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Larval quality is shaped by matrix effects: implications for connectivity in a marine metapopulation

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Abstract. Variation in the phenotype or "quality" of dispersing individuals can shape colonization success and thus local dynamics and patterns of connectivity in a metapopulation. In marine reef systems, larval dispersal typically connects fragmented populations, and larval quality may be shaped by developmental history at the natal reef (e.g., parental effects) and/or by conditions in the pelagic environment (e.g., food, temperature, hydrodynamics, predator regime). We extract information recorded within the incremental bands of fish "ear stones" (otoliths) to reconstruct the early life histories of reef fish, to evaluate whether larval quality is a function of natal populations, dispersal histories, or both. We sampled sagittal otoliths from 282 common triplefins (*Forsterygion lapillum*) collected at approximately weekly intervals between December 2003 and March 2004, from three sites within Wellington Harbor (New Zealand) and three sites along the adjacent Wellington South Coast. We used image analysis to quantify otolith traits and to reconstruct five larval phenotypes (pelagic larval duration, size-at-hatch, early larval growth, late larval growth, and an instantaneous larval growth rate), followed by a principal components analysis to derive a composite measure of larval quality. We used laser ablation-inductively coupled plasma-mass spectrometry to quantify otolith microchemistry, followed by a set of cluster analyses (based upon 13 statistical descriptors of time series for each of 11 elemental ratios) to identify and characterize two putative natal "source populations" and two putative "larval dispersal histories." We evaluated the relationship between larval quality, source populations, and dispersal histories using two-way ANOVA and MANOVA, and determined that larval quality of *F. lapillum* is a function of larval dispersal history and not source population identity. Specifically, larvae of *F. lapillum* with microchemical signatures consistent with retention and/or entrainment in the nutrient-enriched Wellington Harbor had traits associated with elevated larval quality (i.e., short pelagic larval durations, small size-at-hatch, fast larval growth, and fast instantaneous growth rates). Our results suggest that conditions in the pelagic larval environment shape larval quality and potentially mediate metapopulation connectivity. In the case of *F. lapillum* from Wellington Harbor, environmentally induced heterogeneity in larval quality may limit connectivity by favoring successful replenishment by locally retained larvae over long-distance dispersers.

Key words: *demographic connectivity; environmental marker;* Forsterygion lapillum; *larval condition; larval dispersal; larval retention; match–mismatch hypothesis; matrix effects; metapopulation dynamics; otolith microchemistry; selective mortality; time-series analysis.*

Introduction

Metapopulation frameworks have emerged as a standard ecological paradigm to conceptualize and study the dynamics and evolution of species residing within spatially distributed populations (Hanski and Gaggiotti 2004) and have proven exceptionally useful in explaining complex dynamics arising from networked local populations (e.g., Saunders et al. 1991). One of the most fundamental and least understood processes affecting metapopulation dynamics is *population connectivity*, or the exchange of individuals between discrete local populations. Empirical estimates of connectivity can be difficult to obtain (Ims and Yoccuz 1997) and are typically modeled as dispersal probabilities (Moilanen and Nieminen 2002). For many organisms, dispersal can be a physiologically demanding event (Baker and Rao 2004, Stamps et al. 2005), and mortality following dispersal events may be high and potentially selective upon individuals with particular dispersal histories (e.g., long-distance dispersers; Matter 2006). Similarly, selective mortality may benefit dispersers that have originated from particular source populations (e.g., with phenotypes well suited to the new environmental conditions; Stamps 2006). In this way, among-individual variation in phenotypes (e.g., physiological condition) of colonizers may effectively mediate patterns of metapopulation connectivity established by initial dispersal events.

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Most marine reef organisms exist as highly fragmented populations interconnected by dispersal of eggs and/or larvae through a pelagic ocean matrix (Roughgarden et al. 1985, Caley et al. 1996, Kritzer and Sale 2004). Eggs and larvae of many reef species exhibit extreme variation in phenotypes (e.g., size, morphology, development time, growth rate, lipid stores), which often have important consequences for subsequent fitness (e.g., growth and/or survival; Pechenik et al. 1998, Phillips 2002, Shima and Findlay 2002, Wilson and Meekan 2002, McCormick and Hoey 2004), and thus may reflect larval quality. For some species, such phenotypic variation has been attributed to parental effects (e.g., Marshall et al. 2003, Green and McCormick 2005, Marshall et al. 2006, McCormick 2006, Gagliano and McCormick 2007) that may be a characteristic of the natal source populations that gave rise to these propagules. For many marine species, particularly those with feeding larvae, conditions in the pelagic larval environment (e.g., food availability, temperature, hydrodynamics, predator regime) may further influence larval phenotypes (e.g., Meekan et al. 2003, Phillips 2004, Sponaugle et al. 2006).

If larval quality is a function of source populations, then an understanding of patterns and processes associated with natal environments may be useful in predicting patterns of connectivity in marine metapopulations. Alternatively, if larval quality is driven primarily by conditions in the pelagic larval environment, then understanding the role of spatial and temporal variation in the pelagic environmental features that affect larval quality may be necessary to accurately predict patterns of demographically meaningful connectivity. Despite the important implications of these hypotheses, the relative importance of natal effects versus larval dispersal history as sources of variation in larval quality is poorly known for marine species (although some laboratory experiments have addressed similar questions under artificial conditions; e.g., Bayne et al. 1975, Gallager and Mann 1986).

Here, we develop and apply a set of analytical approaches to extract information archived within the incremental bands of fish "ear stones" (otoliths). Using matched pairs of otoliths, we (1) quantify phenotypic traits indicative of larval quality and (2) reconstruct putative source population identities and dispersal histories for individuals that recently settled to natural reef-based populations in a harbor and an adjacent open-coast setting. We integrate these complimentary sets of information to ultimately evaluate whether larval quality is a function of natal populations, dispersal histories, or both.

Methods

Study system and sampling

Our work examines phenotypic variation and larval dispersal history of the common triplefin, *Forsterygion lapillum* (Family: Tripterygiidae). *F. lapillum* is one of the most abundant species in shallow rocky reef habitats of New Zealand (Clements 2003, Feary and Clements 2006, Wellenreuther et al. 2007), where it feeds upon a range of small invertebrates (Feary 2001, Clements 2003), and is likely an important prey species for larger reef predators. Females of the species spawn benthic egg masses on cobbles, which are defended and cared for by males for ~2 weeks prior to hatching (Thompson 1979, Francis 2001; J. S. Shima and S. E. Swearer, *unpublished data*). Unlike most other New Zealand triplefins, *F. lapillum* appear to remain reproductively active for most of the year (Wellenreuther and Clements 2007). Juveniles settle to the fronds of macrophytic brown algae (McDermott and Shima 2006) between December and March, after a mean pelagic larval duration of 52 d (SD = 9 d; J. S. Shima and S. E. Swearer, *unpublished data*). Larvae complete development in the pelagic water column, where they are patchily distributed (Kingsford and Choat 1989) and present for most of the year (Hickford and Schiel 2003).

We sampled recently settled *F. lapillum* at approximately weekly intervals from December 2003 to March 2004, the seasonal peak in recruitment (J. S. Shima and S. E. Swearer, *unpublished data*), using standardized monitoring units for recruitment of reef fishes (SMURFs; sensu Ammann 2004). Our SMURFs followed the design of Ammann (2004): each SMURF consisted of a cylinder of plastic mesh (garden fencing, 2.5 cm grid) that measured 1.0 m in length × 0.35 m in diameter, filled with haphazardly folded plastic mesh (roadside safety fencing). SMURFs were deployed on or near rocky reef habitat, from permanent mooring lines, set 2 m above the substrate, and at a mean water depth of 6 m (SD = 4 m). This placement of SMURFs was chosen to mimic the canopies of macroalgae that are more typically used by settling *F. lapillum*. SMURFs were deployed in triplicate to each of six sites, stratified within two regions (Wellington Harbor, Wellington South Coast, New Zealand). The three sites within the Harbor were located at Kaiwharawhara (41°15′30″ S, 174°47′48″ E), Eastbourne (41°17′6″ S, 174°54′0″ E), and Shelly Bay (41°17′46″ S, 174°49′12″ E); the three sites along the adjacent South Coast were located at Island Bay (41°20′48″ S, 174°46′24″ E), Princess Bay (41°20′48″ S, 174°47′6″ E), and Moa Point (41°20′54″ S, 174°48′54″ E). Wellington Harbor is a semi-enclosed, roughly circular basin that receives substantial discharge from the Hutt River (mean flow for 2004, 3×10^6 m^3/d; peak flow, 92×10^6 m^3/d on 2/16/04; J. S. Shima, *unpublished data*). Tidal exchange between the harbor and open coast is limited (roughly 4.5% of the total harbor volume per tidal cycle, Maxwell 1956), and point-source inputs of heavy metal contaminants and nutrients have been identified within the harbor (e.g., Stoffers et al. 1986, Pilotto et al. 1998). Consequently, the harbor is more typically a nutrient-enriched environment, likely with unique water chemistry. By contrast, the Wellington South Coast borders Cook

Strait and is continuously flushed by oceanic water from the Tasman Sea. Sites along the South Coast are characterized by limited terrestrial inputs and relatively low primary productivity (Bowman et al. 1983, Harris 1990, Gardner 2000; J. S. Shima and S. E. Swearer, *unpublished data*). We sampled sites within these two adjacent regions over four months to capture the range of variation in larval *F. lapillum* phenotypes, source populations, and/or pelagic larval dispersal histories. Specifically we hypothesized that *F. lapillum* larvae coming from populations within Wellington Harbor and/or entrained early in their pelagic development within harbor waters would be of higher quality and possess unique chemical signatures relative to fish that were spawned and/or retained predominately within the nutrient- and chemically depleted waters of the open coast.

Quantifying larval quality

To quantify larval phenotypes, we extracted and analyzed sagittal otoliths of recently settled *F. lapillum* sampled from SMURFs. Otoliths are calcium carbonate structures within the vestibular apparatus of teleost fishes, analogous to the inner ear bones of other vertebrates, and used by fishes for hearing and balance (Popper and Coombs 1980, Riley and Moorman 2000). Sagittal otoliths are roughly ellipsoidal in shape and typically form in a pattern of daily growth increments (Pannella 1971, Campana and Thorrold 2001) that, when viewed in cross section under a microscope, can be used to estimate the age, previous growth rates, and major physiological events (e.g., hatch date, settlement date) in the early life history of fishes (Secor et al. 1995, Campana and Thorrold 2001, Takahashi et al. 2001, Pasten et al. 2003). Otolith growth rates appear to be well correlated with somatic growth rates across many species (Francis 1990, Campana and Jones 1992, Hare and Cowen 1997, Shima 1999, Shima and Findlay 2002, Sponaugle et al. 2006).

Otoliths were extracted from 616 recently settled *F. lapillum*, though a random subsample of these was selected and analyzed for this study (~10 individuals per site for each collection date, else all individuals if sample size was <10). Following extraction, one sagittal otolith from each fish was set aside for microchemistry analysis (described in *Methods: Reconstructing larval dispersal history and source population identity*), and the remaining otolith was embedded in cyanoacrylate and polished along the sagittal plane with 3 μm diamond lapping film (3M, St. Paul, Minnesota, USA) to expose daily growth increments across the postrostral axis (daily increments were validated with calcein staining in a separate study; J. S. Shima and S. E. Swearer, *unpublished data*; see also Kohn 2007). Polished samples were clarified in immersion oil for ~24 h prior to image acquisition. A set of digital images was collected for each sample, using an image analysis system comprised of a Leica compound microscope (Leica Microsystems, Wetzlar, Germany) fitted with a Nikon CoolPix (Nikon, Chiyoda-ku, Tokyo, Japan) digital camera and connected to a PC operating ImagePro Plus v5.0 (MediaCybernetics, Bethesda, Maryland, USA). Images for increment analysis were typically acquired with 400× magnification (though occasionally, larger otoliths were sampled using 200×). Growth increments along the postrostral axis were tagged using the Caliper Tool package of ImagePro Plus; individual increment widths and an estimate of radius (measured from the otolith's core to the trailing edge of a given increment) were recorded to the nearest 0.1 μm for each tagged increment. Samples were read only once, by a single observer (J. S. Shima), who was blind with respect to metadata associated with each sample (e.g., collection site, date, size of fish, and other variables). The visible presence of a "hatch check" and "settlement check" facilitated identification and differentiation of three distinct life-history stages within each otolith: a "pre-hatch stage" (i.e., daily otolith increments formed while the individual was still encapsulated in its egg), a "pelagic larval stage" (i.e., daily otolith increments formed during pelagic larval development), and a "post-settlement stage" (i.e., daily otolith increments formed after settlement to SMURF, but prior to collection). Hatch checks were identified and generally characterized by an abrupt (~50%) increase in increment widths. Settlement checks were identified and generally characterized by an abrupt (~50%) decrease in increment widths, which were also typically coincident with a change in the optical density of the otolith (see also Kohn [2007] for further validation of settlement marks in *F. lapillum*).

Daily increments from the pelagic larval stage of sampled otoliths facilitated estimates of five phenotypic variables that we used to characterize larval quality of recently settled *F. lapillum*: (1) "Pelagic larval duration (PLD)" is an estimate of larval development time in days, and was estimated by the number of daily otolith increments counted in the larval stage of each sample (i.e., the interval between hatch check and settlement check). (2) "Early larval growth" was estimated as the mean increment width across the first 5 days of larval growth following hatching. (3) "Late larval growth" was estimated as the mean increment width across the final 5 days of larval growth prior to settlement. (4) "Size-at-hatch" was estimated as the postrostral radius from core to hatch check. (5) "Instantaneous larval growth rate" was estimated using a maximum likelihood approach (NLIN procedure, SAS v. 9.1; SAS, Cary, North Carolina, USA) that fit an exponential model to the larval otolith growth trajectory of each fish (after Shima and Findlay 2002):

$$L_t = a \times \exp^{bt} \quad (1)$$

where L_t is the otolith increment width (μm) at time t (d) in the larval stage, a is the maximum-likelihood estimate of width at $t = 0$, and b is the maximum-likelihood estimate of instantaneous growth rate (i.e., a measure of

the "per μm" rate of increase over a short time interval; units = $\mu m \cdot \mu m^{-1} \cdot d^{-1}$). We applied an exponential growth model to our data because we observed otolith growth patterns to be exponential in form.

Because these five measures of larval phenotype provide complimentary information but may be interrelated, we used a principal component analysis (PRINCOMP procedure, SAS v. 9.1) to generate a composite measure of larval quality, estimated as the first principal component score for each fish.

Reconstructing larval dispersal history and source population identity

We used chemical signatures recorded within the remaining sagittal otolith of each fish to characterize and discriminate among putative "source populations" and "pelagic larval dispersal histories" of recently settled *F. lapillum*. In addition to recording useful demographic information for fishes (e.g., described previously), otoliths also incorporate trace elements found in seawater, particularly divalent cations occurring naturally in seawater and/or enhanced via anthropogenic inputs (Campana 1999, Swearer et al. 1999, 2002). Resultant microchemical signatures recorded within the embryonic otolith (i.e., for *F. lapillum*, the region of the otolith formed at the natal site, prior to hatching) comprise an "environmental fingerprint" of a putative source population (sensu Barbee and Swearer 2007). Similarly, microchemical signatures recorded across the pelagic larval growth axis characterize larval environmental history experienced by recently settled *F. lapillum*.

To reconstruct larval dispersal history and source population identity, sagittal otoliths were first cleaned of adhered tissue and surface contaminants using a 15% H_2O_2 solution (buffered with 4 g NaOH/L solution) for 24 hr followed by five 5-min rinses in ultra pure (18 Mohm) H_2O, air-dried in a class 100 laminar-flow cabinet, and then embedded in a chemically inert resin (Buehler Epothin; Buehler, Lake Bluff, Illinois, USA). Samples were then mounted on a South Bay Technologies multilap polishing fixture and ground in the sagittal plane to within 10 μm of the otolith core using 9 μm diamond lapping film (3M®) mounted on an 8 inch (20 cm) lapping wheel (Model 920; South Bay Technologies, San Clemente, California, USA). Polished otoliths were cleaned a second time prior to analysis following methods of Patterson and Swearer (2007).

Quantification of the concentrations (relative to Ca, the internal standard) of the following elements (detection limits, μmol element/mol Ca, in parentheses): ^{7}Li (5.19), ^{11}B (21.4), ^{24}Mg (13.5), ^{31}P (60.2), ^{34}S (177), ^{55}Mn (2.96), ^{63}Cu (0.960), ^{66}Zn (2.29), ^{88}Sr (0.349), ^{138}Ba (0.0342), and ^{208}Pb (0.0357) in recruit otoliths was performed on a Varian (Palo Alto, California, USA) inductively coupled plasma mass spectrometer (ICP-MS) fitted with a HelEx (Laurin Technic, Narrabunda, Australia and the Australian National University, Canberra, Australia) laser ablation (LA) system constructed around a Compex 110 (Lamda Physik; Coherent, Santa Clara, California, USA) excimer laser operating at 193 nm (see Eggins et al. [1998] for a description of the LA system). Otoliths were run in blocks of eight samples selected randomly from all sites and collection dates (see Barbee and Swearer 2007 for details of LA-ICP-MS methods). Two different analyses were performed on each otolith using LA-ICP-MS. The first analysis (used to characterize putative source populations) was performed using a stationary laser with a 19-μm spot to drill down through the otolith core. This acquisition produced a "time-series" of concentrations for each of the 11 elemental ratios, measured through the core of each otolith. The second analysis (used to characterize larval dispersal histories) was performed using a moving laser (scan rate, 2.5 scans/s; stage movement rate, 3 μm/s) with a 5 × 80 μm rectangular spot, resulting in a high resolution "transect" (80 μm wide) across the postrostral growth axis of the otolith (i.e., running from the otolith core to the postrostrum edge). This constant rate of acquisition produced a "time-series" of concentrations for each of the 11 elemental ratios, measured across the postrostral growth axis of each otolith (i.e., from core to otolith edge). The time series relating to otolith cores were truncated because ablated drill sequences included some post-hatch (i.e., non-natal) material. Mn and Ba concentrations are known to be enriched in otolith cores (Ruttenberg et al. 2005, Barbee and Swearer 2007), and were therefore used as a diagnostic to truncate (i.e., constrain) time series to otolith core regions indicative of a natal signature. Because drill sequences through the core of the otolith produced roughly symmetrical patterns in elemental time series around the otolith primordium (inferred from local maximum in Mn concentration), we included only the second half of each elemental time series in our analyses (i.e., from primordium to edge of core). The second half was chosen in order to eliminate any artifacts in the time series resulting from surface contamination. Elemental time series relating to pelagic larval dispersal history were similarly truncated to include only the pelagic larval period of each sample (i.e., excluding material sampled from the "pre-hatch" and "post-settlement" regions of each otolith). This truncation was facilitated by known positions of hatch and settlement checks (estimated from increment analysis of the paired sagittal otolith, described previously). We used this same approach to estimate and represent chemical signatures on a daily time scale by averaging across successive LA-ICP-MS scans that occurred within the same daily otolith growth increment.

A series of multivariate statistical approaches was used to first characterize and subsequently cluster fish with similar chemical signatures into a discrete number of groups with respect to (1) otolith core microchemistry (i.e., putative source populations) and (2) larval otolith

transect microchemistry (i.e., pelagic larval dispersal histories). For each case, our data sets consisted of time series of 11 elemental ratios. Time series varied in length depending upon the size of the otolith core and/or the pelagic larval duration of the fish; this, combined with the large number of data points for each time series, precluded a conventional cluster analysis of the raw data without some form of data reduction. To capture patterns of variation and covariation among the elemental ratio time series (i.e., to facilitate a subsequent cluster analysis with a high discriminatory power), we decomposed each time series to a set of 13 statistical properties, or "extracted features" (sensu Wang et al. 2006). To estimate this comprehensive set of univariate descriptors, which consisted of a *serial correlation* function, a *nonlinear* function, a *skewness* function, a *kurtosis* function, a *hurst* function, a *lyapunov* function, a *frequency* function, a *trend* function, a *seasonal* function, a *trend and seasonally adjusted (TSA) serial correlation* function, a *TSA nonlinear* function, a *TSA skewness* function, and a *TSA kurtosis* function, we used R (R core development team; *available online*).[4]

Trend and seasonality are common components of time series that respectively describe a long-term change in mean levels through time (trend) and repeating sequences over fixed intervals of time (seasonality). Frequency is the estimated number of observations over which repeating cycles (i.e., seasonality) occurs. Several of the extracted features (e.g., serial correlation, nonlinear, skewness, and kurtosis) can be estimated following statistical removal of trend and seasonality components (e.g., TSA serial correlation and other components), which has the advantage of further highlighting otherwise cryptic properties of time series (e.g., noise and chaos; Wang et al. 2006). Serial correlation reflects the degree to which successive observations within the time series are correlated (e.g., autocorrelated) through a time series. The nonlinear function characterizes the magnitude of deviation from underlying linear models. Skewness is a measure of the lack of symmetry with respect to the midpoint of a time series. Kurtosis describes the tendency of the data to be peaked (positive values) or flattened (negative values) with respect to a normal distribution. Hurst provides a measure of self-similarity in the time series; lyapunov is a measure of chaos dynamics. See Wang et al. (2006) and references therein for more detailed descriptions and interpretations of each extracted feature.

This set of extracted features was estimated for each of the 11 time series of elemental ratios. The resultant 143 descriptors were then standardized (mean = 0, SD = 1) and used in a hierarchical cluster analysis (CLUSTER procedure, SAS v. 9.1) to determine the number of clusters by evaluating consensus among the cubic clustering criterion, pseudo F statistic, and pseudo t^2 (SAS Institute 1999). These are among the best diagnostics currently available to objectively determine the number of clusters in a data set (Milligan and Cooper 1985, Legendre and Legendre 2006). Cluster identities were subsequently determined using a K-means clustering algorithm (FASTCLUS procedure, SAS v. 9.1). This general approach was implemented separately to partition all fish into discrete clusters of (1) putative source populations (based upon otolith core features) and (2) putative larval dispersal histories (based upon larval otolith transect features).

[4] ⟨http://cran.r-project.org⟩

Sources of variation in larval quality

We used two-way ANOVA (GLM procedure, SAS v. 9.1) to evaluate whether larval quality of recently settled *F. lapillum* varied as a function of putative source population and/or pelagic larval dispersal history. The first principal component score resulting from a PCA on five measured larval phenotypes (described above) comprised the dependent variable in this analysis. Cluster identities for (1) putative source populations and (2) putative pelagic larval dispersal histories comprised the orthogonal explanatory variables in this analysis. In addition, we analyzed overall patterns of variation in the five estimated phenotypic traits (PLD, early larval growth, late larval growth, size-at-hatch, and instantaneous larval growth rate) among "source population" and "dispersal history" clusters using two-way MANOVA.

Results

Larval phenotypes to estimate larval quality

We estimated larval phenotypes and corresponding microchemistry from the paired sagittal otoliths of 282 fish. Larval phenotypes varied widely among individuals. We estimated the mean pelagic larval duration (PLD) of recently settled *Forsterygion lapillum* to be 51.5 d (SD = 9.3), with a range of 33–101 d. Early larval growth (mean daily otolith growth increment width) ranged from 1.0 to 3.7 μm/d (mean = 2.1, SD = 0.5), while late larval growth ranged from 2.5 to 12.6 μm/d (mean = 5.8, SD = 1.5). Measured size-at-hatch of the sampled otoliths ranged from 23.8 to 46.2 μm (mean = 32.7, SD = 3.5). Modeled instantaneous growth rates of larval otoliths ranged from 0.017 to 0.053 $\mu m \cdot \mu m^{-1} \cdot d^{-1}$ (mean = 0.035, SD = 0.006).

We used principal components analysis to construct a composite variable of these five larval phenotypic measures. The first principal component (PRIN 1) accounted for 52% of the overall variation in the data set of larval phenotypes. PLD loaded negatively on PRIN 1 (–0.54), as did size-at-hatch (–0.28). Positive loadings on PRIN 1 were observed for early larval growth (0.27), late larval growth (0.47), and instantaneous larval growth rate (0.58). Fish with high PRIN 1 scores derived from this PCA therefore hatched with a smaller otolith sizes (i.e., indicative of more rapid development within eggs), had shorter PLDs (i.e., rapid

larval development), and had otoliths that grew more quickly relative to fish with low PRIN 1 scores. We therefore deemed PRIN 1 to be an effective composite measure of larval quality.

Characterizing putative source populations and pelagic larval dispersal histories

We used a set of 143 "extracted features" of elemental ratio time series to cluster 282 recently settled *F. lapillum* into groups with similar microchemistry signatures for (1) otolith cores (a natal or "source population" signature) and (2) pelagic larval otolith growth axes (a "larval dispersal history" signature). Objective metrics derived from hierarchical clustering procedures (i.e., cubic clustering criterion, pseudo F statistic, and pseudo t^2) suggested the presence of two significant source population clusters and two significant larval dispersal history clusters. These conclusions were based upon a consensus among the cubic clustering criterion, pseudo F statistic, and pseudo t^2. K-means clustering was then used to assign cluster membership.

Because the 143 extracted features of time series used to cluster fish into source- and larval-dispersal history clusters do not readily yield intuitive characterizations of the otolith microchemistry of each cluster, we calculated a mean time series for each element, for both source- and larval-dispersal history clusters. For presentation purposes, and to control for known ontogenetic variation of elemental concentrations in these time series (J. S. Shima and S. E. Swearer, *unpublished data*), we present mean concentrations (± 1 SE) that were calculated after first standardizing all time series to a common length scale. We standardized time series to a common scale using a ranking procedure (RANK procedure, SAS v. 9.1), which assigned observations from longer time series homogeneously across a number of "bins" determined by the length of the shortest time series. We emphasize, however, that actual clustering assignments were based upon 143 extracted features of time series that were estimated from true time series lengths (i.e., PLDs of variable duration, otolith cores of varying size). We present characteristic patterns of variation in 11 elemental ratios that approximate each source population cluster (Fig. 1) and each larval dispersal history cluster (Fig. 2); we give univariate statistics and canonical loadings for all 143 extracted features in the Appendix (Table A1).

All 11 elemental ratios had components (i.e., extracted features) of their time series that varied significantly between otoliths assigned to the two putative source population clusters (based upon univariate t tests; Fig. 1; Appendix). Relative to cluster 1, otoliths assigned to cluster 2 became increasingly enriched in Li through time (evidenced by significant differences in both hurst and trend). Otoliths in cluster 2 were also enriched in B, Mg, P, Mn, and Zn early in their time series, though concentrations of these elements converged with values typical of cluster 1 closer to the outer edge of otolith cores (i.e., closer to hatch dates). This general pattern was principally captured by differences in the nonlinear, hurst, trend, and seasonal descriptors (Fig. 1, Table A1). Mean time series of S and Cu for the two clusters appeared superficially similar in overall patterns, however, finer scale heterogeneity useful in discriminating between the two clusters was captured by five of the 13 extracted features for both elements (Fig. 1; Appendix). Temporal patterns of variation in Sr and Ba differed markedly between otoliths from the two clusters. Relative to cluster 1, otoliths assigned to cluster 2 were strongly depleted in Sr early in their time series (showing evidence of U-shaped patterns), though concentrations of Sr increased rapidly through time in cluster 2 otoliths, and ultimately exceeded those measured near the outer edges of otolith cores assigned to cluster 1. This pattern of variation in Sr profiles between clusters was principally captured by differences in the nonlinear, hurst, trend, and skewness descriptors (Fig. 1; Appendix). Ba concentrations from otolith cores assigned to cluster 2 peaked in the middle of the time series (i.e., exhibiting a hump-shaped pattern) and were substantially elevated relative to cluster 1, though concentrations of Ba in both clusters fell to similar low levels toward the outer edges of otolith cores (as reflected by differences in the nonlinear, kurtosis, hurst, trend, and skewness descriptors; Fig. 1; Appendix). Finally, relative to otoliths in cluster 2, otoliths from cluster 1 had Pb concentrations that were elevated early in time series and generally more variable overall. Extracted features that differentiated Pb time series between the two clusters included kurtosis, hurst, trend, seasonality, and TSA-serial correlation (Fig. 1; Appendix).

All elements were also useful in discriminating between otoliths assigned to the two putative larval dispersal history clusters (Fig. 2; Appendix). Relative to cluster 2, otoliths assigned to cluster 1 were generally enriched in Li and Pb, but depleted in B, S, Cu, Zn across much of their pelagic larval period of development. Concentrations of Mg and P in otoliths assigned to cluster 2 exhibited an enrichment peak during the latter half of the larval period, while Sr and Ba concentrations became depleted relative to cluster 1 at a similar time in the second half of the pelagic larval stage. Mn concentrations for both clusters peaked toward the end of the pelagic larval stage (left shifting of the cluster 2 peak is an artifact of standardizing length scales). In general the time series differences between the two clusters were driven primarily by higher serial correlation, hurst, lyapunov, and trend values in cluster 2, and higher frequency and seasonality values in cluster 1 (Fig. 2; Appendix).

Is larval quality explained by source and/or pelagic larval dispersal history?

Larval quality (as estimated by PRIN 1) varied as a function of pelagic larval dispersal history (two-way ANOVA, $F_{1,278} = 10.38$, $P = 0.0014$) but not source

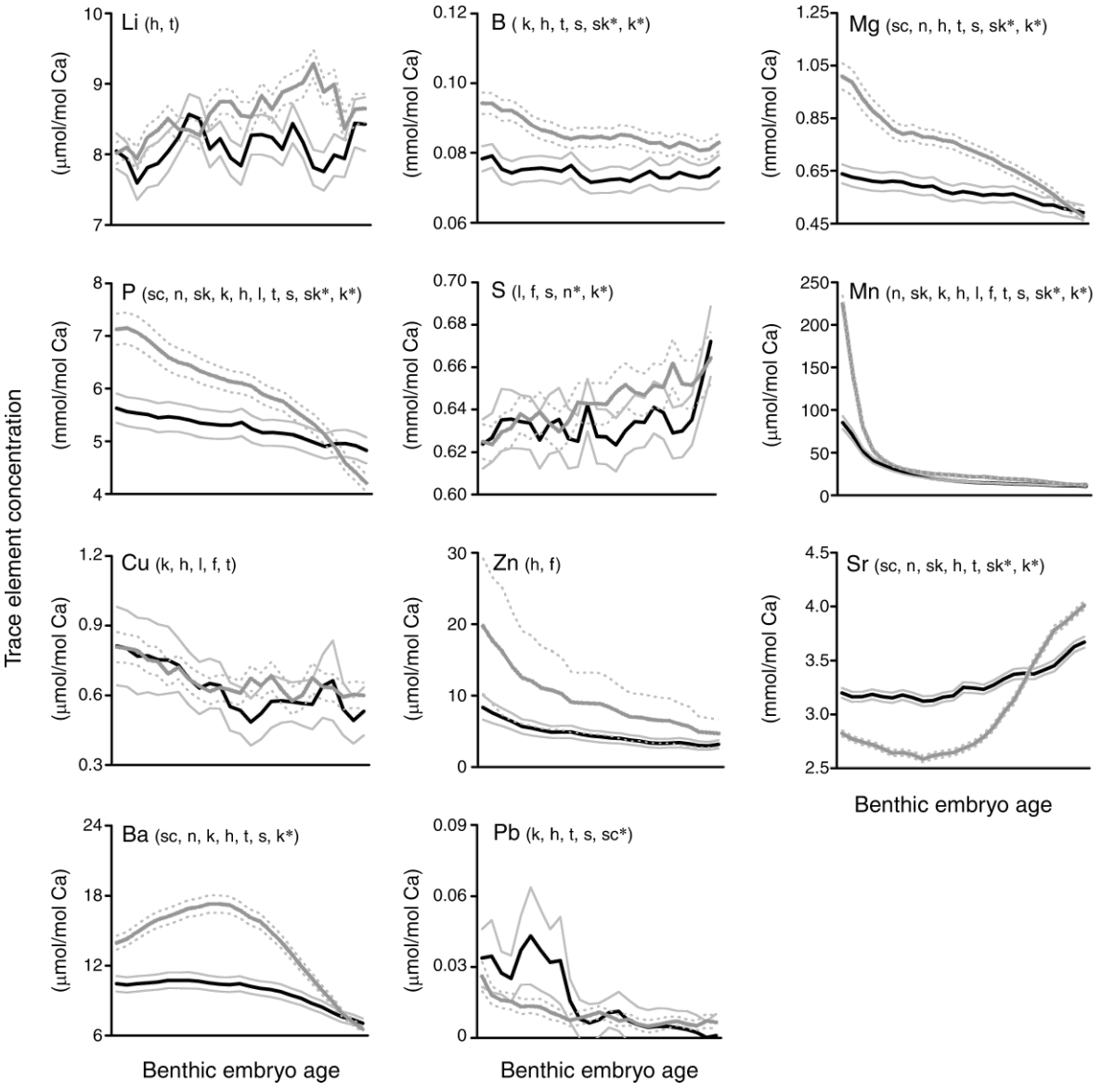

FIG. 1. Microchemical signatures associated with two separate putative "source populations" for recently settled common triplefins (*Forsterygion lapillum*). Given are mean concentrations (bold lines) of 11 elemental ratios through time (the *x*-axis represents a percentage distance from start to end of the age of the sample), with ±SE (fine lines), measured through otolith cores using laser ablation-inductively coupled plasma-mass spectrometer (LA-ICP-MS). Two discrete source populations were discriminated with a cluster analysis of the "extracted features" (sensu Wang et al. 2006) of these time series (bold black lines represent 80 fish with similar natal source signatures that were assigned to cluster 1; bold gray lines represent 202 fish with similar natal source signatures that were assigned to cluster 2). A listing of extracted features that differed ($P < 0.05$) between the two clusters is given after each element symbol: sc, serial correlation function; n, nonlinear function; sk, skewness function; k, kurtosis function; h, hurst function; l, lyapunov function; f, frequency function; t, trend function; s, seasonal function. Terms sc*, n*, sk*, and k* have been trend and seasonally adjusted (TSA). Supporting statistics are given in the Appendix: Table A1. Mean time series were calculated after standardizing all samples to a common length scale and are given here to illustrate the characteristic microchemistry of each cluster.

population identity ($F_{1, 278} = 0.13$, $P = 0.72$) or an interaction between source and dispersal history ($F_{1, 278} = 0.30$, $P = 0.58$). Fish assigned to dispersal history cluster 2 had higher PRIN 1 scores than those assigned to dispersal history cluster 1 regardless of source population cluster assignment (mean [SD] of PRIN 1 scores for source and dispersal cluster combinations as follows: $\text{source}_1 \times \text{dispersal}_1 = 0.38$ [1.65]; $\text{source}_1 \times \text{dispersal}_2 = -0.18$ [1.53]; $\text{source}_2 \times \text{dispersal}_1 = 0.42$ [1.42]; $\text{source}_2 \times \text{dispersal}_2 = -0.37$ [1.68]). Results of two-way MANOVA suggest a similar overall pattern of variation: estimated phenotypic traits varied with larval dispersal history (two-way MANOVA, Wilks' $\lambda = 0.93$, $F_{5, 274} = 4.09$, $P = 0.0014$) but not source population identity (Wilks' $\lambda =$

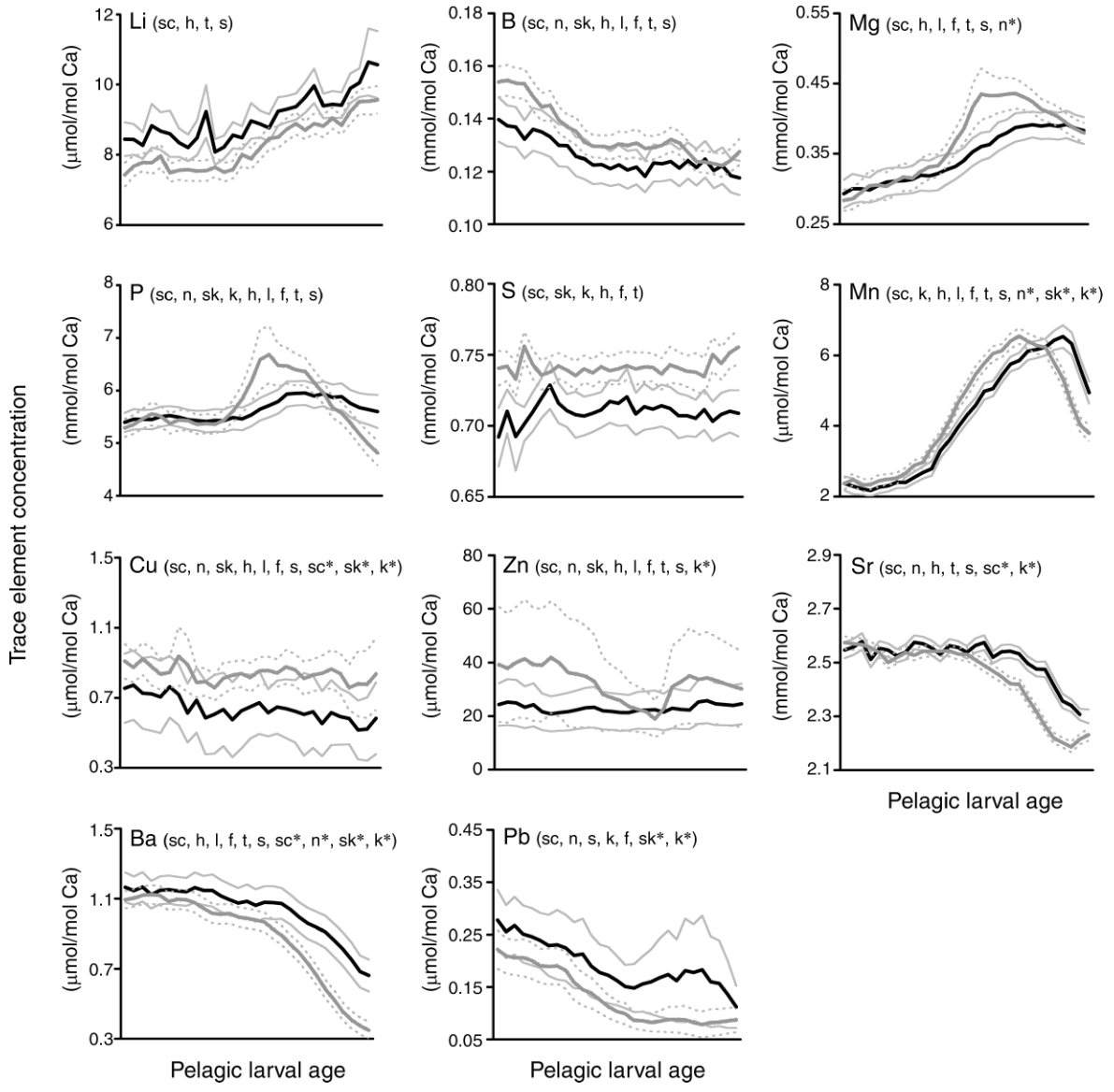

FIG. 2. Microchemical signatures associated with two separate putative "dispersal histories" for recently settled *F. lapillum*. Given are mean concentrations (bold lines) of 11 elemental ratios through time, with ±SE (fine lines), measured across the pelagic larval otolith growth axis using laser ablation-inductively coupled plasma-mass spectrometer (LA-ICP-MS). Two discrete dispersal histories were discriminated with a cluster analysis of the "extracted features" (sensu Wang et al. 2006) of these time series (bold black line with solid SEs represent 124 fish with similar larval dispersal signatures that were assigned to cluster 1; bold gray lines with dashed SEs represent 158 fish with similar larval dispersal signatures that were assigned to cluster 2). A listing of extracted features that differed ($P < 0.05$) between the two clusters is given after each element symbol, as in Fig. 1. Mean time series for each cluster were calculated after standardizing all samples to a common length scale and are given here to illustrate the characteristic microchemistry of each cluster.

0.99, $F_{5,274} = 0.45$, $P = 0.81$) or an interaction term (Wilks' $\lambda = 0.99$, $F_{5,274} = 0.29$, $P = 0.92$).

Because some of the elements (e.g., P, S, Cu) used to inform our classifications of samples to source and dispersal history clusters were potentially subject to isobaric interferences in ICP-MS analyses, and because Zn is known to vary between right and left otoliths for some species (Campana et al. 2000), we repeated all classifications and subsequent analyses excluding the extracted features that related to these elements. Removal of these descriptors did not substantially modify classifications of our samples; results for two-way ANOVA and two-way MANOVA were qualitatively identical to those reported previously.

DISCUSSION

Theoretical explorations of metapopulation dynamics often model connectivity as dispersal events or proba-

bilities (Hanski 2002, Moilanen and Nieminen 2002). In many natural systems, phenotypes of dispersers that are directly linked to fitness may change during dispersal. Examples include seeds of terrestrial plants that are dispersed and simultaneously modified (in some cases, improved in fitness) while passing through the guts of frugivorous animals that act as vectors for long-distance seed dispersal (reviewed in Samuels and Levey 2005). For many organisms, dispersal may reduce physiological condition of individuals, as a consequence of additional energetic expenditure and/or limited feeding opportunities (e.g., Roff 1977, Elkin and Reid 2005). For such systems, patterns of dispersal may differ from patterns of realized demographic connectivity, because fitness (i.e., post-dispersal survival) of migrants may vary as a function of dispersal pathways and/or past histories.

In marine reef systems, dispersal is most typically undertaken by larvae whose phenotypic traits may be shaped by parental effects (Marshall et al. 2003, Green and McCormick 2005, Marshall et al. 2006, McCormick 2006, Gagliano and McCormick 2007) and/or dispersal pathways (Meekan et al. 2003, Phillips, 2004, Sponaugle et al. 2006). If phenotypic traits that determine fitness are a function of source populations (e.g., because maternal provisioning or paternal care is spatially heterogeneous), then some source populations may contribute proportionally more successful dispersers to connectivity pathways (relative to numerical reproductive output alone). These producers of high-quality offspring may also function as more important sources (in a source/sink context) relative to other populations producing lower quality propagules. If, alternatively, features of the pelagic larval environment are important determinants of individual fitness, then certain dispersal pathways may be disproportionately favored over other pathways, relative to predictions based solely on migratory rates. Under either scenario, patterns of connectivity in marine metapopulations may be mediated by larval quality. The degree to which larval quality may be a function of source populations and/or larval dispersal history is largely unknown for marine reef species.

Our results suggest that a composite measure of larval quality for the common triplefin, *Forsterygion lapillum*, is best predicted by features associated with dispersal pathways and not natal populations. We used clustering approaches based upon microchemical signatures recorded within fish otoliths to identify two discrete source clusters and two discrete larval dispersal history clusters. Fish assigned to larval dispersal history cluster 1 had short pelagic larval durations, small size-at-hatch, fast early and late larval growth, and fast instantaneous growth rates. These otolith-based traits have been associated with higher fitness in other studies (Searcy and Sponaugle 2001, Shima and Findlay 2002, Wilson and Meekan 2002, McCormick and Hoey 2004, Raventos and Macpherson 2005, Grorud-Colvert and Sponaugle 2006, Meekan et al. 2006, Sponaugle et al. 2006).

Under conditions of limited larval mixing, source and dispersal histories are likely to be interdependent (i.e., specific larval source clusters may be linked to particular dispersal histories). For *F. lapillum*, with a mean pelagic larval duration of 51.5 d, the comparatively short residence times for parcels of water within the Wellington Harbor (estimated at 10.7 d; Heath [1985]) may have facilitated sufficient decoupling between source and dispersal history clusters (i.e., samples were distributed among source and dispersal clusters in a roughly orthogonal manner), which enabled us to evaluate our hypothesis with two-way ANOVA.

Without additional studies, we can only speculate on the geographic interpretations of source and larval dispersal history clusters that may be represented by microchemical signatures in this study. However, to provide a context for our discussion, we do so here with caution. The two identified source clusters differed in attributes of all 11 measured elemental ratios. Source cluster 2 was generally enriched in Mg, P, Mn, Zn, and Ba, which are elements that have been hypothesized to be linked with elevated otolith organic content (i.e., higher protein : mineral ratios) in other studies (Ruttenberg et al. 2005, Lenaz et al. 2006, Miller et al. 2006). Consequently, we hypothesize that source cluster 2 may be indicative of natal sources (either spatially discrete uniform populations or individual mothers within heterogeneous populations) with greater maternal provisioning of eggs. Source cluster 2 was also depleted in Sr concentrations initially (possibly indicative of lower salinities; Campana 1999) but then increased to higher values by the end of the embryonic period (possibly indicative of warmer temperature; Martin et al. 2004). These observations, coupled with the numerical dominance of source cluster 2 in our sampling of *F. lapillum* recruits (i.e., *F. lapillum* also have larger population sizes inside Wellington Harbor relative to the adjacent open coast, McDermott 2005), suggest to us that source cluster 2 may represent fish spawned from nutrient-replete Harbor-based populations. By contrast, source cluster 1, with characteristically lower signals of maternal provisioning, may reflect fish spawned from populations located along the cooler and (comparatively) nutrient-depleted open coast.

Components of all 11 measured elemental ratios also differed between the two identified larval dispersal history clusters. Larval dispersal history cluster 1 was generally enriched in Li, Ba, and Pb and depleted in B, S, Cu, and Zn (generally consistent with larval development in coastal waters; e.g., Swearer et al. 1999, Hamer et al. 2003). Enriched Mg and depleted Sr in the latter half of the cluster 2 time series may reflect reduced otolith growth (for Mg) and/or water temperature (for Sr) as such effects have been observed in the larval stages of other marine fish (e.g., Martin et al. 2004, Martin and Thorrold 2005). Furthermore, the higher serial correlation, hurst, lyapunov, and trend values associated with cluster 2 indicate greater changes

in elemental concentrations during the larval period, consistent with individuals migrating between coastal and open ocean environments. In contrast, the higher frequency and seasonality values in cluster 1 suggest that elemental concentrations exhibit strong and periodic fluctuations, consistent with the predicted stronger effects of tidal mixing of coastal and oceanic waters within Wellington Harbor. Overall patterns of elemental concentrations recorded for larval dispersal histories suggest to us that larval dispersal history cluster 1 may reflect fish that spent the majority of their larval life in Harbor waters, while fish assigned to larval dispersal history cluster 2 may have experienced predominately open ocean conditions during larval development.

If we are correct in our geographic interpretations of identified clusters, then we can further infer for our system that *F. lapillum* larvae that developed predominately within Wellington Harbor are of higher quality regardless of whether they were spawned from populations located in either Wellington Harbor or the Wellington South Coast. Consequently, dispersal history (i.e., local retention or early entrainment of larvae within harbor waters) largely dictates fitness of dispersers and may mediate patterns of connectivity (i.e., propagule exchange between these two regions). To the extent that retention of locally produced larvae may be more common than entrainment of larvae produced from outside the Wellington Harbor system, then populations of *F. lapillum* within the harbor may be largely self-recruiting (sensu Swearer et al. 2002), and may also represent an important source of recruits for populations along the adjacent outer coast. However, patterns of connectivity between the open coast and harbor populations may depend upon patterns of larval transport relative to larval ontogeny. For example, if larvae from open coast populations are entrained within Wellington Harbor early in larval development, and ultimately settle within the harbor in good physiological condition (and are thus more likely to survive), then connectivity between these two regions may be relatively high. Alternatively, given an identical hydrographic regime, if the timing of reproduction is such that larvae from open coast populations are entrained late in larval development and ultimately settle within the harbor in relatively poor condition (and likely die), then connectivity between these two regions may be comparatively low. Similar scenarios can be envisioned that might influence the relative importance of Wellington Harbor-based populations as sources (in a source/sink context) of recruits for populations along the Wellington South Coast. These interpretations are consistent with an extension of the "match–mismatch hypothesis" of Cushing (1975), whereby large recruitment events are predicted to follow a good "match" between reproduction and seasonal food availability for developing larvae, and recruitment failures arise from mismatches in reproductive timing and food availability. Here, our data suggest that match–mismatch dynamics may be important in shaping demographic connectivity in marine metapopulations.

Our results complement recent findings of other studies, which highlight both the importance (Swearer et al. 1999, Cowen et al. 2000) and complexity (Cowen et al. 2006) of patterns of dispersal and connectivity in marine metapopulations. Earlier conceptual models that marine larval pools are well mixed and composed of passive dispersers are no longer supported by the emerging evidence. Instead, a growing body of evidence suggests that connectivity in marine metapopulations may represent a composite of occasional longer distance dispersal and substantial natal retention (Jones et al. 1999, Swearer et al. 1999, Swearer et al. 2002, Jones et al. 2005, Almany et al. 2007), with the latter facilitated by both physical (e.g., Gaylord and Gaines 2000, Sponaugle et al. 2002) and behavioral mechanisms (Thorrold et al. 2001, Kingsford et al. 2002). In our system we primarily focused upon dispersal and connectivity between two regions (a harbor and an adjacent open coast), and we expect that source/sink frameworks (e.g., Crowder et al. 2000) may be a useful tool in which to quantify and further explore the importance of connectivity mediated by larval quality. Our observations that larvae developing within semi-enclosed embayments appear to be of higher quality are consistent with the findings of Gaines and Bertness (1992) and suggest that coastal geomorphology may be an important source of environmentally induced heterogeneity in larval quality for coastal reef organisms.

Models are increasingly employed to estimate patterns of dispersal and connectivity in marine metapopulations (e.g., Cowen et al. 2000, 2006, Siegel et al. 2003). Such models may be useful in fisheries management (e.g., to identify spatial arrangements of stock-recruitment relationships; e.g., Cowen et al. 2006) and conservation (e.g., to inform decisions about siting of marine reserves; e.g., Botsford et al. 2001). Recent appreciation that larval behavior can substantially modify patterns of larval transport and thus connectivity (because larvae can readily migrate vertically between stratified flows and/or can swim against prevailing currents; reviewed in Montgomery et al. 2001, Kingsford et al. 2002, Leis 2006) has resulted in calls for incorporation of "larval behavior" parameters into particle tracking models (Kingsford et al. 2002). Our results indicate heterogeneity in larval quality driven by features of pelagic environments (i.e., "matrix effects") may similarly modify predicted patterns of larval transport and connectivity, particularly if variation in larval quality has a direct impact on larval behavior (e.g., Sclafani et al. 1993) or swimming ability (e.g., Grorud-Colvert and Sponaugle 2006). The role of matrix effects on patterns of connectivity is receiving increasing theoretical and empirical attention across many non-marine systems (e.g., Ricketts 2001, Vandermeer and Caravajal 2001, Hanski et al. 2004, Haynes and Cronin 2004, Murphy and Lovett-Doust 2004, Revilla et al. 2004). We suggest

that matrix effects may play a particularly important role in marine metapopulations and should therefore be (1) a focus of future empirical research and (2) included as a central component of future models of marine larval dispersal and metapopulation connectivity.

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Literature Cited

Almany, G. R., M. L. Berumen, S. R. Thorrold, S. Planes, and G. P. Jones. 2007. Local replenishment of coral reef fish populations in a marine reserve. Science 316:742–744.

Ammann, A. J. 2004. SMURFs: standard monitoring units for the recruitment of temperate reef fishes. Journal of Experimental Marine Biology and Ecology 299:135–154.

Baker, M. B., and S. Rao. 2004. Incremental costs and benefits shape natal dispersal: theory and example with *Hemilepistus reaumuri*. Ecology 85:1039–1051.

Barbee, N. C., and S. E. Swearer. 2007. Characterizing natal source population signatures in the diadromous fish *Galaxias maculatus*, using embryonic otolith chemistry. Marine Ecology Progress Series 343:273–282.

Bayne, B. L., P. A. Gabbott, and J. Widdows. 1975. Some effects of stress in the adult on the eggs and larvae of *Mytilus edulis* L. Journal of the Marine Biological Association of the UK 55:675–689.

Botsford, L. W., A. Hastings, and S. D. Gaines. 2001. Dependence of sustainability on the configuration of marine reserves and larval dispersal. Ecology Letters 4:144–150.

Bowman, M. J., A. C. Kibblewhite, R. A. Murtagh, S. M. Chiswell, and B. G. Sanderson. 1983. Circulation and mixing in greater Cook Strait, New Zealand. Oceanologica Acta 6: 383–391.

Caley, M. J., M. H. Carr, M. A. Hixon, T. P. Hughes, G. P. Jones, and B. A. Menge. 1996. Recruitment and the local dynamics of open marine populations. Annual Review of Ecology and Systematics 27:477–500.

Campana, S. E. 1999. Chemistry and composition of fish otoliths: pathways, mechanisms and applications. Marine Ecology Progress Series 188:263–297.

Campana, S. E., G. A. Chouinard, J. M. Hanson, A. Fréchet, and J. Brattey. 2000. Otolith elemental fingerprints as biological tracers of fish stocks. Fisheries Research 46:343–357.

Campana, S. E., and C. M. Jones. 1992. Analysis of otolith microstructure data. Otolith microstructure examination and analysis. Canadian Special Publication of Fisheries and Aquatic Science 117:73–100.

Campana, S. E., and S. R. Thorrold. 2001. Otoliths, increments, and elements: keys to a comprehensive understanding of fish populations? Canadian Journal of Fisheries and Aquatic Sciences 58:30–38.

Clements, K. 2003. Triplefins. Pages 160–167 *in* N. Andrew and M. Francis, editors. The living reef: the ecology of New Zealand's rocky reefs. Craig Potton Publishing, Nelson, New Zealand.

Cowen, R., K. M. M. Lwiza, S. Sponaugle, C. B. Paris, and D. B. Olson. 2000. Connectivity of marine populations: open or closed? Science 287:857–859.

Cowen, R. K., C. B. Paris, and A. Srinivasan. 2006. Scaling of connectivity in marine populations. Science 311:522–527.

Crowder, L. B., S. J. Lyman, W. F. Figueira, and J. Priddy. 2000. Source–sink population dynamics and the problem of siting marine reserves. Bulletin of Marine Science 66:799–820.

Cushing, D. H. 1975. Marine ecology and fisheries. Cambridge University Press, Cambridge, UK.

Eggins, S. M., L. P. J. Kinsley, and J. M. G. Shelley. 1998. Deposition and element fractionation processes during atmospheric pressure laser sampling for analysis by ICP-MS. Applied Surface Science 129:278–286.

Elkin, C. M., and M. L. Reid. 2005. Low energy reserves and energy allocation decisions affect reproduction by Mountain Pine Beetles, *Dendroctonus ponderosae*. Functional Ecology 19:102–109.

Feary, D. 2001. Trophic morphology, diet and habitat use of New Zealand triplefins (Family Tripterygiidae). Thesis. University of Auckland, Auckland, New Zealand.

Feary, D. A., and K. D. Clements. 2006. Habitat use by triplefin species (Tripterygiidae) on rocky reefs in New Zealand. Journal of Fish Biology 69:1031–1046.

Francis, M. 2001. Coastal fishes of New Zealand. Reed Publishing, Auckland, New Zealand.

Francis, R. I. C. C. 1990. Back-calculation of fish length: a critical review. Journal of Fish Biology 36:883–902.

Gagliano, M., and M. I. McCormick. 2007. Maternal condition influences phenotypic selection on offspring. Journal of Animal Ecology 76:174–182.

Gaines, S. D., and M. D. Bertness. 1992. Dispersal of juveniles and variable recruitment in sessile marine species. Nature 360:579–580.

Gallager, S. M., and R. Mann. 1986. Growth and survival of larvae of *Mercenaria mercenaria* (L.) and *Crassostrea virginica* (Gmelin) relative to broodstock conditioning and lipid content of eggs. Aquaculture 56:105–121.

Gardner, J. P. A. 2000. Where are the mussels on Cook Strait (New Zealand) shores? Low seston quality as a possible factor limiting multi-species distributions. Marine Ecology Progress Series 194:123–132.

Gaylord, B., and S. D. Gaines. 2000. Temperature or transport? Range limits in marine species mediated solely by flow. American Naturalist 155:769–789.

Green, B. S., and M. I. McCormick. 2005. Maternal and paternal effects determine size, growth and performance in larvae of a tropical reef fish. Marine Ecology Progress Series 289:263–272.

Grorud-Colvert, K., and S. Sponaugle. 2006. Influence of condition on behavior and survival potential of a newly settled coral reef fish, the bluehead wrasse *Thalassoma bifasciatum*. Marine Ecology Progress Series 327:279–288.

Hamer, P. A., G. P. Jenkins, and B. M. Gillanders. 2003. Otolith chemistry of juvenile snapper *Pagrus auratus* in Victorian waters: natural chemical tags and their temporal variation. Marine Ecology Progress Series 263:261–273.

Hanski, I. 2002. Metapopulation ecology. Oxford University Press, New York, New York, USA.

Hanski, I., C. Erälahti, M. Kankare, O. Ovaskainen, and H. Sirén. 2004. Variation in migration propensity among individuals maintained by landscape structure. Ecology Letters 7:958–966.

Hanski, I., and O. E. Gaggiotti. 2004. Ecology, genetics and evolution of metapopulations. Elsevier Academic Press, San Diego, California, USA.

Hare, J. A., and R. K. Cowen. 1997. Size, growth, development, and survival of the planktonic larvae of *Pomatomus saltatrix* (Pisces: Pomatomidae). Ecology 78:2415–2431.

Harris, T. F. W. 1990. Greater Cook Strait. DSIR (Department of Scientific and Industrial Research). Marine and Freshwater, Wellington, New Zealand.

Haynes, K. J., and J. T. Cronin. 2004. Confounding of patch quality and matrix effects in herbivore movement studies. Landscape Ecology 19:119–124.

Heath, R. A. 1985. A review of the physical oceanography of the seas around New Zealand—1982. New Zealand Journal of Marine and Freshwater Research 19:79–124.

Hickford, M. J. H., and D. R. Schiel. 2003. Comparative dispersal of larvae from demersal versus pelagic spawning fishes. Marine Ecology Progress Series 252:255–271.

Ims, R. A., and N. G. Yoccoz. 1997. Studying transfer processes in metapopulations: emigration, migration, and colonization. Pages 247–265 *in* I. A. Hanski and M. E. Gilpin, editors. Metapopulation biology: ecology, genetics, and evolution. Academic Press, London, UK.

Jones, G. P., M. J. Milicich, M. J. Emslie, and C. Lunow. 1999. Self-recruitment in a coral reef fish population. Nature 402: 802–804.

Jones, G. P., S. Planes, and S. R. Thorrold. 2005. Coral reef fish larvae settle close to home. Current Biology 15:1314–1318.

Kingsford, M. J., and J. H. Choat. 1989. Horizontal distribution patterns of presettlement reef fish: are they influenced by the proximity of reefs? Marine Biology 101:285–297.

Kingsford, M. J., J. M. Leis, A. Shanks, K. C. Lindeman, S. G. Morgan, and J. Pineda. 2002. Sensory environments, larval abilities and local self-recruitment. Bulletin of Marine Science 70(Supplement):309–340.

Kohn, Y. 2007. Pelagic larval duration in New Zealand triplefin fishes. Thesis. University of Auckland, Auckland, New Zealand.

Kritzer, J. P., and P. F. Sale. 2004. Metapopulation ecology in the sea: from Levins' model to marine ecology and fisheries science. Fish and Fisheries 5:131–140.

Legendre, P., and L. Legendre. 2006. Numerical ecology. Elsevier, Oxford, UK.

Leis, J. M. 2006. Are larvae of demersal fishes plankton or nekton? Advances in Marine Biology 51:57–141.

Lenaz, D., M. Miletic, E. Pizzul, S. Vanzo, and G. Adami. 2006. Mineralogy and geochemistry of otoliths in freshwater fish from Northern Italy. European Journal of Mineralogy 18:143–148.

Marshall, D. J., T. F. Bolton, and M. J. Keough. 2003. Offspring size affects the post-metamorphic performance of a colonial marine invertebrate. Ecology 84:3131–3137.

Marshall, D. J., C. N. Cook, and R. B. Emlet. 2006. Offspring size effects mediate competitive interactions in a colonial marine invertebrate. Ecology 87:214–225.

Martin, G. B., and S. R. Thorrold. 2005. Temperature and salinity effects on magnesium, manganese, and barium incorporation in otoliths of larval and juvenile spot *Leiostomus xanthurus*. Marine Ecology Progress Series 293: 223–232.

Martin, G. B., S. R. Thorrold, and C. M. Jones. 2004. Temperature and salinity effects on strontium incorporation in otoliths of larval spot (*Leiostomus xanthurus*). Canadian Journal of Fisheries and Aquatic Sciences 61:34–42.

Matter, S. F. 2006. Changes in landscape structure decrease mortality during migration. Oecologia 150:8–16.

Maxwell, B. E. 1956. Hydrobiological observations for Wellington Harbour. Transactions of the Royal Society of New Zealand 88:493–503.

McCormick, M. I. 2006. Mothers matter: crowding leads to stressed mothers and smaller offspring in marine fish. Ecology 87:1104–1109.

McCormick, M. I., and A. S. Hoey. 2004. Larval growth history determines juvenile growth and survival in a tropical marine fish. Oikos 106:225–242.

McDermott, C. J. 2005. Understanding patterns of habitat use in reef fish: implications of ontogenetic shifts in habitat-use for population demography. Thesis. University of Wellington, Victoria, New Zealand.

McDermott, C. J., and J. S. Shima. 2006. Ontogenetic shifts in microhabitat preference of the temperate reef fish *Forsterygion lapillum*: implications for population limitation. Marine Ecology Progress Series 320:259–266.

Meekan, M. G., J. H. Carleton, A. D. McKinnon, K. Flynn, and M. Furnas. 2003. What determines the growth of tropical reef fish larvae in the plankton: food or temperature? Marine Ecology Progress Series 256:193–204.

Meekan, M. G., L. Vigliola, A. Hansen, P. J. Doherty, A. Halford, and J. H. Carleton. 2006. Bigger is better: size-selective mortality throughout the life history of a fast-growing clupeid, *Spratelloides gracilis*. Marine Ecology Progress Series 317:237–244.

Miller, M. B., A. M. Clough, J. N. Batson, and R. W. Vachet. 2006. Transition metal binding to cod otolith proteins. Journal of Experimental Marine Biology and Ecology 329: 135–143.

Milligan, G. W., and M. C. Cooper. 1985. An examination of procedures for determining the number of clusters in a data set. Psychometrika 50:159–179.

Moilanen, A., and M. Nieminen. 2002. Simple connectivity measures in spatial ecology. Ecology 83:1131–1145.

Montgomery, J. C., N. Tolimieri, and O. Haine. 2001. Active habitat selection by pre-settlement reef fishes. Fish and Fisheries 2:261–277.

Murphy, H. T., and J. Lovett-Doust. 2004. Context and connectivity in plant metapopulations and landscape mosaics: does the matrix matter? Oikos 105:3–14.

Pannella, G. 1971. Fish otoliths—daily growth layers and periodical patterns. Science 173:1124–1127.

Pasten, G. P., S. Katayama, and M. Omori. 2003. Timing of parturition, planktonic duration, and settlement patterns of the black rockfish, *Sebastes inermis*. Environmental Biology of Fishes 68:229–239.

Patterson, H. M., and S. E. Swearer. 2007. Long-distance dispersal and local retention of larvae as mechanisms of recruitment in an island population of a coral reef fish. Austral Ecology 32:122–130.

Pechenik, J. A., D. Wendt, and J. R. Jarrett. 1998. Metamorphosis is not a new beginning. BioScience 48:901–910.

Phillips, N. E. 2002. Effects of nutrition-mediated larval condition on juvenile performance in a marine mussel. Ecology 83:2562–2574.

Phillips, N. E. 2004. Variable timing of larval food has consequences for early juvenile performance in a marine mussel. Ecology 85:2341–2346.

Pilotto, P. J., J. R. Goff, and D. C. Weatherburn. 1998. A contemporary contamination record of stormdrain and harbor sediments, Wellington, New Zealand. Environmental Geology 36:159–166.

Popper, A. N., and S. Coombs. 1980. Auditory mechanisms in teleost fishes. American Scientist 68:429–440.

Raventos, N., and E. Macpherson. 2005. Effect of pelagic larval growth and size-at-hatching on post-settlement survivorship in two temperate labrid fish of the genus *Symphodus*. Marine Ecology Progress Series 285:205–211.

Revilla, E., T. Wiegand, F. Palomares, P. Ferreas, and M. Delibes. 2004. Effects of matrix heterogeneity on animal dispersal: from individual behavior to metapopulation-level parameters. American Naturalist 164:131–153.

Ricketts, T. H. 2001. The matrix matters: effective isolation in fragmented landscapes. American Naturalist 158:87–99.

Riley, B. B., and S. J. Moorman. 2000. Development of utricular otoliths, but not saccular otoliths, is necessary for vestibular function and survival in zebrafish. Journal of Neurobiology 43:329–337.

Roff, D. 1977. Dispersal in dipterans—its costs and consequences. Journal of Animal Ecology 46:443–456.
Roughgarden, J., Y. Iwasa, and C. Baxter. 1985. Demographic theory for an open marine population with space-limited recruitment. Ecology 66:54–67.
Ruttenberg, B. I., S. L. Hamilton, M. J. H. Hickford, G. Paradis, M. Sheehy, J. D. Standish, O. Ben-Tzvi, and R. R. Warner. 2005. Elevated levels of trace elements in cores of otoliths and their potential use as natural tags. Marine Ecology Progress Series 297:273–281.
Samuels, I. A., and D. J. Levey. 2005. Effects of gut passage on seed germination: do experiments answer the questions they ask? Functional Ecology 19:365–368.
SAS Institute. 1999. SAS/STAT User's Guide, Version 8. SAS Institute, Cary, North Carolina, USA.
Saunders, D. A., R. J. Hobbs, and C. R. Margules. 1991. Biological consequences of ecosystem fragmentation: a review. Conservation Biology 51:18–32.
Sclafani, M., C. T. Taggart, and K. R. Thompson. 1993. Condition, buoyancy and the distribution of larval fish: implications for vertical migration and retention. Journal of Plankton Research 15:413–435.
Searcy, S. P., and S. Sponaugle. 2001. Selective mortality during the larval–juvenile transition in two coral reef fishes. Ecology 82:2452–2470.
Secor, D. H., J. M. Dean, S. E. Campana, and A. B. Miller. 1995. Recent developments in otolith research. University of South Carolina Press, Columbia, South Carolina, USA.
Shima, J. S. 1999. Variability in relative importance of determinants of reef fish recruitment. Ecology Letters 2: 304–310.
Shima, J. S., and A. M. Findlay. 2002. Pelagic larval growth rate impacts benthic settlement and survival of a temperate reef fish. Marine Ecology Progress Series 235:303–309.
Siegel, D. A., B. P. Kinlan, B. Gaylord, and S. D. Gaines. 2003. Lagrangian descriptions of marine larval dispersion. Marine Ecology Progress Series 260:83–96.
Sponaugle, S., R. K. Cowen, A. Shanks, S. G. Morgan, J. M. Leis, J. S. Pineda, G. W. Boehlert, M. J. Kingsford, K. C. Lindeman, C. Grimes, and J. L. Munro. 2002. Predicting self-recruitment in marine populations: biophysical correlates and mechanisms. Bulletin of Marine Science 70(Supplement): 341–375.
Sponaugle, S., K. Grorud-Colvert, and D. Pinkard. 2006. Temperature-mediated variation in early life history traits and recruitment success of the coral reef fish *Thalassoma bifasciatum* in the Florida Keys. Marine Ecology Progress Series 308:1–15.
Stamps, J. A. 2006. The silver spoon effect and habitat selection by natal dispersers. Ecology Letters 9:1179–1185.
Stamps, J. A., V. V. Krishnan, and M. L. Reid. 2005. Search costs and habitat selection by dispersers. Ecology 86:510–518.
Stoffers, P., G. P. Glasby, C. J. Wilson, K. R. Davis, and P. Walter. 1986. Heavy metal pollution in Wellington Harbour. New Zealand Journal of Marine and Freshwater Research 20:495–512.
Swearer, S., J. Caselle, D. W. Lea, and R. R. Warner. 1999. Larval retention and recruitment in an island population of a coral reef fish. Nature 402:799–802.
Swearer, S. E., J. S. Shima, M. E. Helberg, S. R. Thorrold, G. P. Jones, D. R. Robertson, S. G. Morgan, K. A. Selkoe, G. M. Ruiz, and R. R. Warner. 2002. Evidence of self-recruitment in demersal marine populations. Bulletin of Marine Science 70:251–271.
Takahashi, M., Y. Watanabe, T. Kinoshita, and C. Watanabe. 2001. Growth of larval and early juvenile Japanese anchovy, *Engraulis japonicus*, in the Kuroshio-Oyashio transition region. Fisheries Oceanography 10:235–247.
Thompson, S. M. 1979. Ecological and behavioural factors influencing the distribution and abundance patterns of tripterygiid fishes with particular reference to *Tripterygion varium*. Thesis. University of Auckland, Auckland, New Zealand.
Thorrold, S. R., C. Latkoczy, P. K. Swart, and C. M. Jones. 2001. Natal homing in a marine fish metapopulation. Science 291:297–299.
Vandermeer, J., and R. Caravajal. 2001. Metapopulation dynamics and the quality of the matrix. American Naturalist 158:211–220.
Wang, X., K. Smith, and R. Hyndman. 2006. Characteristic-based clustering for time series data. Data Mining and Knowledge Discovery 13:335–364.
Wellenreuther, M., P. T. Barrett, and K. D. Clements. 2007. Ecological diversification in habitat use by subtidal triplefin fishes (Tripterygiidae). Marine Ecology Progress Series 330: 235–246.
Wilson, D. T., and M. G. Meekan. 2002. Growth-related advantages for survival to the point of replenishment in the coral reef fish *Stegastes partitus* (Pomacentridae). Marine Ecology Progress Series 231:247–260.

APPENDIX

Variation in 13 extracted features of time series for each of 11 trace elemental ratios recorded in the otoliths of *Forsterygion lapillum* (*Ecological Archives* E090-081-A1).