

Postsettlement survival linked to larval life in a marine fish

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There is a growing realization that the scale and degree of population connectivity are crucial to the dynamics and persistence of spatially structured populations. For marine organisms with complex life cycles, experiences during larval life may influence phenotypic traits, performance, and the probability of postsettlement survival. For a Caribbean reef fish (*Thalassoma bifasciatum*) on an oceanic island, we used otolith (ear stone) elemental profiles of lead (Pb) to assign recent settlers to a group that developed in waters elevated in Pb concentrations throughout larval life (i.e., nearshore signature) and a group that developed in waters depleted in Pb (i.e., offshore signature), potentially dispersing from upstream sources across oceanic waters. Larval history influenced early life history traits: offshore developers initially grew slowly but compensated with fast growth upon entering nearshore waters and metamorphosed in better condition with higher energy reserves. As shown in previous studies, local production contributed heavily to settlement: at least 45% of settlers developed nearshore. However, only 23% of survivors after the first month displayed a nearshore otolith profile. Therefore, settlers with different larval histories suffered differential mortality. Importantly, selective mortality was mediated by larval history, in that the postsettlement intensity of selection was much greater for fish that developed nearshore, potentially because they had developed in a less selectively intense larval environment. Given the potential for asymmetrical postsettlement source-based survival, successful spatial management of marine populations may require knowledge of “realized connectivity” on ecological scales, which takes into account the postsettlement fitness of individuals from different sources.

larval-juvenile transition | otolith chemistry | realized connectivity | selective mortality | *Thalassoma bifasciatum*

Populations of many coastal marine species are connected primarily by dispersal during a relatively short pelagic larval phase (i.e., days to months), because most species have limited adult movement. For much of the last 30 years, researchers assumed that marine populations were demographically open. Models of open populations (1) suggested that larval supply was decoupled from local demographic rates (2). This view was reinforced by the assumption that larvae behaved as passive particles dispersed widely by ocean currents (e.g., ref. 3). However, recent studies have elucidated the importance (4, 5) and apparent ubiquity of self-recruitment (i.e., retention of locally produced young) for population replenishment in many tropical species (6–11) and the potential for limited dispersal along open coasts in temperate systems (12–15). Both physical oceanographic processes (16) and larval behavior (17) may prevent advection and promote the retention of developing larvae in nearshore waters.

Despite the recent evidence for local replenishment in island systems, the young that recruit to an island are rarely wholly of local origin (the obvious exception being island endemics). Jones *et al.* (6) estimated that 15–60% of damselfish recruits to Lizard Island were locally produced, whereas Almany *et al.* (11) recently estimated that 60% of successful recruits of two coral reef fishes

with widely different larval durations originated locally in a small island marine reserve. Spatiotemporal variation in the proportion of self-recruiting fish has been reported (30–90%; refs. 7 and 18) and should be expected given the highly dynamic nature of ocean circulation. These results support an emerging view of marine metapopulations that are replenished both by local and distant sources (9), but that replenishment is measured in numbers of arriving young. Although the importance of connectivity for metapopulation persistence has been recognized (4, 5), researchers are just beginning to appreciate the role of larval experiences and postsettlement selective processes in influencing the survival of individuals with different larval histories (e.g., refs. 19–21). Intense postsettlement mortality is often cited as a demographic bottleneck (22), and thus the identity of surviving fish could determine which sources contribute to population persistence. Understanding the influence of larval history on the performance, condition, and fate of successful settlers is critical for management, because it is the fitness of survivors that will directly determine “realized connectivity.” Here, we define realized connectivity as the proportion of settled individuals from different larval sources that survive to reproduce.

Researchers have yet to address this issue because of the difficulty of identifying the sources and dispersal histories of individual larvae. However, recent advances using elemental fingerprints of water mass residence, permanently recorded in hard parts such as balance and hearing structures (fish otoliths, ref. 23; gastropod statoliths, ref. 24) and larval shell material (15), have been successfully applied to reconstruct migration and dispersal pathways and to identify spawning grounds and juvenile nursery habitats (7, 12, 15, 25). Water masses differ in their chemical composition, and nearshore waters along coastal margins are often enriched in trace metals relative to offshore oceanic waters (26), because many of these elements have anthropogenic or terrestrial origins. The process of elemental uptake and incorporation into aragonitic structures is complex and element-specific (27); however, higher ambient concentrations generally result in elevated concentrations of most trace elements in hard parts such as otoliths (23). Discrete water masses in the ocean also commonly differ in their physical (e.g., temperature) and biological (e.g., species composition, prey availability) properties, and these may influence the phenotypic traits and performance of larvae entrained within them (20, 28, 29). Often, nutrients and prey resources are locally enriched near islands because of the nearshore retention of coastal runoff or vertical mixing (e.g., the island mass effect; refs. 30 and 31).

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It is well known that larval experiences can profoundly influence the traits and performance of individuals at the time of settlement (32, 33), and that early life experiences can carry over to affect survival at later life stages (19, 34–36). However, it is unknown how larvae that develop in distinct water masses, potentially arising from different sources, may survive differentially after the larval–juvenile transition. Based on the distribution of trace elements in coastal seawater (26) and the elemental profiles of otoliths from larvae collected in oceanic waters (> 20 km offshore), Swearer (18) determined that otolith lead (Pb) concentrations were the best environmental marker of nearshore development for two species of coral reef fish in St. Croix, U.S. Virgin Islands. We extend previous work (7, 18) and use the well studied bluehead wrasse (*Thalassoma bifasciatum*) population on the island of St. Croix to examine how the water mass in which a fish develops influences larval performance and early life history (ELH) traits of successful settlers. We also use a cohort-based analysis (37) to investigate the survival potential of fish with particular larval histories by focusing on the differential effects of phenotypic selection on individuals with similar elemental profiles. Here, we show that ELH traits, the probability of survival, and the intensity of postsettlement selection are functions of the water mass in which larvae developed.

Results

Effects of Dispersal History on ELH Traits. We used a Markov chain Monte Carlo simulation model to assign 87 (40%) recently settled bluehead wrasse (i.e., recruits) into a group that developed in waters characterized by elevated Pb concentrations and 134 (60%) recruits into a group that developed in a water mass depleted in Pb (see *Materials and Methods*). The proportion of recruits assigned to each water mass differed significantly among months [high-Pb group: June = 52%, July = 41%, August = 28%; $\chi^2 = 7.05$, $P = 0.03$; sample sizes in [supporting information \(SI\) Table 1](#)] and between two sites (high-Pb group: BB = 48%, JB = 30%; $\chi^2 = 5.24$, $P = 0.022$, [SI Table 2](#)) situated on opposite shores of the island, which agreed well with previous findings regarding spatiotemporal variation in dispersal histories of recent settlers to St. Croix (see refs. 7 and 18). Elemental profiles of Pb were consistent with cross-shore dispersal in that concentrations peaked at the core, when larvae hatched, decreased throughout the early and middle portions of larval development, and were elevated before settlement (Fig. 1). The assignment model produced results independently consistent with findings from a previous study by Swearer (18): recruits classified into the low-Pb group had Pb concentrations lower than the maximum levels detected in larvae captured in oceanic waters (>20 km upstream of St. Croix) during those developmental periods when they could theoretically have resided offshore (Fig. 1) but were elevated at the end of the larval period, likely signifying a return to nearshore waters. In contrast, recruits classified into the high-Pb group had Pb concentrations that remained elevated over the maximum levels of oceanic larvae for all developmental periods (Fig. 1), likely indicating nearshore residence throughout the larval phase.

Bluehead wrasse that developed in water masses differing in Pb concentrations also differed in ELH trait distributions (Fig. 2), and the trends were consistent for each monthly cohort ([SI Table 1](#)) and at each site ([SI Table 2](#)). We did not detect significant differences in pelagic larval duration [PLD; Kolmogorov–Smirnov two-sample tests (K-S test): $Z = 1.04$, $P = 0.23$; Fig. 2a] or size at settlement ($Z = 0.67$, $P = 0.76$) between fish that developed in different water masses. Despite a poor start compared with fish that developed in a high-Pb water mass, recruits developing in the low-Pb water mass grew significantly faster on average ($Z = 1.48$, $P = 0.025$; Fig. 2b), largely because of accelerated growth in the 2 weeks before settlement [repeated-measures ANOVA (RM-ANOVA): age \times water mass term,

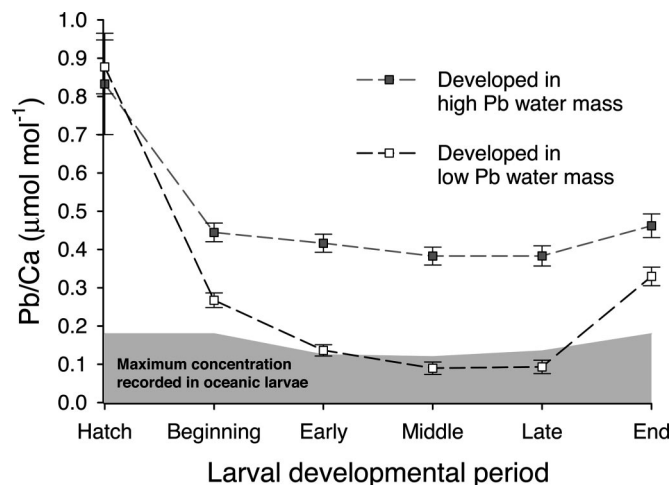


Fig. 1. *T. bifasciatum* otolith elemental profiles depicting average Pb/Ca concentrations (± 1 SE) along temporal transects for fish classified into high- (filled symbols) and low-Pb (open symbols) water masses using a Markov chain Monte Carlo assignment model (see *Materials and Methods*). The gray-filled region represents the maximum Pb/Ca concentration measured in oceanic larvae captured >20 km upstream of St. Croix in 1997 as part of a separate study (modified from ref. 18). Fish from 2001 that were classified into the low-Pb development group generally had Pb concentrations lower than the maximum values measured in oceanic larvae for those developmental periods when they were likely to have resided in offshore waters.

Greenhouse–Geisser (G-G) $\varepsilon = 0.195$, $F_{5.6, 1116.8} = 2.82$, $P = 0.012$; [SI Table 3](#), Fig. 3]. Hindcast growth histories differed among monthly cohorts (posthoc contrasts: Aug > July > June) and between sites [Jacks Bay (JB) > Butler Bay (BB)], but the qualitative growth history patterns presented in Fig. 3 remained consistent between low- and high-Pb-classified fish (i.e., no significant interaction terms including water mass and site or month; [SI Table 3](#)). Larvae that developed in low-Pb water masses emerged from metamorphosis with larger lipid reserves ($Z = 1.63$, $P = 0.01$; Fig. 2c) and correspondingly wider otolith metamorphic bands (a proxy for condition, see *Materials and Methods*; $Z = 1.51$, $P = 0.025$; Fig. 2d).

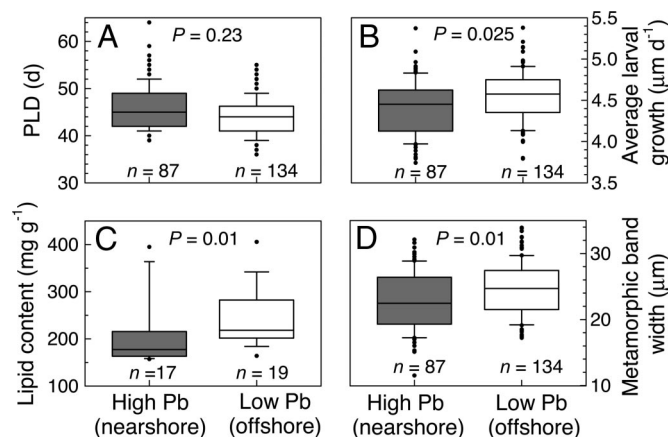


Fig. 2. Box plots depicting distributions of ELH traits for new recruits of *T. bifasciatum* that were classified as having developed primarily in high- (nearshore) or low-Pb (offshore) water masses based on elemental profiles of Pb/Ca concentrations. Shown are distributions of PLD (A), average larval otolith growth (B), total lipid content (C), and metamorphic band width (D). Box plots show median values (line), 25% and 75% quantiles (box), 5% and 95% quantiles (whiskers), and outliers (points).

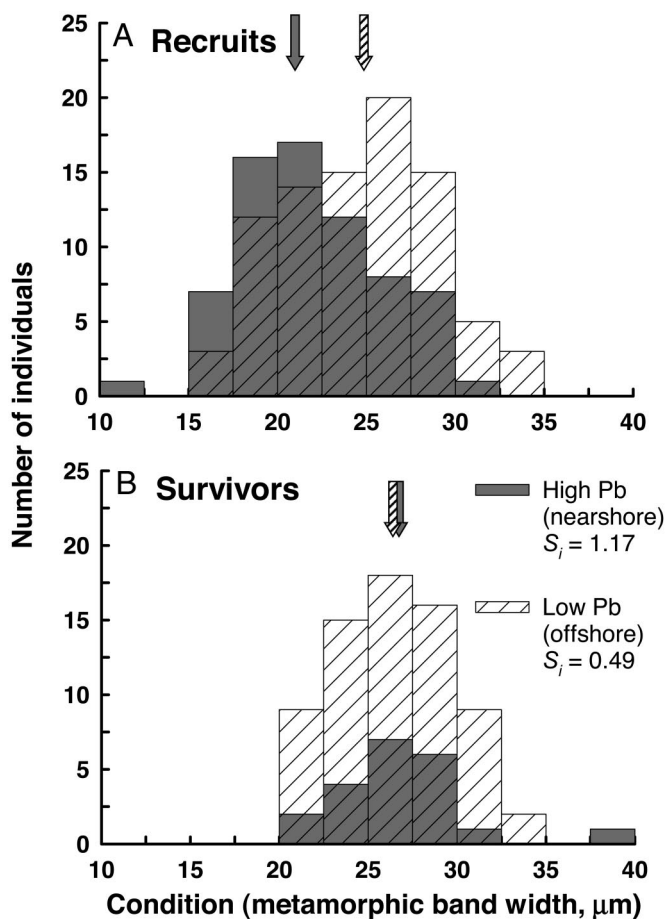


Fig. 5. Distributions of the width of the metamorphic band (a proxy for condition; ref. 19; S.L.H., unpublished work) for new recruits (0–7 d postsettlement) (A) and survivors (1 month postsettlement) (B) of cohorts that were classified as developing in high- (gray bars) or low-Pb (diagonal hatched bars) water masses based on elemental profiles of otolith Pb/Ca concentrations. Arrows above frequency histograms represent the mean metamorphic band width for that group. S_i measures changes in metamorphic band widths from recruit to survivor classes.

waters off St. Croix (collected >20 km offshore in 1997; ref. 18). If onshore–offshore gradients in Pb concentration were similar between these two studies, it is especially likely that these fish developed in offshore waters.

As they pass by St. Croix, mesoscale eddies propagating from the Amazon and Orinoco Rivers may temporarily mask coastal trace element enrichment signatures (18, 41), and thus coastal waters may have distinct elemental composition only during typical flow conditions. These dynamic circulation features may also entrain and transport developing larvae of coral reef fishes from distant sources (42) while simultaneously influencing larval traits (20). An influx of fish with a depleted Pb signature may be indicative of just such a dispersal event (e.g., August cohort, SI Table 1). Indeed, mesoscale eddy activity occurs predictably in late August and September, and large-scale eddy-induced current reversals around St. Croix have been associated with island-scale patterns of replenishment consistent with long-range dispersal (18, 41, 43). Despite the potential for oceanographic events to disrupt typical coastal seawater composition, in 2001, we detected consistent differences in ELH traits that were associated with water mass characteristics experienced during larval life. These patterns remained consistent even in the face of spatiotemporal variation in the proportion of fish that developed in high- and low-Pb waters.

Settlers are the survivors of larval life. We found evidence that larval history (as indicated by residence in distinct water masses) was associated with strikingly different growth rates and physiological performance. Fish that developed in water masses depleted in Pb grew more slowly in the beginning and middle portions of the larval phase, as might be expected for larvae residing in oceanic waters that are relatively depleted in nutrients and potential prey items (31). Those offshore-developing fish that successfully settled exhibited rapid compensatory growth at the end of the larval phase, likely upon reentering nearshore waters, and consequently settled at a size similar to fish that spent their entire larval life in waters enriched in Pb. Importantly, these fish were on average in better physiological condition than nearshore-developing fish. A compensatory growth response in fishes commonly occurs after exposure to reduced rations (44). Fish adapted to restricted rations (i.e., perhaps characteristic of the offshore environment) have been shown to have higher assimilation efficiencies (45), and this may promote a compensatory growth response when prey availability increases.

The relatively poor performance of fish that developed in the high-Pb water mass was not likely caused by toxic Pb poisoning, because even nearshore seawater concentrations of Pb in St. Croix are detectable only in trace amounts ($150.1 \text{ pmol}\cdot\text{liter}^{-1}$ or $11.9 \text{ nmol}\cdot\text{mol}^{-1} \text{ Ca}$; ref. 18). These are far below levels considered toxic for larval fishes ($30 \text{ }\mu\text{g liter}^{-1}$, ref. 46) and are unlikely to deleteriously affect physiological performance. Significantly elevated Pb/Ca concentrations occurred at the end of larval development for the low-Pb group, signifying a change in water mass. The concurrent compensatory growth response we observed is opposite to what would be predicted if nearshore waters were heavily contaminated. Although unlikely in this system, covariation between Pb and other unmeasured contaminants cannot be ruled out. In other locations, pollution by heavy metals and organic contaminants could impair larval growth, development, and the survival of larvae that remain in nearshore waters. This possibility requires further investigation.

The survival and fitness of any individual can be largely determined by its experiences early in life (19, 33–36), so variability in ELH traits could have great ramifications for the postsettlement success of reef fishes. Despite this well documented concept, the studies that have identified settlers to source have assumed a direct correspondence between settlement intensity and eventual recruitment to the adult population (6, 7, 11, 15). Although the reported high levels (30–90%) of self-recruitment of bluehead wrasse to St. Croix emphasize the importance of larval retention (7, 18), the episodes of postsettlement selection that we monitored suggested that fish who developed in high-Pb, likely nearshore, water masses suffered much higher mortality. These surprising effects of larval history on postsettlement mortality were mediated by large differences in recent growth and condition (i.e., metamorphic band width) at settlement. Researchers have documented strong links between environmental conditions experienced by larvae and the width of the metamorphic band in bluehead wrasse (20, 47), but a direct relationship between metamorphic band width and physiological performance has only recently been identified (S.L.H., unpublished work). This proxy for condition is an important determinant of postsettlement selective mortality (19), apparently because of the effects of individual quality on swimming performance and risk-taking foraging behavior (48).

Condition-mediated selection is an important driver of survival during critical life history transitions in many species that exhibit complex life cycles (21, 33). We found that intense selection occurred in the high-Pb group for wide metamorphic bands and rapid growth during the last 2 weeks before settlement but not for the survivors of the low-Pb group. Asymmetries in the strength of selection between groups that experienced distinct larval histories may arise from differences in the timing of

selective mortality. We collected only fish that survived the larval period, and mortality may have been particularly intense in offshore compared with nearshore waters during the planktonic period. In that case, only the best-performing larvae that developed offshore were able to pass through this selective filter and survive until settlement. In contrast, fish that spent their larval life in a high-Pb water mass developed in a less selectively intense environment, and both high- and low-quality nearshore fish successfully settled, potentially because of the increased likelihood of encountering suitable adult habitat at the end of the larval period, but poor-performing individuals were subsequently selectively removed. Thus, accurately measuring the contribution of different sources to local populations is only the first step in describing connectivity, because larvae that developed in different places may have very different fates once they arrive on the reef.

Spatial management of fisheries requires knowledge of population connectivity, including information on self-recruitment and the contribution from distant sources (4, 5). A potential important metric for management purposes is not the proportion but the subsequent fitness (i.e., survival and reproductive output) of individuals that arrive from different sources, which we term “realized connectivity.” Recent detailed oceanographic models of larval dispersal that incorporate realistic larval behaviors have begun to reveal the scale of connectivity across ocean basins (9). A more complete picture of metapopulation dynamics will be achieved when we can predict the ecological scale of realized connectivity, because these patterns should be more congruent with phylogeographic patterns that geneticists routinely measure over evolutionary timescales. Techniques to estimate the actual population contributions from distinct sources will be vital tools in closing the gap between ecological and evolutionary studies of connectivity in marine systems.

Materials and Methods

Species Background and Study System. The bluehead wrasse, *T. bifasciatum*, is an omnivorous labrid common on shallow reefs throughout the Caribbean. Larvae settle to reefs after a PLD of ≈ 47 d (range 35–78 d, refs. 49 and 50), affording considerable potential for long-distance dispersal. In St. Croix, settlement is broadly lunar cyclic with peak intensity around the new moon, and recruitment fluctuates monthly, usually peaking in summer and early fall (49). Upon settlement, bluehead wrasse undergo metamorphosis over a 3- to 5-day nonfeeding period while sequestered in the sand or reef substrate (50). Newly emerged recruits prefer benthic low-relief rubble or coral crevices and initially remain solitary or in small groups for several weeks before joining juveniles to shoal in the water column. St. Croix, U.S. Virgin Islands (17.75° N, 64.75° W), is a relatively small (40 × 7-km) island in the northeast Caribbean Sea, 90 km southeast of Puerto Rico. We studied recent settlers from two reefs on opposite shores of St. Croix, BB on the leeward and JB on the windward shore. Both sites were located near the outer-reef slope and were primarily composed of flat coral pavement with sparse patches of living and dead coral, interspersed with patches of rubble and sand (see ref. 49 for details). These sites were chosen because they receive consistent levels of recruitment (43) and differ in the spatiotemporal contribution of self-recruitment to population replenishment (7).

Collections and ELH Trait Measurements. To examine the effects of dispersal history on ELH traits and postsettlement survival of bluehead wrasse, we sampled an initial group of new recruits (i.e., preselection group) from three cohorts (June, July, and August 2001) at BB and JB and then returned to sample survivors (i.e., postselection group) after bouts of mortality after ≈ 30 days (June and July cohorts only). Samples were preserved by freezing at -80°C . To obtain measurements of ELH traits, we used the permanent record of age, growth rate (daily otolith growth, micrometer per day $^{-1}$), and relative size at age contained within otoliths (accretionary calcium carbonate structures in the inner ears of fish; SI Fig. 7). For bluehead wrasse, Victor (51) validated the deposition of daily otolith increments and identified the presence of conspicuous settlement and emergence marks; this is termed the metamorphic band and represents otolith accretion during a 3- to 5-day nonfeeding metamorphic period. For a subset of individuals ($n = 36$), we examined the influence of dispersal history on condition by measuring total lipid content. Lipid content

was determined gravimetrically by using chloroform–methanol extraction (52). Duplicate aliquots of solvent extract were dried to a constant weight at 60°C and weighed to the nearest 0.01 mg. Duplicate means were then expressed as total lipid in milligram per gram $^{-1}$ dry weight (coefficient of variation between duplicates = 5.5%, among samples = 30.7%). Previous work revealed a strong positive relationship between lipid content and the width of the metamorphic band ($r^2 = 0.62$; S.L.H., unpublished work).

Sagittal otoliths were dissected from a haphazardly selected subsample of new recruits and juveniles using standard techniques. We placed the right otolith into medium viscosity immersion oil for a minimum of 30 days to enhance ring clarity. The left otolith was stored dry for chemical analysis. All otoliths were read two to three times by one person (S.L.H.), and all unclear or abnormally shaped otoliths were discarded ($<5\%$). Daily otolith growth measurements were made along the longest axis of the otolith in the sagittal plane, from the core to the outermost complete ring, by using a compound microscope at $\times 400$ with polarized transmitted light attached to an image analysis system (ImagePro 4.5, Media Cybernetics). Otolith increment width was used as a proxy for somatic growth, based on the demonstration that there is a strong relationship between somatic and otolith growth for this species (19).

To determine whether ELH traits differed among fish with different dispersal histories or between the initial and survivor groups of a particular dispersal history, we examined shifts in trait-frequency distributions using K-S tests. We back-calculated the settlement date of each individual and included survivors in further analyses only if they settled within the same 8-day window as the new recruits each month. New recruits were defined as fish aged 0–7 d postemergence, whereas survivors included individuals from those same cohorts that were ≈ 30 d postemergence. We estimated the intensity of linear directional selection (S_i) as

$$S_i = \frac{\bar{z}_{\text{after}} - \bar{z}_{\text{before}}}{SD_{\text{before}}}, \quad [1]$$

where \bar{z}_{before} and \bar{z}_{after} are the phenotypic trait means before and after the selective event, and SD_{before} is the standard deviation of the trait before selection (37). We analyzed hindcast (backwards from settlement) daily growth histories because of the broad range of PLD for this species, and because the past 1 or 2 weeks of growth may affect survival potential, independent of growth at a particular age. PLD varied among fish, but we examined only the last 30 d to maximize sample sizes for analysis regardless of PLD. Larval growth histories were compared statistically using RM-ANOVA. In cases where the assumption of within-class sphericity was not met, we used the G-G adjustments of degrees of freedom following Von Ende (53), in JMP 6.0 (SAS Institute).

Otolith Elemental Analyses and Dispersal History Classification. The left sagitta from each fish was mounted sulcal side up on plastic slides using low-viscosity epoxy resin (Epo-Thin epoxy resin, Buehler). Sagittae were polished to within 5–15 μm of the core using a lapping wheel and 9- and 3- μm 3M diamond polishing film to expose inner-growth layers. To remove contaminants from the otolith surface before analysis, sagittae were rinsed in ultrapure water (N-pure, resistivity >18.1 M Ω), soaked in semiconductor grade 15% H_2O_2 buffered with Suprapur 0.05 N NaOH (Merck) in acid-leached plastic trays for 1 h, rinsed again in N-pure, soaked and sonicated three times in N-pure for 5 min, rinsed a final time with N-pure and air-dried in a class-100 flow bench. We used a Finnegan MAT Element 2 sector field ICP-MS and a VG-UV microprobe Nd:YAG 266-nm laser ablation system for chemical analysis (see ref. 54 for more details). We ablated and analyzed the composition of individual pits along a transect stretching from the core to edge of the otolith (along the longest axis). Each pit consisted of eight laser pulses of 0.1 mJ at 3 Hz and ablated a volume ≈ 30 μm in diameter and ≈ 10 μm deep. Before acquiring data, we preablated using two laser pulses to remove any surface contamination. For each fish, six to nine pits were ablated between the core and the settlement mark (SI Fig. 7), and each pit was categorized into one of six developmental periods (see Fig. 1) based on the fraction of PLD elapsed. If multiple pits fell within one developmental period, the concentrations of each element were averaged. Pits that overlapped with the settlement mark were excluded to ensure that all elemental concentrations were from larval development only. Consequently, most end-of-the-larval-phase pits correspond to a time period of ≈ 7 d presettlement. In each sample pit, we collected counts for the isotopes ^{24}Mg , ^{48}Ca , ^{55}Mn , ^{88}Sr , ^{138}Ba , and ^{208}Pb . Molar ratios of analyte to Ca were calculated by using the ratio of each isotope to ^{48}Ca and an elemental mass bias correction calculated from calibration standards (repeated after every three to five otoliths) with known analyte-to-Ca ratios. We analyzed solid glass standard reference material (National Institute of Stan-

dards and Technology 612) along with the samples to maintain instrument analytical precision; estimates of precision and limits of detection are located in SI Table 5.

To group fish into different dispersal histories based on otolith elemental profiles, we used a Markov chain Monte Carlo simulation that extends the maximum-likelihood method developed by Sandin *et al.* (55). The model produces output similar to a *k*-means cluster analysis in that fish are assigned into groups based on chronological similarities in elemental concentrations. Previous results indicated that elemental profiles of Pb could serve as reliable environmental markers of nearshore or offshore larval residence (18), leading us to focus exclusively on Pb in this analysis. Our model assumes two distinct water masses (offshore and nearshore), each characterized by an unknown mean and variance in Pb concentration. We further assume that fish may conform to one of two dispersal histories: Given *k* chronologically ordered otolith sample pits, "nearshore" fish are those for which all *k* pits reflect the nearshore water mass; in contrast, "offshore" fish are those for which pits 1 to *s* reflect the offshore water mass, and pits *s* + 1 to *k* reflect the nearshore water mass. Beginning with initial guesses for the Pb concentrations, we used a Gibbs sampling approach to simulate the probability that each fish conforms to each dispersal mode. First, we randomly selected a dispersal history for each fish,

conditional on the current water mass means and variances. Then we updated the two sets of means and variances to their maximum-likelihood values, given the current dispersal histories of all fish. This alternation of steps was repeated 1,000 times after an initial burn-in of 100 steps. We subsequently classified fish as nearshore if they were identified as nearshore in >50% of simulations and as offshore otherwise. Note that classification reliability was high, with >80% of fish conforming to a particular dispersal history in at least 90% of the simulations (SI Fig. 8).

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