate age estimates for the period between metamorphosis and capture. Therefore, juvenile durations may have been underestimated in Depoe Bay fish or overestimated in Otter Crest fish along the central Oregon coast. Juvenile durations may have been underestimated in East Island Rock fish and overestimated in Nellie's Cove fish, relative to Orford Reef fish, along the southern Oregon coast.

The implications for growth rate estimates from this assessment of increment count errors is that juvenile and total growth rates may have been overestimated in Depoe Bay fish or underestimated in Otter Crest fish, along the central Oregon coast. Likewise, juvenile and total growth rates may have been overestimated in East Island Rock fish and underestimated in Nellie's Cove fish, relative to Orford Reef fish, along the southern Oregon coast.

Based upon the observation that larger otoliths, from larger fish, tended to exhibit more sub-daily increments than smaller otoliths, one would expect juvenile durations to be overestimated and growth rates to be underestimated in fish with larger otoliths, and that fish with the smallest otoliths probably yielded the most accurate age and growth rate estimations. This expectation coincides with the pattern observed along the southern Oregon coast, where otoliths were largest from Nellie's Cove fish, which were estimated to parturate and metamorphose earliest, and otoliths were smallest from East Island Rock fish, which were estimated to parturate and metamorphose latest (Fig. 4). If estimates of ages and growth rates are regarded as most accurate for East Island Rock fish due to their small otolith sizes, then the juvenile durations estimated for Nellie's Cove and Orford Reef fish were overestimates and the juvenile and total growth rates for these two sites were underestimates, with a more severe error for Nellie's Cove estimates than for Orford Reef. However, these expectations do not coincide with otolith size patterns for fish along the central Oregon coast, where there is no apparent difference in otolith sizes between fish from Depoe Bay and Otter Crest ($p > 0.10$), despite differences in estimated parturition dates (Fig. 4).

Parturition dates, metamorphosis dates, and metamorphosis ages did not differ between regions (Fig. 4), and otolith sizes were roughly the same from both regions, although nearly all fish from East Island Rock had smaller otoliths than fish from both the central coast sites and other southern coast sites (Fig. 3). It is possible, therefore, that juvenile durations are overestimated in all sites from both the central and southern Oregon coast, except East Island Rock, and that total and juvenile growth rates are underestimated in all sites except East Island Rock. The influence of East Island Rock fish on the southern region may have contributed to faster average estimated growth rates in the southern Oregon coast than in the central Oregon coast.

An alternative explanation for the observed differences in parturition dates among sites is that fish from each site constitute distinct cohorts, with different maternal populations from potentially different geographic locations of origin (Burford 2001), or that cohorts from each site arose during separate parturition events (Pasten et al. 2003). These conclusions imply that fish from different sites within each region did not mix in the plankton as pelagic larvae and may have either dispersed with discrete water masses, been locally retained by oceanographic features such as eddies and gyres, or exhibited behavioral mechanisms for limited dispersal capabilities (Jones et al. 1999, Swearer et al. 1999, Cowen et al. 2000, Swearer et al. 2002, Taylor and Hellberg 2003). Evidence of limited larval dispersal in black rockfish (*S. melanops*) along the Oregon coast (Miller and Shanks *In Press*) and of genetic subdivisions of copper rockfish (*S. caurinus*) populations (Buonaccorsi et al. 2002) supports an explanation of local larval retention for establishing distinct cohorts among sites.

2) *Do larval, juvenile, or total growth rates vary between regions or among local sites along the Oregon coast?*

Larval growth rates did not differ between regions or among sites within each region along the Oregon coast (Fig. 5). However, larval growth rates by mass were faster for fish that metamorphosed at heavier masses, and the effect of mass at metamorphosis on larval growth rates was stronger on the southern Oregon coast than on the central Oregon coast (Fig. 5).

Juvenile growth rates did not differ between regions, but did appear to differ among sites within each region (Fig. 6). In the central Oregon coast, fish in Otter Crest grew faster as juveniles than fish in Depoe Bay. In the southern Oregon coast, fish in East Island Rock grew faster than fish in Orford Reef, and fish in Nellie's Cove grew slower than fish in Orford Reef. Juvenile growth rates were faster for fish that were captured at longer lengths or heavier masses.

Total growth rates appeared to differ between regions, and total growth rates by length appeared to differ among sites within each region along the Oregon coast (Fig. 7). Faster total growth rates, by length and by mass, were observed in the southern region than in the central region. In the central region, fish from Otter Crest grew faster by length than fish from Depoe Bay. In the southern region, fish from East Island Rock grew faster by length than fish from Orford Reef and Nellie's Cove, and fish from Nellie's Cove grew slowest by length. Total growth rates were faster for fish that were captured at longer lengths or heavier masses.

Estimated larval growth rates from collected young-of-year rockfish roughly corresponded with published growth rates for the early life history stages of other species in the Genus *Sebastes* (Love et al. 2002). Estimated larval growth rates by length for the collected fish ranged between 0.163 mm/day and 0.369 mm/day, with a median larval growth rate of 0.212 mm/day (and a mean of 0.216 mm/day). Published growth rates for other species of rockfish during their larval and pelagic juvenile stages range from 0.13 mm/day to 0.17 mm/day documented for young larvae, and growth rates between 0.36 and 0.57 mm/day documented for older larvae and pelagic juveniles (Love et al. 2002). Estimated juvenile growth rates ranged between -0.0327 mm/day and 0.435 mm/day,

with a median juvenile growth rate of 0.226 mm/day (and a mean of 0.235 mm/day). The juvenile growth rate estimates for three fish were negative, implying shrinkage of fish during the juvenile stage, likely due to gross overestimations of sizes at metamorphosis from back-calculations. In these fish, the back-calculated length at metamorphosis actually exceeded the measured length at capture. Estimated total growth rate by length for the collected fish ranged between 0.167 to 0.287 mm/day, with a median total growth rate of 0.218 mm/day (and a mean of 0.223 mm/day).

Growth rates were calculated as absolute growth rates, or changes in size per unit of time (mm/day or g/day), rather than proportional growth rates, or changes in the percent of body size per unit of time (proportional growth rate = %/day = absolute growth rate/fish size). Therefore, the observed increase in juvenile and total growth rates and larval mass growth rates with increasing sizes at capture may indicate approximately constant proportional growth rates throughout the early juvenile stage. Proportional growth rates were not calculated due to the large time period over which larval and juvenile growth rates were averaged for fish. In contrast to absolute growth rates, which don't change based upon the size of fish, the accuracy of proportional growth rates decreases as the time period over which they are calculated increases because body size at time of measurement is the denominator in the calculation. Thus, proportional growth rates are best calculated over shorter intervals of time, such as daily or weekly, which can be achieved by back-calculating sizes at daily or weekly intervals using radial measurements of daily otolith growth increments. The otoliths that I examined did not exhibit a consistent radial counting path, a necessary prerequisite for daily increment measurements in asymmetrical otoliths (Campana 1992), due to many cracks and obscurities radiating outwards from the nucleus. Therefore, only coarse estimates of absolute growth rates averaged over the larval and juvenile periods were feasible.

Observed differences in total growth rates and larval mass growth rates between regions indicated that young-of-year rockfish grew faster on the southern Oregon coast than on the central Oregon coast, which contrasts previous findings for invertebrate growth rates (Freidenburg 2002). Faster total length growth rates on the southern Oregon coast were confirmed by a steeper length-age relationship in the southern region than in the central region (Appendix V: Fig. F). These results are somewhat counterintuitive because water temperatures are typically colder along the southern Oregon coast than along the central Oregon coast (Appendix V: Fig. A), due to persistent upwelling south of Cape Blanco (Parrish et al. 1981, Barth and Smith 1998). Colder water temperatures generally lower metabolism rates, and thus growth rates, in fish, although excessively high temperatures may induce physiological stress and inhibit growth (Jones 2002).

However, oceanographic conditions along the central Oregon coast during summer 2002 were highly atypical, highlighted by a severe upwelling-driven hypoxia zone that formed along the shallow inner shelf approximately 12 km south of Depoe Bay (Grantham et al. 2004), the southernmost of the two central Oregon coast sites. This hypoxia event occurred from July to September 2002 (fish were collected in late August and early September 2002). Intense upwelling conditions persisted during these months, resulting in cold water temperatures throughout the water column and anomalously high chlorophyll *a* concentrations (Wheeler et al. 2003, Grantham et al. 2004). Although the hypoxic zone itself did not impinge on the central coast sites, the growth rates of young-of-year rockfish may have been depressed along the central Oregon coast as a

consequence of lowered water temperatures during this intense upwelling period (Jones 2002). The 2002 summer hypoxia event along the central Oregon coast may signal an ecosystem-level regime change in the northeast Pacific (Grantham et al. 2004) and serve as an indicator for repeated future hypoxic events. Such long-term oceanographic shifts could have dramatic implications for rockfish recruitment and growth rates, with coinciding consequences for fisheries, as well as the general health of temperate nearshore communities such as kelp forests and rocky reefs. Indeed, preliminary data collected during summer 2004 tentatively indicates the formation of another hypoxic zone along the central Oregon coast (Service 2004).

The 2002 summer upwelling period was preceded by several intermittent, strong downwelling events during June and early July, when surface water temperatures exceeded 15°C (Grantham et al. 2004). These relatively high water temperatures may possibly have induced warming-related physiological stress in the young-of-year rockfish, then in their pelagic larval stage, and contributed to slower larval mass growth rates in the central region (Fig. 5) (Jones 2002). However, a negative growth response to downwelling conditions is unlikely since intermittent downwelling is normal along the central Oregon coast in the summer (Huyer 1983).

In addition to, and perhaps as a consequence of, the anomalous hypoxia event, recruitment and growth of *Nereocystis* kelp was very poor on deep and mid-depth reefs (15 and 10 meters depth) along the central Oregon coast in summer 2002 (T.H. Young, personal observation, M.H. Webster, personal communication). *Nereocystis* kelps were absent from most rocky reef sites that were occupied by expansive, emergent *Nereocystis* canopies in previous years (M.S. Webster and M.H. Carr, personal communication). The few existing kelp forests observed along the central Oregon coast consisted either of 1) almost exclusively year-old, perennial *Nereocystis* that had managed to survive the winter (*Nereocystis* is typically an annual kelp on the central Oregon coast that is destroyed during seasonal, winter storms; Abbott and Hollenberg 1976), or 2) dense kelp recruits in shallow water (5 meters depth) (T.H. Young, personal observation, M.S. Webster, personal communication). The poor condition of kelp along the central Oregon coast may have contributed to slower growth rates of young-of-year rockfish, as juvenile nearshore rockfish are often dependent upon kelp for settlement habitat (Carr 1991, Ammann 2004), refuge from predators (Carr 1994b), and as a habitat for principle prey such as amphipods (Love et al. 1991, Carr 1994b). Limited availability of settlement habitat on the central Oregon coast may have caused crowding in recruited juvenile rockfish, precipitating density-dependent growth inhibition due to post-settlement intracohort competition within the sparse kelp canopy (Jones 1988, Booth 1995).

The recruitment and growth failure of *Nereocystis* on deep and mid-depth reefs in the central Oregon coast during summer 2002 may have been caused by competition for light with large phytoplankton blooms (Grantham et al. 2004) and shading by dense zooplankton, particularly mysid shrimp (T.H. Young, personal observation). Additionally, high purple urchin densities (*Strongylocentrotus purpuratus*) along the central Oregon coast may have indicated a possible shift of kelp forests to urchin barrens in 2002 due to overgrazing (M.S. Webster, personal communication, T.H. Young, personal observation, Steneck et al. 2002, Scheibling et al. 1999), hinting at the significance of community-level trophic dynamics for juvenile rockfish growth (Love et al. 1991). In contrast, kelp forests in the southern Oregon coast sites appeared relatively

robust and healthy, with expansive canopy cover of large *Nereocystis* compared to the central coast sites (T.H. Young, personal observation). However, the spatial extent of kelp forests on the southern Oregon coast in 2002 did not necessarily exceed that of previous years and may have actually been a significant reduction from 2001 kelp forests (M.S. Webster and M.H. Carr, personal communication), although not nearly to the level of the central coast.

Regional variation in total growth rates may also result from differences in the species composition of fish collected between the central Oregon coast and the southern Oregon coast. Although all fish identified genetically on the central Oregon coast were quillback rockfish (*Sebastes maliger*), only two-thirds of fish identified on the southern Oregon coast were quillbacks; the remaining one-third southern fish were copper rockfish (*S. caurinus*) and gopher (*S. carnatus*) or black-and-yellow rockfish (*S. chrysomelas*). These results indicate that a higher species diversity of rockfish may be represented in the collection from the southern Oregon coast. Differences in species composition between the two regions may have produced regional differences in growth rates, independent of environmental influences, if the different species experience distinct endogenous growth and ontogenetic rhythms or if their growth rates respond differently to various exogenous, or environmental, factors. The importance of species composition for structuring spatial patterns in growth rates is explored in the following section, along with a discussion of spatial patterns in juvenile physical conditions (Question #3).

Consistent regional differences in growth rates were observed for total growth rates (Fig. 7) and larval mass growth rates (Fig. 5). Thus, regional differences in total mass growth rates can be attributed to differences in growth rates that occur during the larval stage, but that do not persist through the juvenile stage. However, there was no evidence of regional differences for juvenile growth rates (Fig. 6) or for larval length growth rates (Fig. 5). Differences in total length growth rates between the southern and central Oregon coast must be occurring during either the larval stage, the juvenile stage, or both, and therefore should be demonstrated by regional differences in one or both of these stages. The exception to this would be if an additive effect were producing a significant difference in total length growth rates by combining non-significant differences in larval and juvenile growth rates. Therefore, the lack of regional spatial patterns in larval and juvenile length growth rates may indicate such an additive effect, or may arise from additional error in larval and juvenile growth rate estimates. The use of back-calculated sizes at metamorphosis to derive juvenile and larval growth rates invariably introduces an additional source of error into growth rate estimations and may preclude the ability to resolve regional differences in larval and juvenile growth rates. In contrast, total growth rates do not require back-calculation and are calculated from direct measurements of size and age.

There is considerable evidence to indicate that an additive effect caused significant regional differences in total growth rates by combining small differences in larval and juvenile growth rates. Parameter estimates for larval and juvenile growth rates, by length and by mass, were consistently faster on the southern Oregon coast than on the central Oregon coast (Fig. 5 and 6), which corroborates the pattern observed for total growth rates (Fig. 7). P-values from t-tests comparing larval and juvenile growth rates between regions were as follows (Nested ANOVAs): Larval Length Growth Rate, $p=0.12$; Larval Mass Growth Rate, $p=0.084$; Juvenile Length Growth Rate, $p=0.016$;

Juvenile Mass Growth Rate, $p=0.14$. Although the effect of Region was not significant for any of these ANOVAs ($p>0.10$), the parameter estimates and their corresponding p -values clearly indicate a consistent difference in larval and juvenile growth rates between the central and southern Oregon coast. P -values from t -tests comparing total growth rates between regions were as follows: Total Length Growth Rate, $p<0.0001$; Total Mass Growth Rate, $p=0.0014$. When larval and juvenile growth rates are pooled together and error from back-calculations is eliminated, a substantial regional difference in total growth rates is produced.

Juvenile growth rates and total growth rates by length appeared to differ at the spatial scale of local sites, and the pattern of growth rate variation among sites within each region was consistent (Fig. 6 and 7). However, it is difficult to evaluate whether this variation among sites is a result of local ecological factors occurring at the scale of one to ten kilometers, such as predation (Metcalf et al. 1987, Connell 1998), selective mortality (Levin et al. 1997, Takasuka et al. 2003), competition (Booth 1995), prey availability (McCormick and Molony 1992), or habitat quality (Love et al. 1991, Tupper and Boutilier 1997); due to temporal effects resulting from different collection dates between sites (Appendix V: Table A); due to differences in species composition among sites; or due to possible systematic biases in age and growth rate estimates between sites.

Spatial variation in growth rates, especially among sites within the southern Oregon coast, may have resulted from spatial differences in allometric growth or ontogenetic stage of fish. In particular, East Island Rock fish were significantly younger, smaller, and faster-growing than fish from all other sites. It is possible that the slower growth rates in the other sites may be associated with a developmental change in growth pattern – an ontogenetic shift to slower growth rates – that all other fish underwent as juveniles but had not occurred yet in the younger East Island Rock fish. Consequently, the growth-size relationships used to test for spatial patterns in growth rates may not adequately describe the growth-size relationship for smaller fish such as those from East Island Rock.

Spatial variation in larval growth rates appears to occur predominantly at the regional scale (Fig. 5), whereas spatial variation in juvenile growth rates occurs almost exclusively at the local site level (Fig. 6). Planktonic larvae tend to be transient and highly mixed on a regional level, and are influenced by processes occurring at the spatial scale of current systems, eddies, gyres, and water masses (Lasker 1978, Iles and Sinclair 1982, Fortier and Gagné 1990). In addition, the habitat characteristics of pelagic, planktonic larvae are defined by the oceanographic properties of the water in which they drift or swim, and such properties tend to vary on larger spatial scales than structural habitats, such as reefs or kelp beds where juveniles reside (Love et al. 1991, T.H. Young, personal observation). Larvae are thought to be entrained in water masses where they may be passively transported long-distance by currents (Roberts 1997) or entrained in meso-scale eddies and regionally or locally retained (Jones et al. 1999, Swearer et al. 1999, Cowen et al. 2000, Taylor and Hellberg 2003). Small-scale spatial variation is difficult or impossible to detect in populations whose larval growth rates are uncoupled from local environmental factors by long-distance dispersal (Roberts 1997). For these transient larvae, important growth factors may include water temperature, salinity, and dissolved oxygen content (Fuiman 2002); zooplankton composition and availability (i.e., food) (McCormick and Molony 1992); degree of upwelling or downwelling and pelagic

productivity (Lasker 1978); circulation patterns relative to available settlement habitat and prey patches (Cowan and Shaw 2002); availability of settlement habitat such as canopy kelp (Carr 1991, Carr 1994a), and intensity or selectivity of predation and competition (Houde 2002).

In contrast, juveniles are local resident fish and exhibit a high degree of site-fidelity, remaining within the same kelp forest canopy before transitioning to the reef below (Love et al. 2002). The growth patterns of juveniles are consequently tightly coupled to local conditions, interactions, and resource dynamics that occur on the scale of the kelp forest or reef. Kelp forest and reef characteristics, which define the habitats of juvenile rockfish, tend to vary on smaller spatial scales than the majority of water mass properties that characterize larval habitats (Broitman and Kinlan *In Review*). For example, local kelp dynamics may be instrumental in determining food and habitat availability (Love et al. 1991), degree of exposure to storm surges and currents (Dayton 1985), intensity of predation and density of predators (Gaines and Roughgarden 1987), density of competitors or congeners within a cohort (Carr 1994a), and overall habitat quality and structural complexity (Carr 1991). Other crucial local factors for juvenile growth rates may include habitat relief or rugosity, and small-scale oceanographic effects from coastline geography and bathymetric features, such as downstream (leeward) effects, eddies, and wave exposure (Broitman and Kinlan *In Review*). The observation that juvenile growth rates varied on a local spatial scale (at the site level) while larval growth rates varied on a regional scale underscores the importance of individual dispersal distances and capabilities or behaviors of movement (e.g., transient or resident) for determining the scale at which influential factors in life history parameters operate. Speculative causes in spatial variation of growth rates at the local scale, among sites, are addressed to greater detail in the next section, alongside a discussion of spatial patterns in juvenile physical conditions (Question #3).

It is important to note that some of the observed spatial patterns in growth rates reflect those that would be predicted from suspected systematic errors in otolith daily increment counts, age estimates, and size back-calculations. Within the southern Oregon coast, differences in estimated parturition dates (Fig. 4) indicate that growth rates for East Island Rock may be overestimated and growth rates from Nellie's Cove may be underestimated. This is corroborated by the observation that estimated juvenile growth rates and total length growth rates along the southern Oregon coast are fastest in East Island Rock and slowest in Nellie's Cove (Fig. 6 and 7). However, differences in estimated parturition dates (Fig. 4) also predict that, within the central Oregon coast, growth rates for Depoe Bay fish may be overestimated and/or growth rates for Otter Crest fish may be underestimated. In contrast, despite these predictions of error, estimated growth rates were fastest in Otter Crest and slowest in Depoe Bay in the central region.

Otolith radii (Fig. 3) may correspond positively with the degree of age overestimation due to sub-daily increments. Within the southern Oregon coast, spatial differences in otolith radii predict that juvenile and total growth rates in East Island Rock should be faster than growth rates in Orford Reef, and that growth rates in Nellie's Cove should be slowest, *ceteris paribus*. Likewise, growth rates for the southern Oregon coast region should be faster than the central Oregon coast. Within the central region, there should be no difference in growth rates between Depoe Bay and Otter Crest, *ceteris paribus*. These predictions are corroborated by observed spatial patterns of juvenile

growth rates and total length growth rates among sites within the southern Oregon coast (Fig. 6 and 7), and by spatial patterns of total growth rates between the two regions (Fig. 7). However, Otter Crest fish exhibited faster juvenile growth rates (Fig. 6) and total length growth rates (Fig. 7) than Depoe Bay fish within the central Oregon coast, despite no significant difference in their otolith radii.

The use of a single regression equation for length back-calculations (Fig. 3), despite regional differences in the slope of otolith-somatic growth relationships, likely caused overestimations in juvenile length growth rates for southern Oregon coast fish and underestimations in juvenile length growth rates for central Oregon coast fish. Conversely, error in back-calculations may have resulted in underestimation of southern coast larval length growth rates and overestimation of central coast larval length growth rates. This is due to the fact that the slope of the otolith-somatic growth relationship for lengths was steeper for the southern Oregon coast than for the central Oregon coast (Appendix V: Fig. E). Therefore, the use of a single linear regression equation for back-calculations in both regions led to underestimation of lengths at metamorphosis for the southern region, and overestimation of lengths at metamorphosis for the central region. There was no difference between regions in otolith-somatic growth relationships for masses ($p > 0.10$). Back-calculation errors are likely not important for mass growth rates, and spatial patterns in mass growth rates probably reflect actual regional variation.

The only measurement for which error derived from back-calculation appears to have been important was larval length growth rate. There was no evidence of regional spatial patterns in either juvenile growth rates by length or by mass (Fig. 6). However, larval mass growth rates exhibited significant regional variation whereas larval length growth rates did not (Fig. 5). Therefore, errors in lengths at metamorphosis from back-calculations may have statistically nullified an important regional pattern in larval length growth rates that was apparent in larval mass growth rates. The slope of larval mass growth rates versus mass at metamorphosis was steeper for the southern Oregon coast than the central Oregon coast and southern coast fish grew faster than central coast fish for heavier masses at metamorphosis (Fig. 5). A similar regional pattern may have been masked in larval length growth rates because of the underestimation of southern larval growth rates and overestimation of central larval growth rates (Appendix V: Fig. E). Additionally, errors in larval length growth rates should be more pronounced for fish with larger lengths at metamorphosis, thereby depressing the slope for larval length growth rates of southern coast fish and steepening the slope for larval length growth rates of central coast fish. These back-calculation errors may have therefore effectively cancelled out a true regional pattern in larval length growth rates, if the regional pattern were similar to that of larval mass growth rates (Fig. 5).

Errors introduced by inaccurate back-calculations in the estimation of juvenile and larval growth rates by length cannot explain the spatial variation observed in total growth rates at the regional level. The equations for calculating total growth rates do not utilize back-calculated sizes at metamorphosis. Therefore, observed regional differences in total growth rates, by mass and by length, are not thought to be associated with any substantial error due to back-calculations (Fig. 7). Additionally, there was no evidence of differences in the otolith-somatic growth relationships for masses between regions. Thus, regional spatial patterns observed in larval mass growth rates cannot be explained by errors in back-calculations of masses at metamorphosis.

Similar significant regional patterns, marked by faster growth on the southern coast than on the central coast, occurred in total growth rates by mass and by length, as well as in larval mass growth rates. Additionally, these regional patterns were corroborated by non-significant differences in juvenile growth rates and larval length growth rates. Therefore, these consistent regional differences may indicate a real spatial pattern, rather than error associated with measurement or back-calculation.

3) *Do juvenile physical conditions (mass-length relationships) vary between regions or among local sites along the Oregon coast?*

The relationship between mass and length differed significantly between sites within each region, but not between the regions themselves (Fig. 8). Along the central Oregon coast, Depoe Bay fish were more massive per unit of length than Otter Crest fish, indicating better physical condition of Depoe Bay fish than Otter Crest fish. Along the southern Oregon coast, Nellie's Cove fish appeared to be more massive per unit of length than Orford Reef fish, and East Island Rock fish appeared to be less massive per unit of length than Orford Reef fish, but these differences were not significant ($p > 0.10$).

Depoe Bay fish were captured approximately three weeks later than Otter Crest fish. Therefore, differences in condition factors (Fig. 9) and in growth rates (juvenile growth rates and total length growth rates, Fig. 6 and 7) between these two central Oregon coast sites may have resulted either from intrinsic local variation in environmental factors operating on a site-level scale (i.e., a spatial effect), or from temporal changes in regional oceanographic conditions along the central Oregon coast between the time of capture of Otter Crest fish and the time of capture of Depoe Bay fish (i.e., a temporal effect). Both Otter Crest and Depoe Bay fish were collected from emergent *Nereocystis* canopy kelp during a protracted period of intense, persistent upwelling along the central Oregon coast (Grantham et al. 2004). Depoe Bay fish experienced a greater duration of exposure to cold sea-surface temperatures due to prolonged upwelling, which may have caused average juvenile and total growth rates of Depoe Bay fish to decrease significantly over time or may have induced an allometric shift in growth, thereby changing condition factors.

Depoe Bay and Otter Crest are dramatically different sites that may be influenced by distinct small-scale oceanographic conditions. Depoe Bay is a small, wide-mouthed bay with low bottom habitat rugosity, while Otter Crest is a shallow, high relief reef located immediately down-current of a major headland, or cape (M.S. Webster and M.H. Carr, personal communication, T.H. Young, personal observation). These two coastal features – bays and headlands, or capes – typically exhibit markedly different oceanographic conditions (Broitman and Kinlan *In Review*). In addition, during summer 2002, the *Nereocystis* kelp in Depoe Bay appeared large, old, and worn, was more sparsely and patchily distributed, and grew deeper than Otter Crest kelp, probably consisting of perennials that survived winter storms (T.H. Young, personal observation). Otter Crest kelps, in contrast, were relatively small, young, healthy, and very dense, grew only in shallow water, and likely consisted of new kelp recruits for that year (T.H. Young, personal observation). The differences in juvenile growth rates and juvenile physical conditions between these sites, although relatively close in proximity to one

another, emphasizes the strong effects of oceanographic and biological variation on a small, local spatial scale for controlling growth patterns and overriding the effects of regional processes for resident fish (i.e., juveniles). Depoe Bay fish were also slightly older at capture than Otter Crest fish, and the difference in condition factors (Fig. 9) may represent an ontogenetic change in allometric growth, although this scenario is unlikely since the average age difference between the two central sites was only approximately 5 days (Appendix V: Table B).

Differences in physical conditions and in growth rates (juvenile growth rates and total length growth rates) between the three southern Oregon coast sites may be a consequence of local spatial variation in environmental factors among sites. Temporal effects would not have been important among these three sites, as fish collections were conducted over a period of only two days. The three southern sites were situated at different distances from the mainland coast, and were probably influenced by distinct oceanographic conditions. Nellie's Cove is a small cove with low relief located directly adjacent to the mainland coast, East Island Rock is a nearshore basalt haystack with high relief situated within a kilometer of the coast, and Orford Reef is a series of high relief basalt pinnacles several kilometers offshore. Consequently, Orford Reef is typically situated within a different oceanographic regime, characterized by more intense upwelling, colder water temperatures, higher water visibility (lower turbidity), lower phytoplankton concentrations, and more expansive kelp forests compared to Nellie's Cove and East Island Rock (M.S. Webster, personal communication, T.H. Young, personal observation).

Environmental differences among these sites were reflected in different algal, invertebrate, and fish communities from subtidal surveys of kelp forests and rocky reefs at these sites (M.S. Webster, personal communication, T.H. Young, personal observation). For instance, very high densities of mysid shrimp and *Nereocystis* kelp were observed at Orford Reef in summer 2002 and 2004, compared to low densities of mysids at both East Island Rock and Nellie's Cove in summer 2002, and low densities of both mysids and *Nereocystis* at East Island Rock in summer 2004 (Nellie's Cove was not surveyed in 2004; M.S. Webster, personal communication, T.H. Young, personal observation). Additionally, species composition of young-of-year juvenile rockfish recruits varied tremendously between Orford Reef and East Island Rock in summer 2004 (T.H. Young, personal observation). Orford Reef recruits consisted primarily of black rockfish (*S. melanops*) and the species group that was identified in this study (quillback, copper, gopher, black-and-yellow). East Island Rock recruits were predominantly blue rockfish (*S. mystinus*), mixed with few black rockfish. These observations underscore the magnitude of local variation in productivity and recruitment among local sites.

These site differences in the southern region imply that spatial variation in growth rates and condition factors should be smallest between Nellie's Cove and East Island Rock, which are located within viewing distance of one another, and greatest between the offshore Orford Reef and one of the other two nearshore coastal sites. However, the opposite is true, where the largest differences in growth rates and condition factors consistently occurred between Nellie's Cove and East Island Rock. Orford Reef fish always occupied the intermediate value in ordered lists of parameter estimates for physical conditions and for all growth rates, with the single exception of total mass

growth rates (which were not significantly different among sites within the southern Oregon coast, $p > 0.10$).

It is possible that bottom habitat relief may play a crucial role in determining juvenile growth rates and condition factors, which would help explain the lack of variation between East Island Rock and Orford Reef, both of which exhibit higher habitat relief. Since juvenile growth rates were faster in these sites, habitat relief may confer some benefit to the growth rates of young-of-year juvenile rockfish. High relief rocky reefs may provide more suitable bottom habitats for juvenile rockfish than low relief reefs, or may accommodate higher densities of benthic crustaceans and other invertebrate prey of juvenile rockfish. The recently settled juveniles may not remain exclusively in the kelp canopy during their early development and may utilize shelter in the rocky reef (T.H. Young, personal observation), perhaps as an alternative habitat for feeding on benthic organisms or as a secondary refuge from predators and competitors. Mysid shrimp that juvenile rockfish may prey upon occurred in dense aggregations along the bottom meter of the water column, directly above the reef, and therefore were not accessible to recruits residing in the kelp canopy.

The dramatic difference in juvenile growth rates and juvenile physical conditions between East Island Rock and Nellie's Cove, despite their almost immediate proximity to one another, underscores the importance of local factors, operating on small scales with a high degree of spatial variability, for driving post-settlement demographics and controlling juvenile growth patterns. During the juvenile stage, any influence of regional factors is overtaken and overwhelmed by the effects of highly spatially variable local processes.

Alternatively, spatial differences in condition factors and growth rates among sites, as well as differences in growth rates between regions, may result from distinct species compositions of fish collections. Although there was no evidence to suggest that species compositions differed between Depoe Bay and Otter Crest, which may both consist entirely of quillback rockfish (*Sebastes maliger*), an insufficient number of fish were genetically analyzed from each of these central Oregon coast sites to ascertain whether or not species compositions differed significantly. There were indications, albeit inconclusive, of differences in species composition among the southern Oregon coast sites. Orford Reef appeared to consist mostly or perhaps entirely of quillback rockfish, while Nellie's Cove contained a mix of quillback and copper rockfish (*S. caurinus*), and East Island Rock contained a mix of quillback rockfish and gopher or black-and-yellow rockfish (*S. carnatus* or *S. chrysomelas*, respectively).

It is conceivable that quillback rockfish, copper rockfish, and gopher/black-and-yellow rockfish exhibit dissimilar physiological tolerances and require distinct conditions and resources for optimal growth, since these species are characterized by differences in geographic distributions and depth ranges, despite considerable overlap in behavior, ecology, and early life history characteristics (Love et al. 2002). Quillback rockfish are a northern species that does not occur south of Point Conception, California and live in water as deep as 274 meters (900 feet) (Yamanaka 2002). In contrast, gopher and black-and-yellow rockfish are southern species that do not occur north of Cape Blanco, Oregon and only reside in water shallower than 80 meters (264 feet) (Larson 2002). The distribution of copper rockfish encompasses the entire geographic ranges of both quillbacks and gophers/black-and-yellows, and coppers have been found as deep as 183

meters (600 feet) (Love 2002). These depth ranges and geographic distributions indicate that quillback rockfish are probably better adapted for colder water temperatures and deeper habitats than are gopher and black-and-yellow rockfish. Conversely, gophers and black-and-yellows are likely better adapted for warmer water temperatures and shallower habitats than quillbacks. Copper rockfish probably represent an intermediate species that is tolerant of both colder and warmer water temperatures and shallow to intermediate depths. Despite their long list of ecological and behavioral similarities, different physiological tolerances or ecological preferences between rockfish species may have profound implications for spatial patterns in growth rates and physical conditions if species compositions are dissimilar between regions or among sites.

Juvenile growth rates, by both mass and length, varied inversely with juvenile physical conditions at the local site level. In other words, sites with faster growing fish consistently had fish that were less massive per unit of length compared to sites with slower growing fish, within the same region (Fig. 6 and 8). Within the central Oregon coast, juvenile growth rates by both mass and length were faster in Otter Crest than in Depoe Bay (Fig. 6), but physical conditions were greater in Depoe Bay than in Otter Crest (i.e., Depoe Bay fish were more massive per unit length) (Fig. 8). Within the southern Oregon coast, juvenile growth rates by both mass and length were faster in East Island Rock than in Orford Reef and slowest in Nellie's Cove (Fig. 6). Physical conditions, in contrast, were greatest in Nellie's Cove and least in East Island Rock (Fig. 8). Total growth rates by length also maintained inverse spatial patterns at the local site level as compared with juvenile physical conditions (Fig. 7 and 8). This local site-level inversion of growth rates and physical conditions may represent an important physiological or ecological trade-off between one measure of fitness in juvenile rockfish – growth rates, and another measure of fitness – physical conditions, or mass-length relationships.

The apparent trade-off between juvenile growth rates and juvenile physical conditions was investigated by plotting condition factors of fish versus juvenile growth rates by length and by mass (Fig. 9). Condition factors appeared to be negatively correlated with juvenile growth rates by length, but were not correlated with juvenile growth rates by mass (Fig. 9). Relationships between condition factors and juvenile growth rates varied considerably among sites but not between regions. These results suggest that the observed trade-off between juvenile length growth rates and physical conditions (i.e., condition factors) occurs at the level of the individual fish, and is reinforced by differences in condition factors among sites that correlate inversely with spatial patterns in juvenile length growth rates. The inverse relationship with condition factors did not extend to juvenile mass growth rates, as expected, since condition factors are determined by the relative rates of growth by mass versus length in fish. Fish are in essence sacrificing their linear growth in order to acquire more mass per unit of length. Whether the strategy of maximizing growth rates by length or attaining optimum condition factors confers greater survivorship, and under what ecological conditions one or the other alternate growth strategy may be preferred, remain to be determined. How environmental or endogenous factors may influence the growth strategy of fish are other important questions to be addressed. Clear variation among sites in this relationship is evidence of local-scale environmental factors playing an important role in the growth strategy of fish. It is not suspected that systematic errors in measurements contributed to

these patterns because no otolith age estimates or size back-calculations were used to calculate condition factors. However, differences in species composition among sites may have been an influential factor for local spatial variation in condition factors.

4) *Do faster growing larvae metamorphose at younger ages, as predicted by the Single Process Concept?*

Larvae with faster growth rates by length metamorphosed at younger ages and experienced shorter larval durations compared to larvae with slower growth rates by length (Fig. 10). The effect of larval length growth rate on age at metamorphosis appeared to be stronger in the central Oregon coast than in the southern Oregon coast (Fig. 10). In contrast, larvae with faster growth rates by mass metamorphosed at older ages and experienced longer durations compared to larvae with slower growth rates by mass (Fig. 10). The effect of larval mass growth rate on age at metamorphosis was stronger in the central Oregon coast than in the southern Oregon coast, and southern coast fish appeared to metamorphose at younger ages than central coast fish for a given larval mass growth rate (Fig. 10).

Multiple studies have found that swimming speeds (Fuiman and Webb 1988, Miller et al. 1988, Williams et al. 1996), predator detection ability (Fuiman 1989, Fuiman and Delbos 1998, Zaunreiter et al. 1991), and escape responses (Fuiman 1989) increase with size and ontogeny in young-of-year fishes. In this context, the observed negative correlation between larval length growth rates and ages at metamorphosis indicates a distinct selective advantage for larval rockfish with faster growth rates by length (Fig. 10). Faster growing fish by length proceed more rapidly through successive developmental stages, experience shorter larval durations, and escape a highly vulnerable planktonic larval existence at younger ages. Therefore, according to the Single Process Concept (Cushing 1975, Houde 1987, Houde 1989) and Stage Duration Hypothesis (Houde 1987, Fuiman 1994, Leggett and DeBlois 1994), faster larval length growth rates likely contribute to higher survivorship (lower mortality rates) and increased chance of recruitment (Bergenius et al. 2002, Cowan and Shaw 2002, Houde 2002).

These results indicate that the timing of metamorphosis may be heavily influenced by larval length growth rates in young-of-year rockfish (Fig. 10). The fact that the rockfish species represented in this study settle almost concurrently with metamorphosis (Love et al. 2002) also highlights the importance of larval growth rates for influencing settlement ages. Given that the pre-settlement environment (pelagic) and lifestyle (planktonic) are thought to be associated with higher mortality rates than benthic habitats and a demersal existence for young-of-year fish (Bailey and Houde 1989), larval growth rates may therefore be a critical factor for determining recruitment rates by mediating the timing of settlement, a pivotal early life history transition.

Larval mass growth rates exhibited a positive relationship with ages at metamorphosis (Fig. 10), contradicting the prediction of the Single Process Concept and presenting a counterpoint to the apparent effect of larval length growth rates. The increase in mass growth rates with age at metamorphosis may be due to the non-linear power function relationship between mass and length (Appendix V: Fig. D). As a result of this mass-length relationship, mass growth rates always increase with age in fish that

are growing by length. This mass growth relationship is a characteristic biometric for the early life history of many fish (Jones 2002).

Another potential mechanism by which the observed pattern may occur is if fish metamorphose upon attaining some critical, or threshold, length (Pasten et al. 2003), and also require appropriate settlement cues, such as available bottom habitat, in order to undergo metamorphosis (Montgomery et al. 2001, Parmentier et al. 2004). If there is a physiological trade-off between larval length growth rates and larval mass growth rates, then fish may “attempt” to shorten their larval duration and expedite metamorphosis by speeding their linear growth (length growth rate) and compromising their mass growth. Although this compromise would increase a larva’s chances of escaping the intense predation typical of the larval stage by metamorphosing early (Houde 2002), the trade-off is that the larvae would be more vulnerable to starvation due to the lack of energy stores (Fuiman 2002). If a fish attains the critical length before encountering the necessary settlement cues, it may hypothetically be capable of delaying metamorphosis, and thus settlement, by slowing its linear growth (Victor 1986, Sponaugle and Cowen 1994, McCormick 1999). Instead of accumulating length, the fish would accrue additional mass to prevent starvation while biding its time to metamorphose and settle. Therefore, fish that settle youngest would exhibit fastest larval length growth rates and slowest larval mass growth rates, whereas fish that metamorphose oldest, by postponing metamorphosis and settlement, would exhibit the reverse pattern: faster mass growth rates and slower larval length growth rates, as indicated in Fig. 10. This process indicates an important trade-off between larval length growth rates and larval mass growth rates.

The natural log of larval mass growth rates was plotted versus the natural log of larval length growth rates in order to investigate this trade-off (Fig. 11). Contrary to the predicted trade-off, which would entail a negative correlation, there was a positive relationship between the natural log of larval length growth rates and the natural log of larval mass growth rates (Fig. 11). This relationship was consistent at both regional and local spatial scales. Therefore, it is not clear why or how larval length growth rates can exhibit an inverse, or negative, relationship with age at metamorphosis while larval mass growth rates exhibit a direct, or positive, relationship with age at metamorphosis.

Spatial variation in the relationships between larval growth rates and ages at metamorphosis suggests that these may not be highly conserved ontogenetic-growth phenomena along the Oregon coast. The nature and strength of these relationships may be influenced by spatially variable environmental factors.

Since the young-of-year rockfish collected represent a group of species that exhibits little or no pelagic juvenile stage (Love et al. 2002), larval rockfish may require a suitable settlement habitat, such as a nearshore rocky reef or kelp canopy, in order to metamorphose. Larvae that have not found such suitable settlement habitat when physiologically ready to metamorphose may be able to actively slow their growth rates, perhaps through behavioral or physiological changes, in order to induce a pause in their development and prevent metamorphosis prior to encountering ideal settlement conditions. Such a capacity to exert endogenous control over growth rates in order to delay metamorphosis also would result in an inverse relationship between age at metamorphosis and larval growth rates. This phenomenon would present a fascinating ontogenetic mechanism by which young-of-year rockfish behaviorally or physiologically

minimize their pelagic juvenile duration so that metamorphosis may coincide with settlement.

The Single Process Concept states that younger settlement and metamorphosis ages should yield higher recruitment rates (Cushing 1975, Houde 1987, Houde 1989). Younger metamorphosis ages may result from increased larval growth and development rates, as predicted by the Single Process Concept and demonstrated in Fig. 10. However, increased mortality rates may also produce younger metamorphosis ages, since high larval mortality rates favor fish that escape the pelagic larval stage at younger ages. If faster larval growth rates do indeed decrease the larval duration, or age at metamorphosis, then higher larval mortality rates would indirectly favor faster larval growth rates. By this mechanism, younger settlement (or metamorphosis) ages and faster larval growth rates may be confounded with higher pre-settlement (or larval) mortality rates, possibly nullifying the hypothesized inverse correlation between recruitment rates and settlement (or metamorphosis) ages. Using the approaches in my study, it would not be possible to determine whether an observed difference in average settlement ages between cohorts or samples is a result of different growth and development rates between the samples, a result of different pre-settlement mortality rates, or both. Higher pre-settlement mortality rates create a directional selective pressure favoring earlier settlement ages, thereby yielding potentially younger average settlement ages in cohorts with lower recruitment rates. Such a pattern would contradict the predicted inverse relationship between recruitment rates and settlement ages because cohorts with higher larval mortality rates would likely exhibit both younger settlement ages *and* lower recruitment rates to the juvenile stage. The scenario predicted by the Single Process Concept would only occur under an assumption of no difference in larval mortality rates between cohorts or samples, combined with a negative effect of larval growth rate on metamorphosis ages.

However, a valid criticism of these results is that the explanatory and response variables for this regression are not independent, since larval duration (age at metamorphosis) is the denominator for the equation of larval growth rate (larval growth rate = larval growth/larval duration). It may thus only be a statistical artifact that these two parameters are inversely related, since an increase in larval duration would cause a decrease in the calculated larval growth rate, unless there is a compensatory increase in larval growth (size at metamorphosis – size at parturition).

5) *Do larval growth rates, size at metamorphosis, or larval duration (i.e., age at metamorphosis) predict juvenile growth rates?*

Larval growth rates appeared to have a negative effect on juvenile growth rates, whereby faster-growing larvae tended to have slower growth rates during the juvenile stage (Fig. 12). Lengths at metamorphosis were also negatively correlated with juvenile growth rates by length; fish that metamorphosed at longer sizes experienced slower juvenile growth rates (Fig. 13). Masses at metamorphosis did not exhibit a significant effect on juvenile growth rates by mass (Fig. 13). Juvenile growth rates also did not appear to be affected by larval duration (i.e., age at metamorphosis) (Fig. 14). These results indicate that juvenile growth rates may be determined, or at least predicted, in part by larval growth rates and size at metamorphosis (particularly length). However, the

apparent influence of larval growth rates and sizes at metamorphosis on juvenile growth rates is an inhibitory effect rather than a reinforcing or enhancing effect, suggesting a trade-off between larval and juvenile growth rates.

All of the above relationships, between juvenile growth rates and larval growth rates, sizes at metamorphosis, or larval durations, varied among sites within each region in a predictable fashion. In the central Oregon coast, fish in Otter Crest exhibited faster juvenile growth rates by length than fish in Depoe Bay, for a given larval growth rate (Fig. 12), length at metamorphosis (Fig. 13), or larval duration (Fig. 14). However, the opposite was true for growth rates by mass: fish in Depoe Bay grew faster as juveniles than Otter Crest fish, for a given larval mass growth rate (Fig. 12), mass at metamorphosis (Fig. 13), or larval duration (Fig. 14).

The consistent reversal in growth rates between Depoe Bay and Otter Crest, with Depoe Bay fish growing faster by mass but Otter Crest fish growing faster by length, may result from the fact that Depoe Bay fish were more massive per unit length than Otter Crest fish (Fig. 8 and 9). In the southern Oregon coast, fish in Nellie's Cove consistently exhibited the fastest juvenile growth rates, by length or by mass, followed by fish in Orford Reef, with East Island Rock fish exhibiting the slowest juvenile growth rates, for a given larval growth rate (Fig. 12), size at metamorphosis (Fig. 13), or larval duration (Fig. 14).

These results suggest that fish that grow faster as larvae subsequently grow slower as juveniles (Fig. 12), and that fish that metamorphose at larger sizes (specifically, longer lengths) grow slower as juveniles (Fig. 13). The negative serial correlation between larval and juvenile growth rates may represent important sequential trade-offs during the early life history of rockfishes and may be induced by changes in physiological responses to developmental rates between the larval and juvenile stages, or may result from dramatic changes in optimal environmental conditions (requirements for optimal growth) between larval and juvenile rockfish. For instance, the inverse correlation between larval growth rates and juvenile growth rates, and between size at metamorphosis and juvenile growth rates can hypothetically result from a switch in food and habitat requirements between the pelagic larval stage and the demersal juvenile stage. Pelagic larval rockfish primarily feed on zooplankton (Love et al. 2002) and would benefit from conditions that retain local pelagic primary and secondary productivity, such as eddies and gyres (Wieters et al. 2003). Upon settlement, demersal juveniles generally exhibit a partial ontogenetic diet shift from zooplankton to benthic crustaceans (Love et al. 2002), which often associate with kelp (T.H. Young, personal observation). Juveniles thus depend on kelp for both habitat and food resources. However, conditions that favor pelagic productivity and larval growth also typically inhibit kelp recruitment and growth due to competition for light and nutrients (Dayton et al. 1999). Pelagic primary productivity (i.e., phytoplankton and chlorophyll-*a* concentrations) is inversely spatially correlated with benthic primary productivity, or kelp and algal growth, along much of the Pacific coastline of North America (Broitman and Kinlan *In Review*). For instance, phytoplankton (and subsequently zooplankton) standing stocks may be reduced near upwelling centers and immediately downstream (in the lee) of capes and headlands, but kelp forest biomass and productivity is enhanced in these areas. Therefore, certain oceanographic conditions may favor the habitat and diets of juveniles while reducing food supplies for larvae, while different oceanographic conditions may favor the diet of

larvae and be detrimental to the diet and habitat of juveniles (i.e., kelp and their associated epifauna).

These apparent early life history trade-offs may have been produced simply by errors in fish size back-calculations, whereby an overestimated size at metamorphosis would yield a slower-than-actual juvenile growth rate and a faster-than-actual larval growth rate. Conversely, an underestimated size at metamorphosis would inflate the juvenile growth rate estimate and deflate or depress the larval growth rate estimate. Thus, larval growth rates and sizes at metamorphosis may be inversely correlated with juvenile growth rates simply due to variation in the degree and direction of errors in back-calculations for size at metamorphosis.

6) *Does growth-selective mortality occur during the early juvenile stage of young-of-year rockfish along the Oregon coast, as predicted by the Growth-Mortality Hypothesis?*

Variances in juvenile growth rates by both length and mass decreased significantly as juvenile duration increased (Fig. 15). Means of juvenile growth rates by both length and mass did not change as juvenile duration increased (Fig. 16). This pattern of stable average juvenile growth rates amidst decreasing variation in juvenile growth rates with increasing time since metamorphosis suggests that stabilizing growth-selective mortality may have occurred during the early juvenile stage of young-of-year rockfish along the Oregon coast. This relationship was consistent between regions and among sites, indicating that the direction and magnitude of growth-selective mortality do not vary spatially along the Oregon coast.

It appears that stabilizing growth-selective mortality may be occurring throughout the juvenile duration for the fish collected (Fig. 15 and 16). The variances of growth rates decrease as juvenile duration increases (Fig. 15), but the mean juvenile growth rates do not appear to change (Fig. 16), implying that the fastest and slowest growing fish are dying first during the juvenile stage. Essentially, outlier fish with extreme juvenile growth rates may be experiencing the highest juvenile mortality rates, being selectively removed from the population faster than fish growing near the median rate. These results contrast the positive directionally selective mortality predicted by the Growth-Mortality Hypotheses (Anderson 1988, Booth and Hixon 1999, Takasuka et al. 2003), whereby mortality rate is inversely proportional to growth rate. This pattern does not vary between regions or among sites within each region ($p > 0.10$), and it is a statistically significant pattern ($p < 0.05$) for both growth rates by length and by mass (Fig. 15).

Since growth-selective mortality during the juvenile stage appears to be largely stabilizing rather than directional in nature, its effects upon spatial patterns in juvenile growth rates should be minimal. Although directional growth-selective mortality was not evident during the juvenile stage, this phenomenon may still have occurred during the larval stage, skewing observed growth rates towards the assumedly faster-growing survivors (Searcy and Sponaugle 2001, Takasuka et al. 2003). Growth-selective mortality during the larval stage was not investigated using this approach because of the difficulty differentiating variance in growth rate changes from systematic deviations in

otolith-somatic growth relationships from the regression used to back-calculate sizes at metamorphosis.

A criticism of this approach to assessing growth-selective mortality is that one might expect to see greater error, and thus greater variances, in juvenile growth rate calculations for fish with shorter juvenile durations and smaller sizes simply as a statistical consequence of using ages and back-calculated sizes at metamorphosis to estimate juvenile growth rates. This pattern (of decreasing variation in juvenile growth rates with increasing juvenile duration) may be caused by the proportionally greater effect of incongruities, or imprecision, between the points used to estimate age at metamorphosis during increment counts (first accessory primordium) and the points used to measure the otolith radius to the first accessory primordium, for fish with shorter juvenile durations and smaller body sizes. The effect of such incongruities (differences between the increment used to measure otolith radii and back-calculate sizes, and the increment used to estimate age at metamorphosis) diminishes with increasing juvenile duration and/or increasing juvenile fish size. In other words, small errors in otolith radial measurements, estimated ages at metamorphosis, and/or size back-calculations translate into proportionally larger errors in estimated juvenile growth rates for smaller fish with shorter juvenile durations compared to larger fish with longer juvenile durations. For fish with longer juvenile durations, these errors are distributed over a greater number of days and are therefore buffered by this longer time period. For fish with larger sizes, errors in back-calculations of size at metamorphosis represent a smaller proportion of growth during the juvenile stage than for smaller fish. Therefore, the observed pattern interpreted as stabilizing growth-selective mortality may in fact indicate a statistical artifact – a systematic sampling bias of juvenile duration on the error, or variation, in growth rate estimates.

An additional statistical artifact that can produce decreased variation in juvenile growth rates with increasing juvenile duration (Fig. 15) is that juvenile growth rates for recently metamorphosed juveniles depend more heavily upon a short period of conditions or upon genetic factors, whereas growth rates for older juveniles are integrated over a longer period of time with greater variation in conditions (Anderson and Sabado 1999, M.S. Webster, personal communication). Therefore, growth rates are more variable among younger juveniles due to the proportionally stronger and more exclusive effect of either beneficial or detrimental conditions, and the greater possibility of experiencing only extreme conditions during their short juvenile durations. The older juveniles each experience a broad range of conditions, including both beneficial and detrimental, that are integrated over their longer juvenile durations. They therefore exhibit less variable juvenile growth rates that reflect the time-average of these conditions.

The phenomenon of growth depensation in younger fish and compensatory growth in older fish may also be important for explaining this pattern (Jones 2002). Growth rates tend to be more idiosyncratic and highly variable in younger fish, particularly during the larval and early juvenile stages (Koebele 1985, Ochi 1986). This growth depensation is due to the cumulative effects of physiological (endogenous) and environmental (exogenous) factors, which may be additive or multiplicative (synergistic) in nature (Jones 2002). Growth depensation may be especially strong throughout the larval stage, during metamorphosis, and immediately following metamorphosis, when growth rates are influenced by a number of asynchronous and idiosyncratic physiological

processes associated with ontogeny and allometric growth. The high variation in growth for younger juveniles reflects the complexity of these processes. As the juvenile stage progresses, and growth changes from allometric to isometric, physiological and environmental effects upon growth become more consistent among individuals, and fish may experience compensatory growth or reduced variability in growth rates (Fuiman 2002, Jones 2002, Ali et al. 2003).

Growth-selective mortality can be detected more finely and resolved with high confidence by back-calculating growth rates or sizes at finer intervals (e.g., daily or weekly) using radial measurements of daily otolith growth increments (Ricker 1969). The otoliths that I examined did not exhibit a consistent radial counting path, a necessary prerequisite for daily increment measurements in asymmetrical otoliths (Campana 1992), due to many cracks and obscurities radiating outwards from the nucleus. Therefore, only coarse estimates of average growth rates over the larval and juvenile periods were feasible in my study.

APPENDIX IV: CONCLUSIONS

Rockfish of the genus *Sebastes* are ecologically and economically important components of nearshore Oregon reef communities but are highly susceptible to overfishing. A number of marine fisheries hypotheses highlight the significance of growth and development in early life history stages for the replenishment of populations. I examined spatial patterns of age and growth in larval and juvenile rockfish along the Oregon coast; I examined the relationships between larval growth, timing of metamorphosis, and juvenile growth; and I tested predictions of two hypotheses: the Single Process Concept and the Growth-Mortality Hypothesis.

Young-of-year rockfish were collected during summer 2002 from five local sites nested within two oceanographic regions – central and south – along the Oregon coast, spanning a prominent oceanographic discontinuity located at Cape Blanco. Otolith microstructures were examined and daily increments counted to estimate ages at capture and ages at metamorphosis, using the first accessory primordium as an indicator of juvenile transformation. Otolith-somatic growth relationships were used to back-calculate sizes at metamorphosis, and growth rates were calculated for the larval and juvenile stages.

Results from Nested ANOVAs suggest that parturition dates varied among sites, which may be a consequence of local larval retention and limited dispersal. Larval growth rates varied on a regional spatial scale, whereas juvenile growth rates varied on a local spatial scale, indicating that the spatial scale of control over early life history demographics is stage-specific. Intense, persistent upwelling and cold water temperatures along the central Oregon coast during summer 2002 may explain slower growth rates in the central region compared to the southern region. Juvenile condition factors also varied on a local spatial scale in the central region, where a time lag between fish collections may have been confounding.

A significant inverse relationship between larval length growth rates and ages at metamorphosis (larval durations) corroborated a prediction of the Single Process Concept that faster growing larvae metamorphose younger, but the strength of this relationship differed between regions.

A positive relationship between larval mass growth rates and ages at metamorphosis may indicate an ability of fish to delay metamorphosis while awaiting appropriate environmental cues such as settlement habitat. Larval growth rates and lengths at metamorphosis exhibited a negative effect on juvenile growth rates, signifying a trade-off in growth between larval and juvenile stages, but there was no effect of age at metamorphosis on juvenile growth rates.

There was no evidence of directional growth-selective mortality during the juvenile stage, contrary to the predictions of the Growth-Mortality Hypothesis. Decreasing variances and unchanging means for juvenile growth rates over the juvenile duration suggest either stabilizing growth-selective mortality, growth depensation in larvae followed by compensatory growth in juveniles, or a statistical artifact of measuring integrated growth rates.

Future research should focus on temporal patterns of growth and recruitment in young-of-year rockfish across nested spatial scales. Long-term studies conducted at multiple spatial scales may assist efforts to identify the effects of oceanographic phenomena and environmental changes on demographics in early life history stages and assist with conservation planning and fisheries management.

APPENDIX V: SUPPLEMENTARY TABLES AND FIGURES

<u>Local Site Name</u>	<u>Geographic Coordinates</u>	<u>Region of Oregon Coast</u>	<u>Date of Capture</u>	<u>Number of Fish Captured</u>	<u>Number of Fish Selected for Analyses</u>	<u>Number of Otoliths Examined</u>
Orford Reef	42°47.148'N 124°35.578'W	Southern	August 22	22	15	15
Nellie's Cove	42°43.987'N 124°30.587'W	Southern	August 23	14	13	12
East Island Rock	42°40.050'N 124°28.487'W	Southern	August 23	15	14	14
Otter Crest	44°45.301'N 124°04.004'W	Central	August 19	40	20	20
Depoe Bay	44°48.683'N 124°04.348'W	Central	September 10	44	20	18
				135	60	57
			Totals			

Table A. Sampling and site characteristics. Southern sites are located south of Cape Blanco and central sites are located near Cape Foulweather. Fish from Orford Reef, Otter Crest, and Depoe Bay were sub-sampled for analyses. All fish from Nellie's Cove and East Island Rock were selected for analyses, with the exception of one heavily damaged fish that was not measured from each site. Otoliths from two Depoe Bay fish and one Nellie's Cove fish were unreadable and excluded from examination.

<u>Local Site Name</u>	<u>Region of Oregon Coast</u>	<u>Total Ages at Capture (days)</u>		<u>Ages at Metamorphosis</u>		<u>Parturition Dates</u>		<u>Metamorphosis Dates</u>	
		Range	Mean	Range	Mean	Range	Mean	Range	Mean
Orford Reef	Southern	70.3 – 99.0	86.8	32.7 – 63.7	51.8	May 15 – June 12	May 27	July 6 – July 29	July 18
Nellie's Cove	Southern	79.7 – 110.3	90.9	40.0 – 64.7	50.9	May 4 – June 4	May 24	June 28 – July 27	July 14
East Island Rock	Southern	60.7 – 79.7	69.3	58.3 – 60.7	52.4	June 4 – June 23	June 14	July 13 – August 23	August 6
Otter Crest	Central	76.0 – 107.3	93.1	39.3 – 79.0	56.1	May 3 – May 27	May 17	June 27 – August 4	July 13
Depoe Bay	Central	82.7 – 113.3	98.2	41.0 – 71.7	55.1	May 19 – June 11	June 3	July 14 – August 22	July 28

Table B. Estimated ages and dates for fish collected from each site. Ranges and means for total ages at capture, ages at metamorphosis (larval durations), metamorphosis dates, and parturition dates are provided for each site.

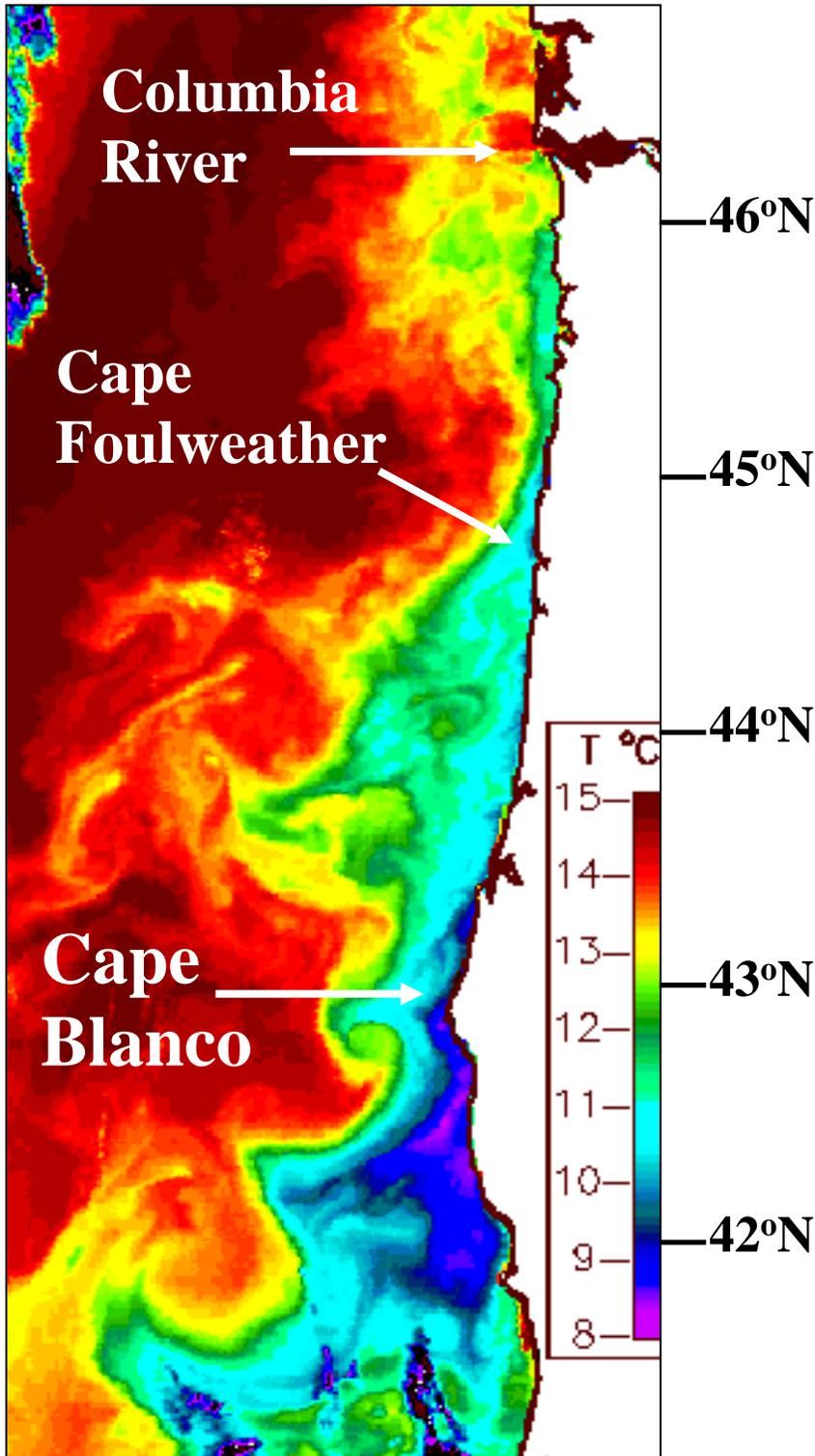


Figure A. Summer sea surface temperatures along the Oregon coast, showing colder region south of Cape Blanco with persistent upwelling and warmer region north of Cape Blanco with intermittent upwelling. The temperature scale on the right is depicted in degrees Celsius

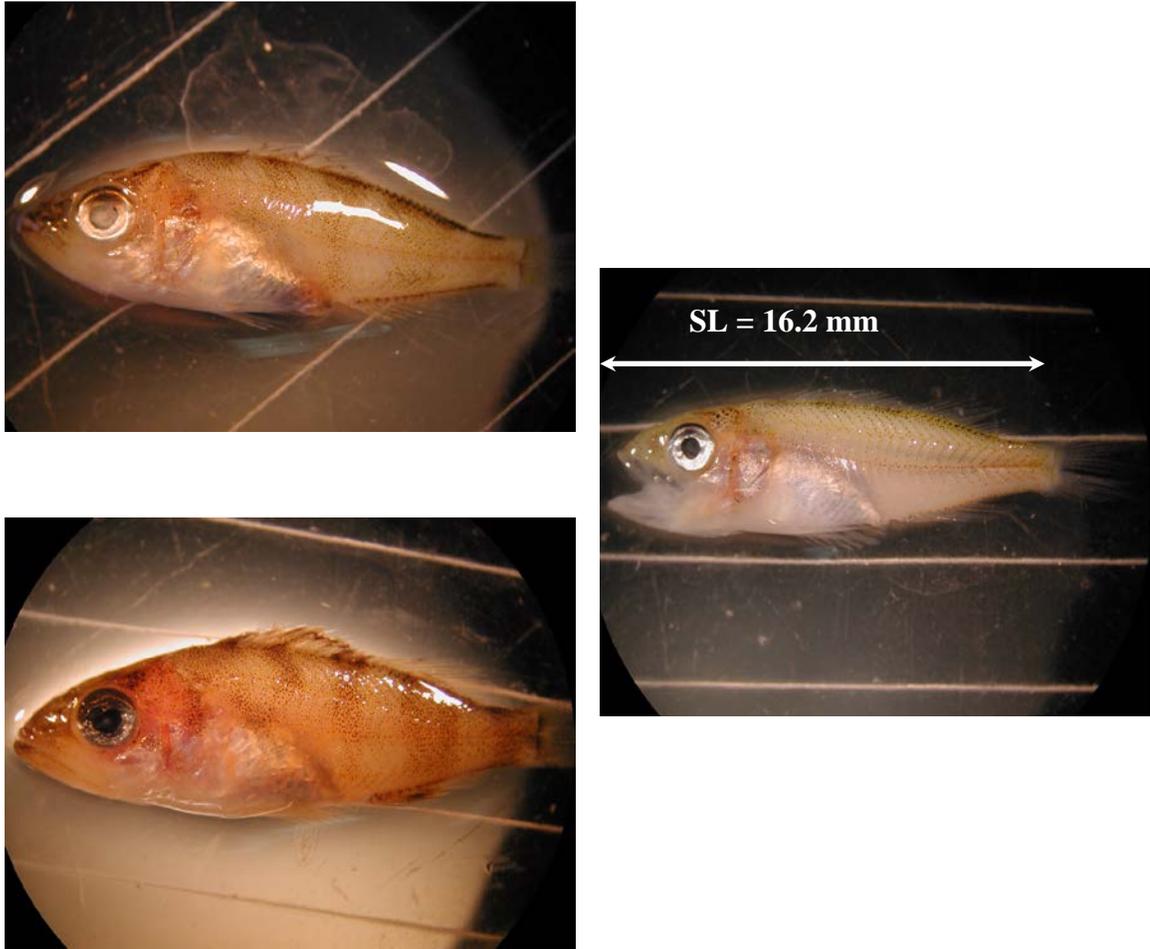


Figure B. Young-of-year juvenile rockfish, collected from Otter Crest (upper left) on the central Oregon coast, from Nellie's Cove (lower left) on the southern Oregon coast, and from East Island Rock (middle right) on the southern Oregon coast. All fish are either *Sebastes maliger* (quillback rockfish), *S. caurinus* (copper rockfish), *S. carnatus* (gopher rockfish), or *S. chrysomelas* (black-and-yellow rockfish). The fish from East Island Rock (right) is a recently metamorphosed juvenile with a standard length of 16.2 millimeters. Standard length is measured from the anterior-most tip of the head (usually the maxilla) to the posterior-most point of the caudal peduncle, not including the caudal fin.



Figure C. Emergent canopy of a bull kelp forest, *Nereocystis luetkeana*, at Otter Crest along the central Oregon coast. Kelp canopy is a structural habitat where juvenile rockfish commonly settle from the plankton along the Oregon coast, transitioning from a pelagic to a benthic environment. Photos taken by Michael S. Webster.

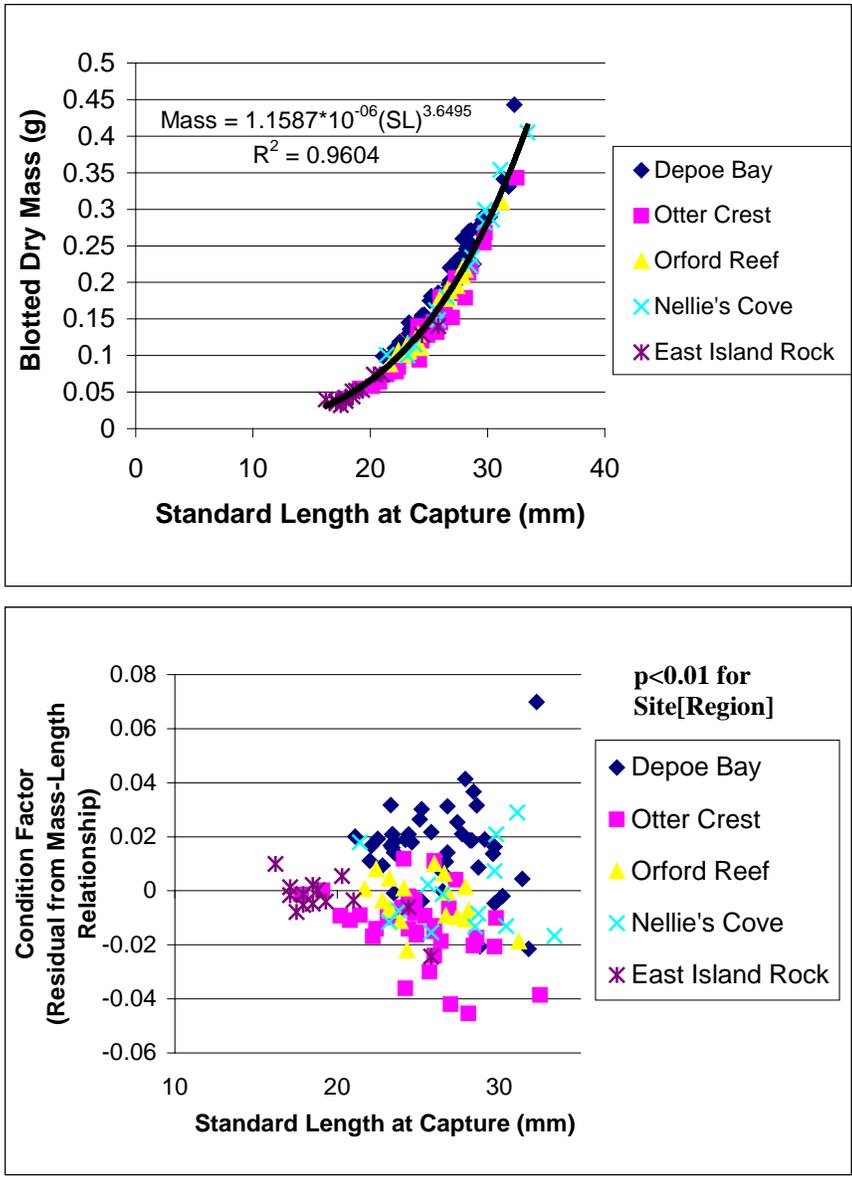


Figure D. Mass-length relationships and condition factors, coded by site. The relationship between blotted dry mass and standard length at capture (top) is the power function equation $Mass = (1.1587 \times 10^{-6}) * (Length)^{3.6495}$, which described 96.0% of variation in the data ($R^2 = 0.9604$). Condition factors (bottom) were calculated as the residuals from this mass-length relationship.

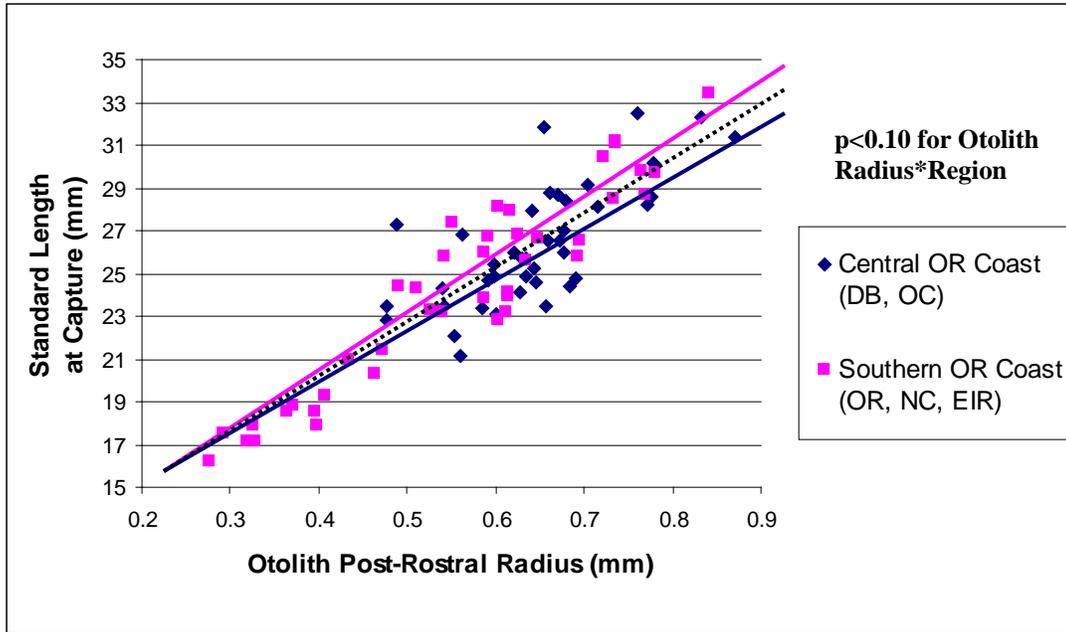


Figure E. Otolith-somatic growth relationships for lengths. Scatter plot of standard length at capture versus otolith post-rostral radius, coded by region. The equation used to back-calculate lengths at metamorphosis for both central and southern regions is represented by a dashed black line, the middle regression line. The actual otolith-somatic growth relationship for the southern Oregon coast is represented by a solid pink line, the upper regression line. The actual otolith-somatic growth relationship for the central Oregon coast is represented by a solid blue line, the lower regression line.

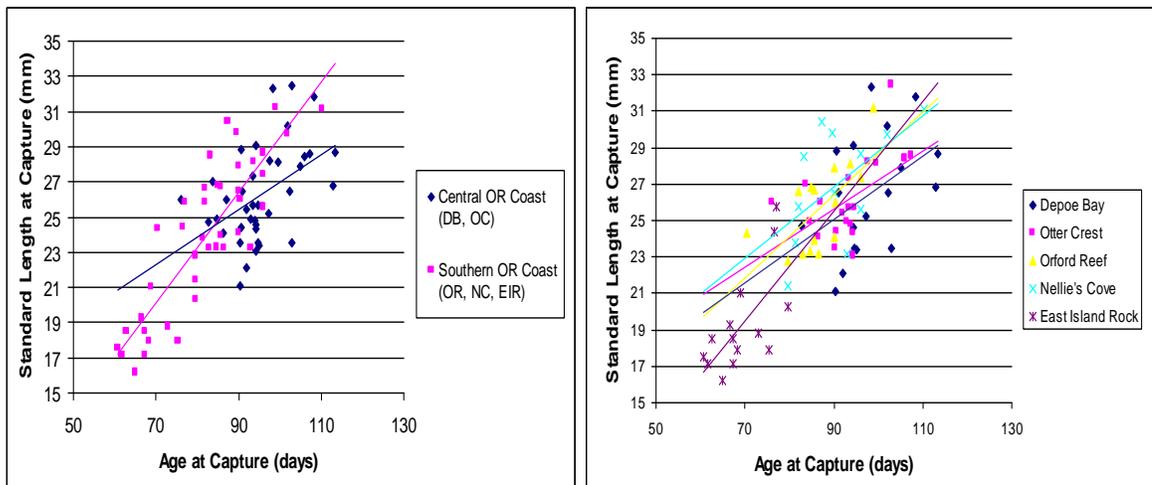


Figure F. Length-age relationships. Scatter plots of standard length at capture versus estimated age at capture, coded by region (left) and site (right).

