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

J.A. Miller and A.L. Shanks

Abstract: Although dispersal distances of marine larvae influence gene flow and the establishment of population structure, few data on realized dispersal distances exist for marine species. We combined otolith microstructure and microchemistry of black rockfish (*Sebastes melanops*) to assess their potential to provide relative estimates of larval dispersal distance. In 2001 and 2002 we measured trace elements at discrete otolith regions, representing the (*i*) egg / early-larval, (*ii*) pelagic larval, and (*iii*) late-larval / early-juvenile periods of fish collected at three locations 120–460 km apart. Discriminant-function analyses based on geochemical signatures at each otolith region accurately grouped an average of 85% (jackknife = 67%) and 87% (jackknife = 81%) of the fish to collection location in 2001 and 2002, respectively. Age at collection ranged from 83 to 174 days and parturition dates within each site were spread over a 22- to 66-day period. Therefore, individuals within sites were not released at similar times. A probable explanation of these data is that larvae from different geographic locations did not mix during ontogeny and possibly did not disperse long distances alongshore. Larval dispersal distances may be appreciably shorter, <120 km, than previously assumed based on models of passive dispersal.

Résumé : Bien que la distance de dispersion des larves marines affecte le flux des gènes et l'établissement de la structure de population, il existe peu de données sur les distances réelles de dispersion des espèces marines. Nous avons évalué le potentiel d'une étude combinée de la microstructure et de la microchimie des otolithes du sébaste noir (*Sebastes melanops*) pour estimer les distances de dispersion des larves. En 2001 et 2002, nous avons mesuré les éléments en traces à des points distincts des otolithes, représentant les périodes (*i*) embryonnaire et larvaire précoce, (*ii*) larvaire pélagique et (*iii*) larvaire tardive et juvénile précoce chez des poissons de trois sites distants les uns des autres de 120–460 km. Une analyse des fonctions discriminantes basées sur les signatures géochimiques dans chacune des régions de l'otolithe regroupe correctement 85 % (67 % après un jackknife) des poissons récoltés en 2001 et 87 % (81 % après un jackknife) en 2002. Les âges à la récolte varient de 83 à 174 jours et les dates de ponte à chaque site s'étendent sur une période de 22–66 jours. Les individus ne sont donc pas relâchés simultanément à tous les sites. Une explication probable de ces données est que les larves des différents sites géographiques ne se mêlent pas entre elles au cours de l'ontogénie et qu'elles ne se dispersent probablement pas sur de grandes distances le long du rivage. Les distances de dispersion des larves sont peut-être considérablement plus courtes, soit <120 km, que l'on estimait antérieurement d'après les modèles de dispersion passive.

[Traduit par la Rédaction]

Introduction

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

Obtaining accurate empirical estimates of larval dispersal distances has been hampered by inadequate analytical techniques. Individual tagging studies are expensive, logistically difficult, and typically not feasible for larval stages, during which mortality often exceeds 90% (but see Jones et al. 1999). Although genetic techniques can underestimate the extent of population structure and offer only indirect information on larval sources and dispersal distances (Kinlan and Gaines 2003; Palumbi 2003), there is evidence for popula-

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tion structure in some *Sebastes* (rockfish) species on relatively small spatial scales, i.e., from 200 to 900 km apart (Withler et al. 2001; Buonaccorsi et al. 2002; Roques et al. 2002). Such studies hypothesize that limited larval dispersal may be one mechanism contributing to the genetic divergence observed (Withler et al. 2001; Buonaccorsi et al. 2002; Roques et al. 2002).

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

Black rockfish (*Sebastes melanops*) range from the Aleutian Islands, Alaska, to southern California. Commercial and recreational harvest began in the late 1800s and continues today. *Sebastes melanops*, combined with blue rockfish (*Sebastes mystinus*) comprised over 90% of Oregon's recreational harvest in 2001 and 2002 (Oregon Department of Fish and Wildlife catch statistics). These long-lived (≤50 years) viviparous fish commonly occur in waters <55 m in depth and reach sexual maturity between 3 and 9 years of age (Cailliet et al. 2001; Love et al. 2002). Larvae and juveniles are pelagic for 3–6 months, although the areas of parturition are unknown. Benthic juveniles initially settle in shallow waters and move into deeper waters as they grow (Love et al. 2002).

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

Unique geochemical signatures have been documented in otoliths of marine fish collected from estuaries and along cross-shelf gradients (Gillanders 2002*a*; Swearer et al. 1999; Thorrold et al. 1998). Similarly, studies on coastal water chemistry typically focus within estuaries or along cross-shelf and depth gradients (Chester 1990; Flegal et al. 1991; Munksgaard and Parry 2001). Although there is some evidence of alongshore gradients in certain trace metals (Sanudo Wilhelmy and Flegal 1991), it is not yet clear whether, or how, otolith elemental composition varies on alongshore gradients. Trace-metal concentrations in seawater vary depending on external inputs (atmosphere and river), physical factors (upwelling, wind mixing), and biological processes (uptake and regeneration) (Cotte-Krief et al. 2002). These factors, i.e., riverine inputs, upwelling intensity, and biological community composition, vary alongshore in marine environments. Therefore, we hypothesized that there would be variation in the otolith chemistry of *S. melanops* collected along the Washington and Oregon coast.

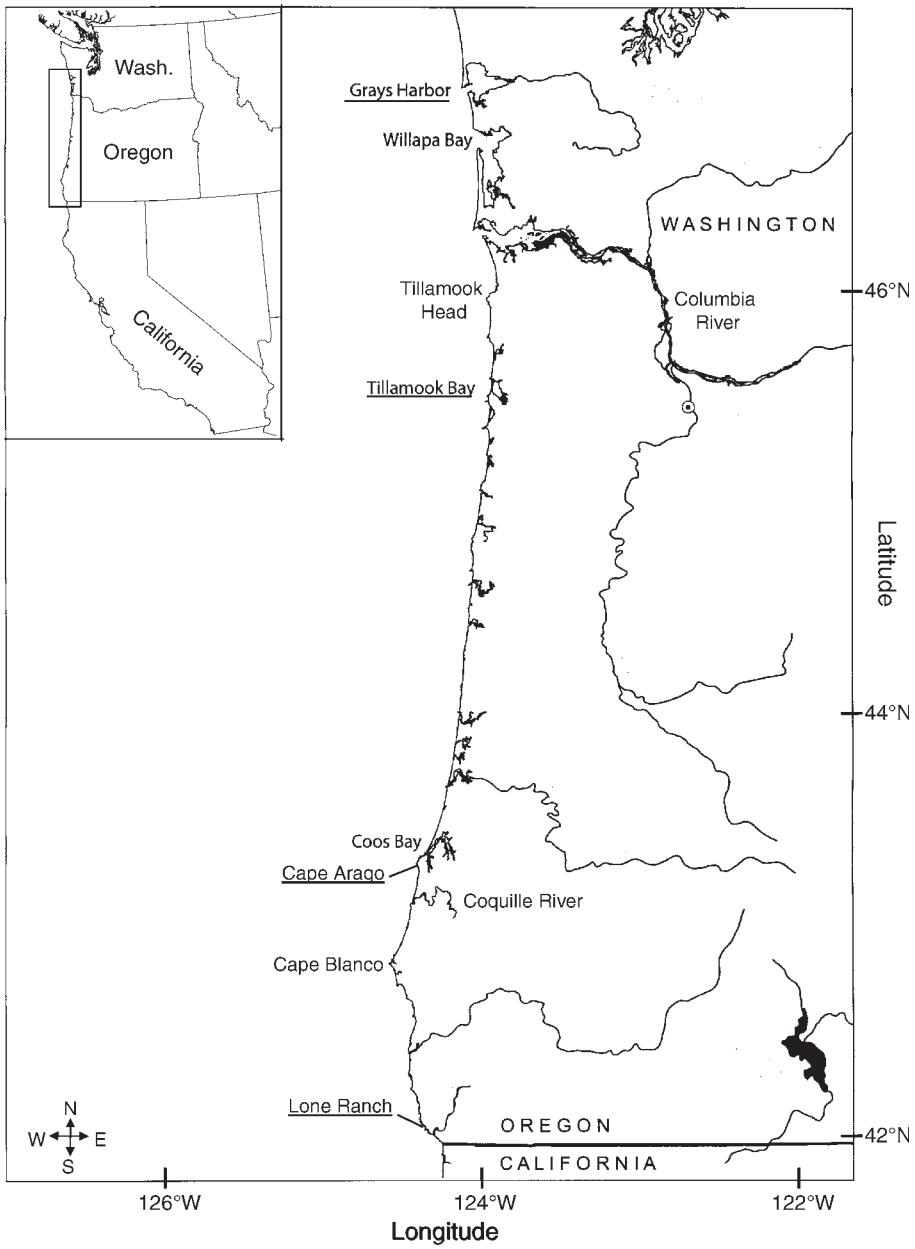
Otolith microchemistry studies typically employ either a "top-down" or "bottom-up" approach when population structure, or connectivity (Thresher 1999), is examined. The top-down approach typically involves assaying adults across a relatively broad region and searching for geographic groupings based on otolith geochemical signatures and, in many ways, is similar to a genetic approach. The bottom-up approach involves attempting to characterize geographic source signatures in otoliths of larvae or juveniles, collecting dispersed adults at a later time, and then identifying the source of those adults by matching the chemical signatures at their otolith cores, which represent natal origins, with those previously observed in larvae and juveniles. These efforts are based on a number of assumptions. Two primary and relatively well-established assumptions are that otolith growth is continuous, with no evidence of resorption, and thus provides a permanent chronological record (Campana 1999; Thresher 1999; Campana and Thorrold 2001). The other major assumption, although not as well established, is that if fish reside in water masses with different chemical properties, those properties will be reflected in otolith microchemistry (Thresher 1999; Campana and Thorrold 2001).

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

The varied geology of the Washington and Oregon coast may contribute to alongshore differences in the elemental composition of otoliths in coastal fishes. Sediments from the Columbia River dominate coastal waters from Grays Harbor, Washington, to Tillamook Head, Oregon (Komar 1997) (Fig. 1). Oregon's Coast Mountain Range extends from the Columbia River southward to The Klamath Mountain Range (Orr et al. 1992). These mountains have different geologies, and the volcanic rocks are different in age and mineralogy. Alongshore differences in salinity and silicate concentrations, primarily due to freshwater discharge from the Columbia River, occur between Oregon's north and south coasts (Landry et al. 1989). In this study, we determined if the trace element composition of *S. melanops* otoliths varied alongshore and throughout the ontogeny.

Sebastes melanops larvae and pelagic juveniles are found associated with upwelling fronts but are also found landward and seaward of such fronts (Larson et al. 1994). In Oregon,

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



larval release typically occurs between February and May and juveniles are found nearshore, and occasionally in estuaries, beginning in June (Love et al. 2002). Hence, early in larval development in *S. melanops*, alongshore flow in the California Current system is predominantly poleward, owing to the Davidson Inshore Counter Current. The subsequent 3- to 6-month pelagic phase extends throughout the spring transition and the initiation of the upwelling season, when dominant flow over the shelf is toward the equator (Strub et al. 1987). If larval dispersal is widespread with extensive (>1 month) periods near the upwelling front, we predicted that otolith elemental signatures from discrete life-history periods would not be useful for discriminating fish on the basis of collection locations. If otolith elemental signatures from discrete periods classify fish to their collection location, then fish most likely stayed together relative to the other collection locations (i.e,. did not mix), did not move appreciable distances alongshore, or both. Alternatively, fish collected at the same location may have followed similar dispersal pathways. Otolith-microstructure analysis provided

information on the timing of parturition, individual age, and otolith growth to aid interpretation of otolith geochemical signatures.

Methods

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

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

Fish collection and otolith preparation

Juveniles were collected by seine in nearshore kelp beds between 14 July and 3 August 2001 and 11 and 16 June 2002. Fish were immediately measured to the nearest 0.5 mm. Sagittal otoliths were removed on the day of collection (2002) or fish were frozen (<2 months) prior to otolith removal (2001). Otoliths were removed with acid-washed plastic forceps, cleaned, weighed (to the nearest 0.01 mg), measured (to the nearest 0.1 mm), embedded, and ground to expose the otolith core. Otoliths were ultrasonically cleaned in NANOpure® water, dried, and stored in acid-washed plastic vials prior to embedding in resin. Otoliths were ground with 3M™ Tri-m-ite wetordry™ paper (240–1200 grit), polished with Buehler AlO_2 powder (12.5 and 3.0 μm), and again cleaned ultrasonically for 15 min.

Yoklavich and Boehlert (1987) validated daily otolith-increment deposition in juvenile *S. melanops*. Therefore, we were able to determine individual ages with otolith-microstructure analysis. Polished otoliths were examined under oil immersion at 1000× magnification with a Leitz Laborlux S compound microscope. Laidig and Ralston (1995) identified a dark check at the edge of the nuclear radius in juvenile otoliths of eight *Sebastes* species. Check marks were located at species-specific radii ranging from 10.93 to 16.96 μm. Ralston et al. (1996) verified, for shortbelly rockfish (*Sebastes jordani*), that the check mark was an extrusion, or parturition, check. We consistently observed a distinct check mark on *S. melanops* otoliths at a radius of 10.6–12.5 μm, with a mean of 11.3 μm. Therefore, we interpreted the check mark as a parturition mark and counted increments, each representing 1 day, from that mark to the otolith's distal edge. If a check mark was not visible, increment counts began at a radius of approximately 11 μm. Otolith counts were independently determined three times. Parturition dates were then determined for each individual. In some cases, fewer individuals were aged than were used in microchemistry studies, owing to inability to adequately discern all growth increments.

Optimas image-analysis software (version 6.0; Optimas Corporation 1996) and a Laborlux S compound microscope at 400× magnification were used to visualize and measure otolith increments within the larval and juvenile transects. A minimum of 15 otolith-increment widths were measured within each transect. No measurements were taken for the early-larval transect because of its short length and poor increment resolution. Individual and site averages were generated for the larval and juvenile transects in both 2001 and 2002. Analysis of variance (ANOVA) was used to determine if there were significant differences in increment width among locations within years.

Trace-element analysis

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

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

analyses indicated no difference in analyte concentrations between transects in the different otolith quadrants (paired t tests, $n = 6$, $p > 0.10$, df = 9). All subsequent transects were located in the anterior dorsal quadrant and extended from the core to the otolith edge. Preliminary analyses indicated that concentrations of the following nine analytes in otoliths were well above background levels: ^{25}Mg, ^{43}Ca, ^{48}Ca, ^{55}Mn, ^{66}Zn, ^{86}Sr, ^{87}Sr, ^{138}Ba, and ^{208}Pb. The average relative standard deviation (%RSD) for National Institute of Standards and Technology (NIST) glass plates during data collection were as follows: ^{25}Mg = 11.3%, ^{43}Ca = 5.6%, ^{48}Ca = 5.6%, ^{55}Mn = 6.4%, ^{66}Zn = 8.4%, ^{86}Sr = 7.7%, ^{87}Sr = 7.3%, ^{138}Ba = 7.5%, and ^{208}Pb = 9.2%. Variation in the average %RSD between the 25- and 120-μm transects was less than 1.5%. VG PQ ExCell ICPMS minimum detection levels are 1–10 parts per trillion for Mg, Ca, Mn, and Zn and <0.1–1 parts per trillion for Sr, Ba, and Pb.

Trace-element compositions in NIST glass standards are homogeneous, and elemental concentrations are reported in Pearce et al. (1997). A NIST standard was run with each otolith sample; this allowed all otolith transects to be standardized to account for instrument drift or day-to-day variations in instrument sensitivity across the atomic-mass range. Background analyte levels were determined with an argon gas blank prior to each transect and subtracted from both mean otolith and NIST glass slide measurements. Elemental data (in counts per second) were standardized by ^{43}Ca to adjust for variability in instrument sensitivity and the amount of ablated material (Campana et al. 1997). Measured element-to-calcium ratios from NIST glass slides were then multiplied by known average NIST concentrations to generate a correction factor. Otolith element-to-calcium ratios were then multiplied by the NIST correction factor collected at the same time as the otolith measurement. Standardized ratios were transformed to attain normality and homogeneity of variance. The only case in which the variance among collection sites could not be stabilized was for ^{25}Mg (Levene's test, $F_{[2,67]} = 3.8$, $p = 0.02$) in the 2002 juvenile signatures. The removal of one outlier from Tillamook Bay (TB) (i.e., ^{25}Mg·^{43}Ca^{-1} >3 standard deviations from the mean) stabilized the variance (Levene's test, $F_{[2,67]} = 2.7$, $p > 0.07$).

Statistical analysis

ANOVA was used to compare the element-to-calcium ratios among sites within each otolith region in 2001 and 2002. Quadratic discriminant function analysis (DFA) was then used to group individuals based on their elemental signatures at each otolith region. Jackknifed classifications were calculated with the removal of one observation a total of N times (N = 55 and 70 in 2001 and 2002, respectively) and averaged. The best validation of a discriminant-function classification is the assignment of new cases (i.e., those not used in the development of the original classification algorithm). Jackknifed predictions are used to provide a more realistic estimate of the ability of the predictor variables to separate groups when sample sizes are not large enough to generate two independent data sets. We also used the classification algorithm based only on the early-larval otolith signatures to predict collection location of individuals using either the larval or juvenile signatures. In this case, the larval and juvenile signatures were treated as new cases, therefore jackknifed classifications were not generated. STATISTICA® (Version 6.0; StatSoft Inc. 2002) and SYSTAT® (Version 9.01; Systat Software Inc. 1998) statistical software programs were used for the above analyses.

Results

Otolith microstructure

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

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

Otolith microchemistry

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

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

The DFA based on the juvenile otolith signatures grouped 88% of the fish to collection location in 2001 (jackknife = 74%) and 88% of the fish to collection location in 2002 (jackknife = 80%; Table 4). The early-larval and larval otolith signatures accurately grouped an average of 85% (jackknife = 64%) of the fish to collection location in 2001 and 86% (jackknife = 82%) in 2002 (Table 4). However, in both years, classification success was relatively good using only ^{25}Mg and ^{87}Sr in the DFA (2001: average = 68% and jackknife = 68%; 2002: average = 77% and jackknife = 76%). The additional elements improved the overall classification success by 17% in 2001 and 9% in 2002. Overall, 67%–87% of the fish were grouped to their collection location based on

Table 1. Sizes, ages, and parturition dates for juvenile black rockfish, *Sebastes melanops*, collected at different locations in 2001 and 2002.

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

Note: Ages and parturition dates were determined from otolith microstructure. TL, total length.

Table 2. Average otolith increment widths (μm) during the larval and juvenile life-history periods in 2001 and 2002.

	Larval period	Juvenile period
2001		
GH	6.7±1.3	3.0±1.3**
CA	7.6±1.2	6.2±0.8
LR	8.2±1.8	5.2±1.6
2002		
TB	7.1±1.5	6.4±1.4
CA	7.1±1.2	6.5±1.4
LR	7.4±1.3	6.5±1.5

Note: CA, Cape Arago; LR, Lone Ranch; GH, Grays Harbor; TB, Tillamook Bay. Values are given as the mean ± SD; **, statistically significant difference at $p < 0.001$.

the early-larval, larval, or juvenile otolith signatures (Table 4), which is considerably better than the prior probabilities of 38% and 33% for 2001 and 2002, respectively, based on sample size and chance alone.

For all otolith regions in both years, the first canonical factor accounted for >75% of the discrimination (Figs. 4 and 5). ^{25}Mg was the most important element in the first factor (i.e., standardized canonical discriminant function (SCDF) > 0.90). Only variables with SCDFs >0.50 will be discussed. ^{208}Pb during the early larval period in both 2001 and 2002 and the juvenile period in 2002 also contributed substantially to the first canonical factor (SCDF > 0.52). ^{87}Sr during the early-larval period in 2001 was the only other variable that contributed substantially to the first canonical factor (SCDF > 0.59). For the second canonical factor, which typically accounted for <10% of the discrimination, ^{66}Zn was the dominant variable in all cases (SCDF > 0.67) except during the early-larval period in 2001, when ^{87}Sr and ^{138}Ba each had SCDF > 0.50. In 2001, ^{138}Ba contributed substantially during the larval period and ^{208}Pb in both the larval and juvenile periods (SCDF > 0.90).

The majority of cases that were misclassified grouped with the closest geographic location. Seventy percent (33 out of 47) of the original misclassifications were placed with the closest collection location, while 61% (51 out of 84) of the jackknifed misclassifications grouped with the closest location. The second most common misclassification, in both years, was for fish from the more northerly locations (GH and TB) to group with LR fish. In both the 2001 and 2002 DFAs, LR fish were located intermediate to the other two collection locations (Figs. 4 and 5), which may account for the more frequent placement of misclassified individuals into the LR group. Furthermore, in 2001, the sample size for LR was only 10 individuals and the 95% confidence ellipses for this group overlapped extensively with those for both GH and CA, which displayed very little overlap (Fig. 4). This would contribute to both the low classification rate for LR fish as well as the misclassification of GH and CA fish to LR. In 2002, when sample sizes were larger and similar (i.e., 23–24 individuals per site), the 95% confidence ellipses displayed much less overlap, and classification success improved for all groups, especially LR (Fig. 5).

To further test the robustness of our classifications, we used a classification algorithm based on only the early-larval otolith signatures to predict collection location of individuals

Table 3. Elements used in discriminant-function analyses (DFA) and the statistical transformations (in parentheses) used to attain normality and homogeneity of variance for different otolith regions (early larval, larval, and juvenile) in 2001 and 2002.

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

Note: *, statistically significant differences among collection locations at $p = 0.05$; **, statistically significant differences among collection locations at $p = 0.01$; ns, no statistical difference. Analysis of variance was used to determine significance.

Fig. 2. The untransformed elemental ratios measured in *S. melanops* otoliths in 2001: ^{25}Mg, ^{55}Mn, ^{66}Zn, ^{87}Sr, ^{138}Ba, and ^{208}Pb. Values are site averages (± standard error) for the early-larval, larval, and juvenile otolith regions at Cape Arago (open circles), Lone Ranch (solid triangles), and Grays Harbor (shaded squares).

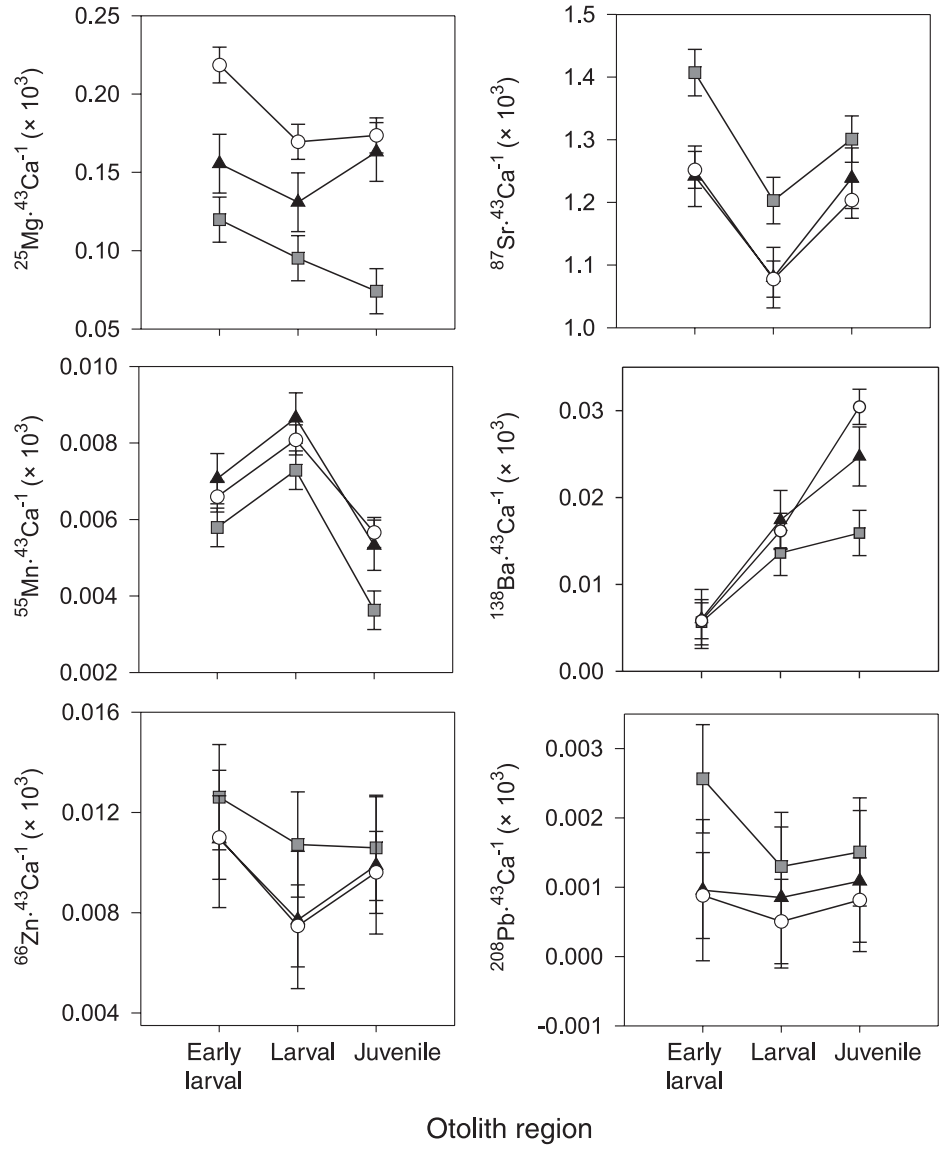
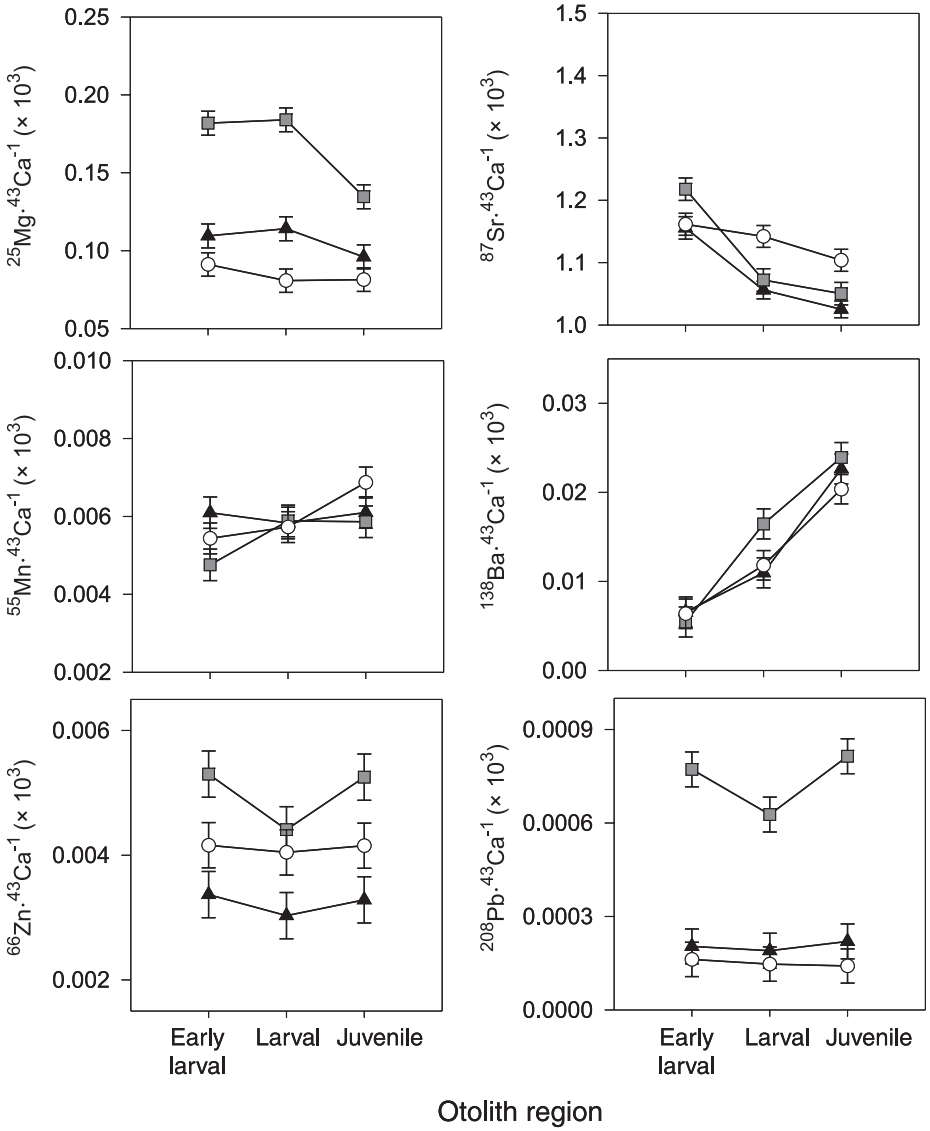


Fig. 3. The untransformed elemental ratios measured in *S. melanops* otoliths in 2002: ^{25}Mg, ^{55}Mn, ^{66}Zn, ^{87}Sr, ^{138}Ba, and ^{208}Pb. Values are site averages (± standard error) for the early-larval, larval, and juvenile otolith regions at Cape Arago (open circles), Lone Ranch (solid triangles),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



based on either their larval or their juvenile signatures. The elements used for those predictions were the same as the previous DFAs except for the removal of Ba in 2001 and Sr in 2002 because classification success was greater without them. The larval otolith signatures, using the early-larval classification algorithm, grouped 66% of the 2001 and 87% of the 2002 individuals to their collection location. The juvenile otolith signatures, using the early-larval classification algorithm, grouped 72% of the 2001 and 75% of the 2002 individuals to their collection location (Fig. 6). Misclassified individuals were most commonly placed with the nearest geographic location (i.e., 68% of misclassifications in 2001 and 62% in 2002). In 2001, the remainder of the misclassifications involved LR fish being placed in GH (25% of misclassifications). In 2002, the second most common misclassification was the placement of TB fish with LR fish (31% of misclassifications).

Discussion

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

Certain characteristics of the otolith geochemical signatures observed in this study warrant further discussion. There were interannual differences in the otolith concentration of some elements (i.e., Mg and Zn) and the discriminatory power of some elements varied between 2001 and 2002

Table 4. The percentages of *S. melanops* accurately classified to collection location based on DFAs using otolith elemental composition for different otolith regions (early larval, larval, and juvenile) in 2001 and 2002.

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

Note: Values in parentheses show the jackknifed percentage correctly assigned. CA, Cape Arago; LR, Lone Ranch; GH, Grays Harbor; TB, Tillamook Bay.

(e.g., Pb was more important in the second discriminant factor in 2001). Multiyear otolith-chemistry studies have often shown that interannual variation can exceed intra-annual variation and prevent accurate classification of fish based on algorithms developed from fish otoliths collected in previous years (Gillanders 2002*b*; but see Hamer et al. 2003). Given that various factors affect coastal water chemistry, including riverine inputs and upwelling intensity, these findings are not surprising. They do, however, warrant further investigation.

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

Thresher (1999), in an extensive review on the use of otolith elemental chemistry for resolving population structure, identified an emerging consistency in such studies. He found that the group IIA elements (Mg, Sr, and Ba) were routinely identified as stock delineators. In this study, we had relatively good jackknifed classification accuracy (68%–76%) using only Mg and Sr. Our results are consistent with Thresher's (1999) finding and indicate that otolith elemental chemistry may provide accurate information on the relative movements of individuals and groups of fish.

What transport mechanisms could have generated the otolith geochemical signatures seen in this study? We consider a number of possibilities: (*i*) fish stayed together relative to the other collection locations (i.e., did not mix); (*ii*) fish did not move appreciable distances alongshore; (*iii*) a combination of *i* and *ii*; or (*iv*) fish from the same collection location followed similar dispersal pathways. Parturition dates within each site were spread over a 22- to 66-day period. Therefore, larvae were not released at the same time. For fish from one location to remain together relative to other locations (*i*), they would have not moved appreciable distances alongshore since parturition (*ii*) or followed similar dispersal pathways for indeterminate distances (*iv*). As stated by Warner et al. (2000), when individuals in groups that settle together differ by weeks in their larval ages, any physical processes associated with accumulation over the duration of larval life must be persistent for that long. As previously mentioned, the predominant sea-surface flow in the California Current system undergoes a seasonal reversal, with predominantly poleward flow during fall and winter and equatorward flow during spring and summer (Huyer et al. 1979; Strub et al. 1987). This transition typically occurs between mid-February and mid-May, occurring later in the year at more northerly locations (Strub et al. 1987). Parturition dates of fish used in this study, i.e., from 2 February to 9 April in 2001 and from 6 February to 21 March in 2002, occurred prior to this transitional period. It is difficult to imagine what physical pathway would persist for a 22- to 66-day period in such an oceanographic regime. A more parsimonious hypothesis may be that larvae do not move appreciable distances alongshore after parturition (*ii*).

If *S. melanops* larvae did not disperse for appreciable distances alongshore during their 3- to 6-month pelagic larval period, they presumably experienced conditions conducive to reduced alongshore flow and (or) have behaviors that minimize alongshore transport. Minimal alongshore transport may occur when advective forces that promote alongshore movement are minimized relative to diffusive forces, e.g., in the nearshore coastal boundary, inshore of wind-driven "upwelling jets", and in coastal eddies. Modeling efforts indicate that coastal species which spawn over many

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

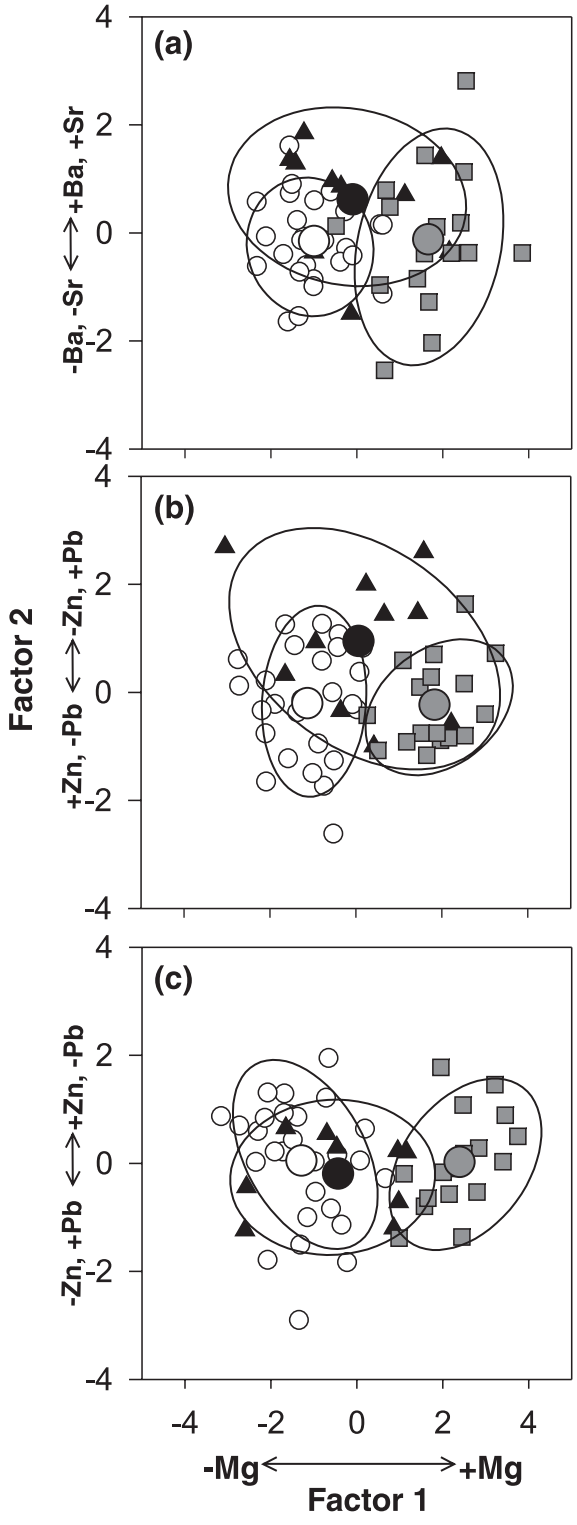


Fig. 5. Discriminant-function classifications based on (*a*) early-larval, (*b*) larval, and (*c*) juvenile otolith elemental signatures for *S. melanops* collected in 2002 at Cape Arago (CA; open circles), Lone Ranch (LR; solid triangles), and Tillamook Bay (TB; shaded squares). The elements responsible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

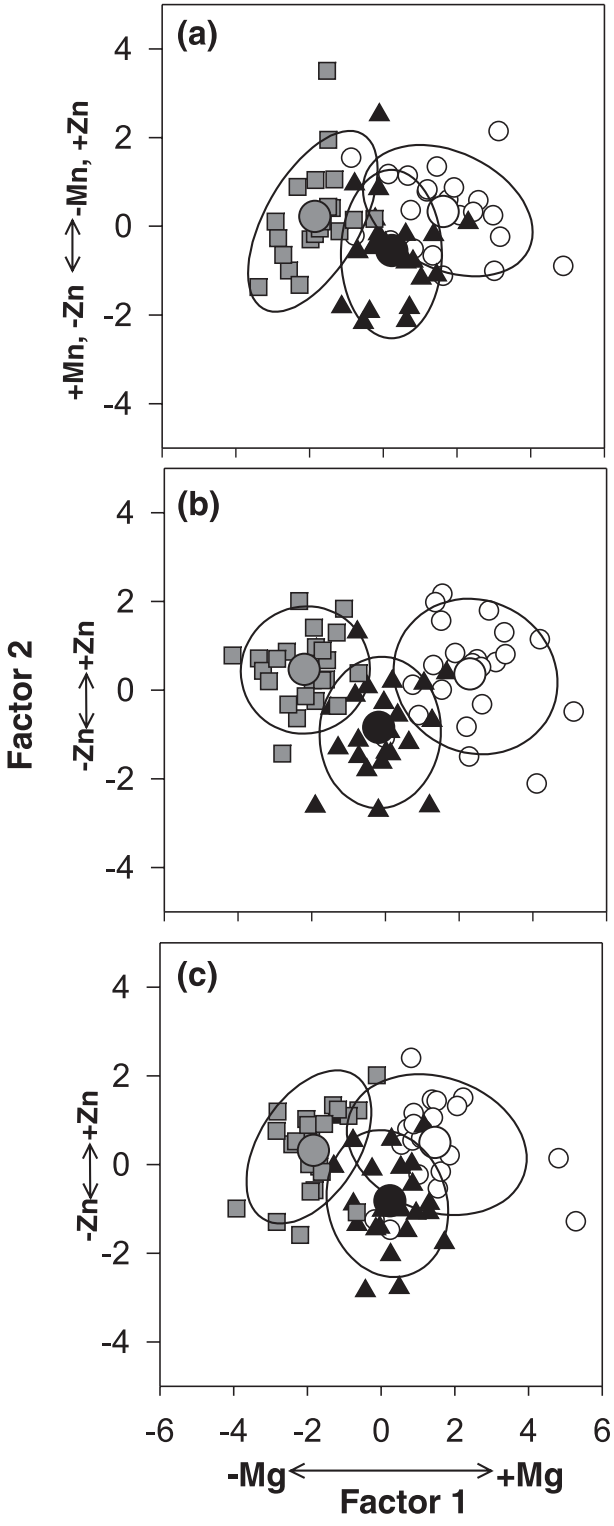
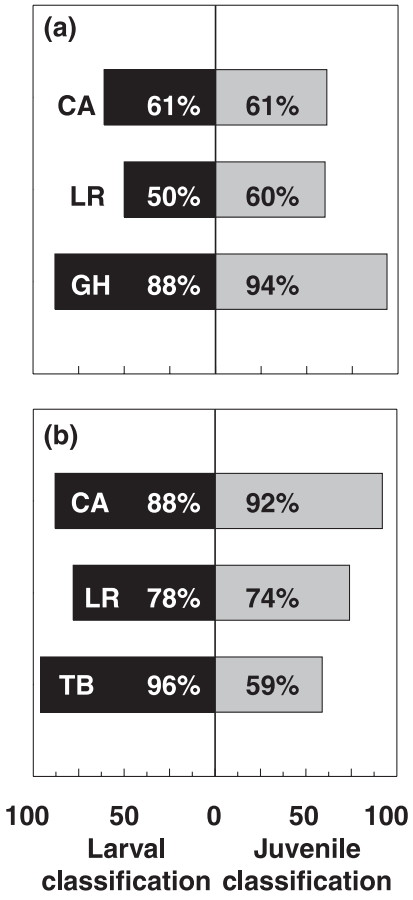


Fig. 6. Discriminant-function classification of larval and juvenile otolith elemental signatures for *S. melanops* based on the early-larval classification algorithm for (*a*) 2001 and (*b*) 2002. Bars represent the percentage of individuals grouped to their collection location based on each of the elemental signatures. Collection locations are as follows: CA, Cape Arago; LR, Lone Ranch; GH, Grays Harbor; TB, Tillamook Bay. For sample sizes see Fig. 5.



years and have extended pelagic-larval periods, two characteristics of most *Sebastes* species, are typically exposed to increased flow variability during larval stages that can, at times, result in greater diffusivity and reduced alongshore transport (Largier 2003). The reduction in alongshore transport due to physical factors could be enhanced by larval behavior (Shanks et al. 2003). Larvae may actively maintain nearshore positions with behaviors similar to those documented in intertidal fishes, including bottom orientation, rheotaxis, and schooling (Largier 2003; Marliave 1986; Montgomery et al. 1997).

Can we estimate larval dispersal distances for *S. melanops*? The closest collection locations in this study were 120 km apart. Given the rate of geographic classification at these two sites throughout ontogeny in both 2001 and 2002 (jackknife average = 63% in 2001 and 78% in 2002), these data suggest that dispersal distances may be <120 km for the majority of individuals. This may represent the dominant dispersal pattern for *S. melanops* but does not preclude the possibility that >10% of the individuals collected at a site came from distances greater than 120 km. Efforts to classify a population as "open", where recruits arrive from outside sources, or "closed", where recruits are locally derived, may not be appropriate if the long-term success of a species and maintenance of its populations depend on a variety of dispersal outcomes over time (Largier 2003).

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

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

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