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 of 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 (30–9%; 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%; χ² = 7.05, P = 0.03; sample sizes in supporting information (SI) Table 1] and between two sites (high-Pb group: BB = 48%, JB = 30%; χ² = 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 × water mass term, Greenhouse–Geisser (G-G) ε = 0.195, F_{5,26} = 11.6, 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. 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.
Selective Mortality of Survivors. Mortality during the first month on the reef was affected by larval history, and most survivors had developed in waters characterized by depleted Pb concentrations. Elemental profiles of Pb showed that nearly 45% of new recruits from June and July developed in a high-Pb water mass, whereas only 23% of survivors from those settlement events developed in these putative nearshore waters ($\chi^2 = 10.7, P = 0.001$, sample sizes in SI Table 4). Distributions of Pb at specific developmental periods corroborated that result and revealed that a higher proportion of survivors developed in waters characterized by low-Pb concentrations (SI Fig. 6). Within the high-Pb group, survivors grew more rapidly as larvae than the initial (i.e., preselection) group of recruits (SI Table 4), mainly because of enhanced late larval growth (RM-ANOVA; G-G $\epsilon = 0.17, F_{5.0, 385.7} = 7.27, P < 0.0001$; Fig. 4a). Within the low-Pb group, in contrast, survivors did not differ from recruits in PLD, size, or average growth rates (SI Table 4). However, late larval growth of survivors did exceed that of recruits (RM-ANOVA; G-G $\epsilon = 0.17, F_{5.1, 823.7} = 2.22, P = 0.048$; Fig. 4b). Phenotypic selection for rapid growth at the end of the larval period was not as extreme for survivors originating from the low-Pb group [selection intensity ($S_i$) last 14 d = 0.24] as that seen in survivors of the high-Pb group ($S_i$ last 14 d = 1.16). Survivors from both groups ended metamorphosis in better condition (i.e., wider metamorphic bands; SI Table 3), but selection intensity on condition was much greater for fish that developed in high- ($S_i = 1.17$) than low-Pb ($S_i = 0.49$) waters (Fig. 5). Despite asymmetries in the strength of phenotypic selection and regardless of the water mass they encountered, survivors did not differ in condition (Fig. 5) or hindcast growth (RM-ANOVA; G-G $\epsilon = 0.18, F_{5.1, 449.3} = 1.01, P = 0.41$).

Discussion
Here, in a marine system, we show that postsettlement selective mortality was associated with larval residence in environments that differed in chemical composition (i.e., high and low Pb). Given previous findings from this system (7, 18), under typical flow conditions, bluehead wrasse that developed in water masses enriched in Pb likely spent much of their larval life developing in nearshore waters and thus were spawned on St. Croix (i.e., self-recruitment). A 4-fold enrichment of Pb occurs in coastal waters near St. Croix (18) compared with oceanic waters offshore (38). This Pb enrichment effect is not unique to St. Croix. For instance, Pb levels reported from coastal waters off Bermuda were 4-fold higher than in oceanic waters in the Sargasso Sea (39, 40). A similar magnitude of difference in Pb/Ca concentrations occurs between fish assigned to high- and low-Pb water masses in this study (i.e., 4.3-fold difference in Pb/Ca in the middle period of larval development). Elevated nearshore concentrations of Pb likely result from urban wastewater discharge and local aeolian inputs from oil and gas production (St. Croix has a large oil refinery).

In contrast, larvae that were resident in the water mass characterized by depleted Pb concentrations likely developed in offshore waters. Fish with low-otolith Pb concentrations had elemental profiles consistent with cross-shore dispersal, in that Pb concentrations were significantly elevated only at the beginning and end of the larval phase but were significantly reduced during the middle of the larval phase. This group may include individuals that dispersed from upcurrent sources across oceanic waters but were entrained nearshore before settlement and fish produced on St. Croix that were advected into offshore waters before returning to their natal island. Otolith concentrations of Pb in the putative offshore-developing fish were lower than the maximum concentration reported for larvae collected in oceanic
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 pmol liter\(^{-1}\) or 11.9 nmol mol\(^{-1}\) Ca; ref. 18). These are far below levels considered toxic for larval fishes (30 \(\mu\)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...
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 (6). 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 phyleogeographic patterns that geneticists routinely measure over evolutionary timescales. Techniques to estimate the actual population contributions from distant 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-d nonfeeding period while sequestered in the sand or reef substrate (50). Newly emerged recruits prefer benthic low-reach 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 northeastern 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 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.

To determine whether ELH traits differed among fish with different dispersal histories or between the initial and survivor groups of a particular cohort, we examined the influence of trait-freezing on PLD 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-d 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 (5) as:

\[ S_I = \frac{z_{\text{after}} - z_{\text{before}}}{S_{\text{before}}} \]

where \( z_{\text{after}} \) and \( z_{\text{before}} \) are the phenotypic trait means before and after the selective event, and \( S_{\text{before}} \) 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 fact survival weeks of growth may affect the 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-6 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 MΩ cm, 0.1 M NaOH and the conductive grade 15% H2O2 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 Finnigan 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 of the otolith from the core to edge of the pit (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 an otolith pit 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 postemergence. In each sample pit, we collected counts for the isotopes 24Mg, 46Ca, 45Mn, 54Mn, 54Si, 88Sr, and 208Pb. Molar ratios of analyte to Ca were calculated by using the ratio of each isotope to 46Ca 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 k reflect the offshore 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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