Trait-based assembly and phylogenetic structure in northeast Pacific rockfish assemblages

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Abstract. If natural communities are assembled according to deterministic rules, coexisting species will represent a nonrandom subset of the potential species pool. We tested for signatures of assembly rules in the distribution of species' traits in Pacific rockfish (*Sebastes* spp.) assemblages. We used morphology, dietary niche (estimated with stable nitrogen isotopes), and distribution data to identify traits that relate to local-scale resource use (the α-niche) and to environmental gradients (the β-niche). We showed that gill raker morphology was related to trophic position (an α-niche axis), while relative eye size was associated with depth habitat (a β-niche axis). We therefore hypothesized that, within assemblages of coexisting rockfish species, the gill raker trait would be overdispersed (evenly spaced) due to limiting similarity, while relative eye size would be clustered due to environmental filtering. We examined the evolutionary relatedness of coexisting species to ask whether phylogenetic community structure and trait distributions gave similar indications about the roles of assembly processes. We tested the trait distributions and phylogenetic structure of 30 published rockfish assemblages against a null model of random community assembly. As predicted, the gill raker trait tended to be more evenly spaced than expected by chance, as did overall body size, while relative eye size was more clustered than expected. Phylogenetic community structure appeared to reflect historical dispersal and speciation and did not provide consistent support for assembly rules. Our results indicate that rockfish community assembly is nonrandom with regard to species' traits and show how distinguishing traits related to the α- and β-niches and incorporating functional morphology can provide for powerful tests of assembly rules.

Key words: α-niche; assembly rules; β-niche; community assembly; environmental filter; gill rakers; limiting similarity; Pacific rockfish assemblages; phylogenetic community structure; Sebastes; *stable isotopes.*

Introduction

Ecologists have long sought to understand how particular combinations of species come together to form communities. If deterministic assembly rules influence community membership though trait-mediated species–species or species–environment interactions, we should see their signatures in the distribution of phenotypes of coexisting species (Ricklefs and Travis 1980, Weiher et al. 1998, Stubbs and Wilson 2004, Cornwell et al. 2006). Two major categories of assembly rules, limiting similarity and environmental filtering, have contrasting effects on the types of species that coexist. Environmental filtering selects species that share certain adaptive traits that allow them to persist in a particular environment. These species may be ecologically similar either because they are close relatives with shared ancestral characteristics, or because they independently evolved similar traits. While environmental filtering will therefore increase the ecological similarity of coexisting species, the principle of limiting similarity

holds that species will be unable to stably coexist if their resource requirements overlap too greatly (MacArthur and Levins 1967). Resource competition has long been thought to influence species co-occurrence and trait evolution (Elton 1946, Hutchinson 1959, Diamond 1975, Schluter 2000). Greater dissimilarity between coexisting species (i.e., even spacing of traits, or "overdispersion") than expected by chance provides observational evidence for competition's role in community assembly (Simberloff and Boecklen 1981, Weiher et al. 1998, Stubbs and Wilson 2004). Trait overdispersion may arise from ecological character displacement, species assortment, or a combination of these mechanisms (Schluter 2000). While the importance of resource competition in community ecology has been at times controversial (e.g., Strong et al. 1979, Hubbell 2001), widespread evidence for trait overdispersion suggests that competition can play an important role in the assembly of communities (Schluter 2000, Dayan and Simberloff 2005).

Environmental filtering and limiting similarity may influence community structure by acting on different types of traits. Recent work (Ackerly et al. 2006, Silvertown et al. 2006, Ackerly and Cornwell 2007) has emphasized a useful distinction between the α- and

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β-niche (first defined by Pickett and Bazzaz [1978] by analogy to α- and β-diversity [Whittaker 1975]). The α-niche describes a species' resource use within local communities, the scale at which competition and other species interactions operate. In contrast, the β-niche describes the types of habitats a species can inhabit, especially its position along dominant environmental gradients (Ackerly and Cornwell 2007). Thus, traits associated with the β-niche may be subject to environmental filtering. Traits reflecting the α- and β-niches may therefore be affected by different types of assembly rules which interact to determine local community structure. If different traits are associated with the α- and β-niche, we predict that the α-niche traits will show a signature of limiting similarity and that the β-niche traits will reflect environmental filtering.

A challenge in trait-based tests of limiting similarity and environmental filtering is identifying and measuring the most important traits on which assembly processes act. An alternative approach that has gained traction in recent years is the use of species' evolutionary relatedness as a proxy for their ecological similarity, on the grounds that most traits show some signal of phylogeny (Blomberg et al. 2003). Early efforts used taxonomic ranks (species/genus ratios) to test whether competition prevented congeners from coexisting locally (Elton 1946). Recently, the greater availability of species-level phylogenies has allowed more powerful analyses using improved measures of relatedness (Webb 2000, Webb et al. 2002, Kraft et al. 2007). When species' traits are conserved (i.e., show a strong signal of phylogeny), the basic predictions of community phylogenetics are that limiting similarity will prevent close relatives from coexisting, while environmental filtering will cause close relatives to co-occur due to their shared traits (Webb 2000, Cavender-Bares et al. 2004). Tests for phylogenetic evenness and clustering are less straightforward when traits are convergent (have low phylogenetic signal); in these cases phylogenetic tests tend to have low power to detect assembly rules, and nonrandom patterns can be more difficult to interpret (Cavender-Bares et al. 2004, Kraft et al. 2007). Phylogenetic community structure also varies with the taxonomic scale of inquiry; Cavender-Bares et al. (2006) found that tree communities exhibited phylogenetic evenness at the genus level but were phylogenetically clustered at higher taxonomic scales. Due to these limitations of phylogenetic methods, it is important to consider both traits and phylogeny when testing for assembly rules.

We used trait-based and phylogenetic analyses to test for assembly rules in the marine rockfish genus *Sebastes*. Rockfish are notable for their diversity in species (~110, including ~70 in the northeast Pacific), color, life history, morphology, and diet (Love et al. 2002). Relationships within the genus are well resolved in a recent molecular phylogenetic appraisal of 99 species, including all common northeast Pacific species (Hyde and Vetter 2007). This ecological and morphological

diversity and the availability of a high-quality phylogeny make *Sebastes* a promising system for the study of adaptive radiation and community assembly.

Sebastes species are differentiated along both α- and β-niche axes. Closely related species coexisting in sympatry often differ in diet and microhabitat. Competition for space has been experimentally demonstrated between sister species *S. carnatus* and *S. chrysomelas* (Larson 1980), and competition for food may be responsible for diet partitioning among other close relatives (Hallacher and Roberts 1985, Murie 1995, York 2005). It is not always straightforward to quantify axes of dietary niche variation, but naturally occurring stable nitrogen isotopes allow the measurement of continuous α-niche axes such as trophic position. If traits related to trophic position and other α-niche axes mediate resource competition between rockfish species, they may show signatures of limiting similarity. Rockfish also vary along environmental gradients (β-niche axes) such as latitude and depth (Love et al. 2002). We identified morphological traits related mainly to the α-niche (gill raker length and number) and the β-niche (relative eye size). We then hypothesized that gill rakers would be evenly spaced in communities due to competition, while eye size would be clustered due to environmental filtering. We tested for these patterns by comparing trait distributions in observed communities to a null model. We also examined phylogenetic community structure to test whether patterns in species' ecological trait similarity were reflected in their evolutionary relatedness.

METHODS

Morphological and ecological data

We measured the morphology of 332 adult individuals from 61 *Sebastes* species, obtained from recreational fishing vessels and collections belonging to research institutions and museums (Appendix A). Sample sizes ranged from 1 to 39 (median = 5) individuals per species. This data set includes all common species in the northeast Pacific with the exceptions of four species endemic to the Gulf of California (*S. cortezi, S. peduncularis, S. exsul,* and *S. spinorbis*) and two recently described cryptic species (*S. crocotulus* [Hyde et al. 2008] and *S. saxicola* Type N [Hyde and Vetter 2007]). Two additional pairs of cryptic species in our morphological data were not distinguished when our community data were collected. We therefore combined measurements of the recently described species (*S. variabilis* and *S. melanostictus*) with their sister species (*S. ciliatus* and *S. aleutianus*, respectively; Orr and Blackburn 2004, Orr and Hawkins 2008), reducing our morphological data to 59 species. The remainder of the northeast Pacific species missing from our data set (*S. gilli, S. lentiginosus, S. moseri, S. notius,* and *S. rufianus*) have restricted geographic ranges and are absent from all community data used in this study, justifying their exclusion from our analyses. For phylogenetic analyses we used an ultra-

TABLE 1. Summary of principal component analysis used to identify axes of morphological differentiation among rockfish (*Sebastes*) species.

Traits and statistics	Factor loadings		
	PC1	PC2	PC3
Head length	**0.26**	−0.06	0.03
Snout length	**0.25**	−0.06	0.01
Snout–pectoral fin distance	**0.26**	−0.03	0.06
Snout–pelvic fin distance	**0.26**	0.01	−0.02
Interopercular width	**0.25**	−0.12	−0.07
Interorbital width	**0.24**	0.23	−0.29
Eye size (horizontal)	**0.25**	0.09	**0.53**
Eye size (vertical)	**0.25**	0.09	**0.49**
Upper jaw length	**0.25**	−0.12	0.00
Lower jaw length	**0.26**	−0.06	−0.02
Gill arch length (lower)	**0.26**	0.00	0.01
Gill raker number	−0.07	**0.76**	−0.27
Gill raker length (longest)	**0.18**	**0.55**	0.22
Pectoral fin length	**0.26**	−0.01	−0.23
Pectoral fin width	**0.25**	−0.10	−0.35
Pelvic spine length	**0.25**	0.02	−0.09
Pelvic fin length	**0.25**	−0.03	−0.30
Eigenvalue (λ)	14.69	1.51	0.27
Variance explained (%)	86.7	8.9	1.6

Notes: All traits except gill raker number were natural-log-transformed prior to analysis. Boldface indicates characters used to interpret principal component "traits."

metric Bayesian 50% majority-rule consensus tree (Fig. 5 in Hyde and Vetter 2007; see Hyde and Vetter 2007 for details). We pruned the phylogeny to include only the 59 species in our data set. Unless otherwise indicated, statistical and phylogenetic analyses were performed in the R environment (R Development Core Team 2008).

We measured 17 morphological characters with potential relevance to habitat and resource use, including gill raker number and length, jaw length, and eye and fin sizes. We could not obtain reliable measurements of total length and gape width for all species as many specimens were partial carcasses or had distorted mouths, but the exclusion of these traits did not affect the interpretation of the principal component analysis. For bilateral traits we averaged measurements from the left and right sides of the body. The same person (T. Ingram) performed all measurements, and measurement error was low in all traits (coefficient of variation < 0.04, based on repeated measurement of 10 arbitrarily chosen specimens). We reduced this data set to major orthogonal axes of morphological variation using a principal component analysis (PCA) on the correlation matrix of species means, all log-transformed to improve normality except gill raker number. The first three principal components explain >97% of morphological variation among species and are clearly interpretable. PC1 reflects overall body size, loading with all linear measurements and correlating strongly ($r = 0.90$) with species' log-transformed maximum total length (Love et al. 2002). PC2 is strongly associated with gill raker length and number, while PC3 is most strongly associated with eye size, with additional loadings on some fin size measurements (Table 1).

The use of PCA provides a sequence of orthogonal combinations of traits, which is desirable when testing for assembly rules as it prevents the same analyses from being performed on correlated characters. We identified associations between principal component traits and α- and β-niche axes to derive a priori predictions about which traits should be more affected by habitat filtering and limiting similarity. For this study we selected trophic position as an α-niche axis and depth habitat as a β-niche axis. While additional niche axes are likely involved in community assembly, we focused on trophic position and depth because they are highly variable in *Sebastes* (Love et al. 2002) and because they are continuous niche axes that can be easily measured for many species.

We estimated trophic position of species using nitrogen stable isotopes. The $\delta^{15}N$ of a species indicates its vertical position in the food web due to its predictable enrichment of approximately 3.4‰ per trophic level (Post 2002). We collected $\delta^{15}N$ data from 222 freshly caught or frozen fish representing 43 species (1–15 individuals per species) from three locations: the continental shelf off the west coast of Haida Gwaii, British Columbia, Canada (HG); Barkley Sound, Vancouver Island, British Columbia (BS); and the Santa Barbara Channel, California, USA (SB). $\delta^{15}N$ values for dorsal muscle tissue were determined with a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK) at the UC Davis Stable Isotope Facility in Davis, California.

When using $\delta^{15}N$ to infer trophic positions of consumers it is often necessary to account for differences in $\delta^{15}N$ at the base of the food web (Post 2002). We were unable to obtain sufficient $\delta^{15}N$ data for baseline organisms at different sites, but we did find that the mean $\delta^{15}N$ of *Sebastes* differed across the three regions (ANOVA; $F_{2,219} = 38.6$, $P < 0.0001$). $\delta^{15}N$ of fish from SB was significantly higher than from BS or HG (Tukey's hsd; $P < 0.0001$), with no difference between BS and HG ($P = 0.95$). This difference is likely to reflect baseline $\delta^{15}N$ differences rather than true differences in trophic position, as for six species sampled in multiple regions the mean $\delta^{15}N$ was consistently higher in SB (paired t test; $t_5 = -7.1$, $P < 0.001$). We accounted for this regional difference by subtracting the mean pairwise difference (1.32‰) from SB $\delta^{15}N$ values. Adjusting by the overall difference between SB and (HG + BS) had an almost identical effect (mean $\delta^{15}N_{SB} - \delta^{15}N_{HG+BS} = 1.25$‰). We present these "adjusted" $\delta^{15}N$ in parts per thousand (‰): this axis can be converted to trophic position by subtracting a baseline $\delta^{15}N$ value and dividing by the average enrichment per trophic level (~3.4‰; Post 2002).

For depth data we used the maximum depth at which each species commonly occurs (Love et al. 2002, Froese and Pauly 2008). For species where this information was unavailable we predicted maximum common depth from

TABLE 2. Results of multiple regression analyses used to identify traits associated with α- and β-niche axes for 43 *Sebastes* species.

Trait	Effect	Standardized slope	P	Partial R^2
PC1	$\delta^{15}N$	0.212	0.16	0.042
	Depth	**0.350**	**0.02**	**0.112**
PC2	**$\delta^{15}N$**	**−0.557**	**0.0002**	**0.284**
	Depth	**0.390**	**0.006**	**0.139**
PC3	$\delta^{15}N$	0.219	0.12	0.044
	Depth	**0.467**	**0.001**	**0.200**

Note: Rows in boldface highlight significant partial regression terms at the α = 0.05 level.

a regression equation of maximum common depth against absolute maximum depth (both log-transformed to improve linear fit, then back transformed to units of meters; $R^2 = 0.75$; $P < 0.0001$). Maximum common depth is a more suitable measure than absolute maximum depth, which often represents rare observations and falls well outside species' normal distributions. Our results were qualitatively identical regardless of which of these two depth measures we used.

We used the $\delta^{15}N$ and depth data to assess which of the PC traits are most related to the α- and β-niche. We used a multiple regression of each PC trait against $\delta^{15}N$ and depth, then calculated the partial coefficients of determination to determine how strongly traits were associated with each of the two niche axes (Table 2, Fig. 1). All traits showed some tendency toward association with both $\delta^{15}N$ and depth, either reaching or approaching significance. We found that PC1 (body size) was relatively weakly related to both $\delta^{15}N$ (partial $R^2 = 0.042$; $P = 0.16$) and depth (partial $R^2 = 0.112$; $P = 0.02$). PC2 (gill rakers) and PC3 (eye size) also showed relationships with both $\delta^{15}N$ and depth, but for PC2 the relationship with $\delta^{15}N$ (partial $R^2 = 0.284$; $P = 0.0002$) was considerably stronger than the relationship with depth (partial $R^2 = 0.139$; $P = 0.006$), while the reverse was true for PC3 ($\delta^{15}N$: partial $R^2 = 0.043$; $P = 0.12$; depth: partial $R^2 = 0.200$; $P = 0.001$). Therefore, while all three of these PC traits appear to have both α and β components, we can conclude that PC2 is predominantly associated with our α-niche axis while PC3 is predominantly associated with our β-niche axis. Relationships with PC1 were weaker, but it appeared to be slightly more related to the β-niche axis. There were no relationships between subsequent PC traits (PC4, PC5, and so on) and niche axes, and as these components explained very little variation (<3% combined) we do not discuss them further.
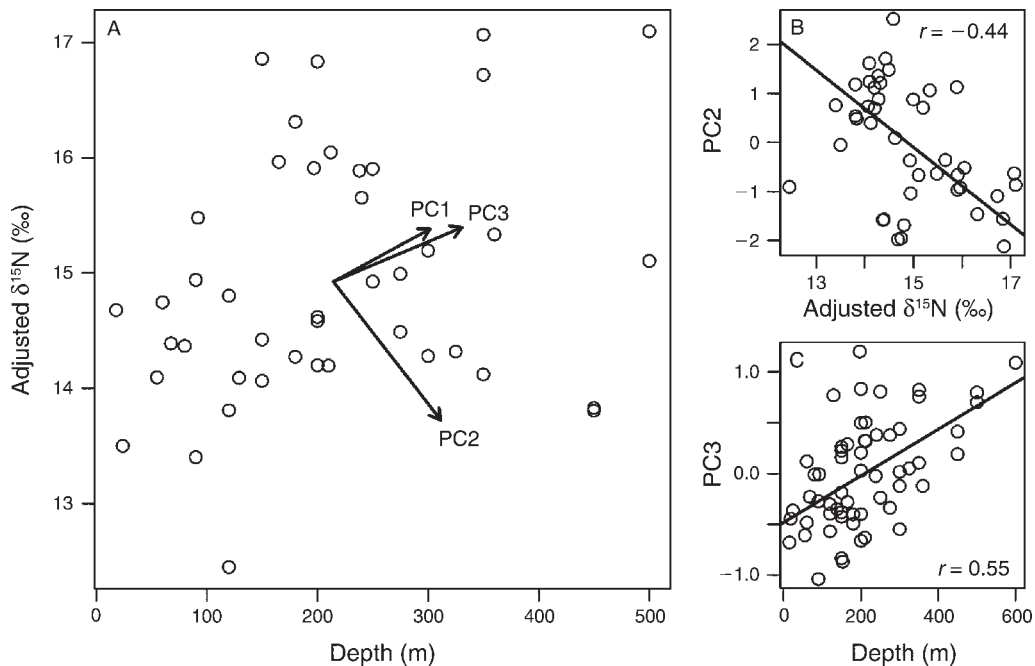

FIG. 1. Relationships between principal component traits and niche axes ($\delta^{15}N$ and depth). (A) Mean adjusted $\delta^{15}N$ vs. maximum common depth for 43 species of Pacific rockfish, *Sebastes*. Arrows indicate the strength of relationships between each trait (PC1, PC2, and PC3) and the two niche axes. Each arrow originates at the bivariate mean of depth and $\delta^{15}N$, and its vertical and horizontal displacement is determined by the standardized partial regression coefficients from the regression of the trait against $\delta^{15}N$ and depth (Table 2). These coefficients are multiplied by the standard deviations of $\delta^{15}N$ and depth, respectively, to rescale the arrows to have the same units as the axes of the figure, and then are multiplied by 2 for improved visibility. The smaller panels show the strongest PC trait–niche axis relationships: (B) PC2 vs. adjusted $\delta^{15}N$, and (C) PC3 vs. depth for 59 species (including 16 with no $\delta^{15}N$ data available for the regression analysis).

Our statistical interpretations of PC2 as a (predominantly) α trait and PC3 as a (predominantly) β trait are also justifiable from functional considerations of these traits. Gill rakers are used for the selective retention of small prey by fishes (Drenner et al. 1984), so a reasonable interpretation of the negative δ^{15}N–PC2 relationship is that species' trophic positions are inversely related to their degree of planktivory. The positive relationship between depth and PC3 is a likely adaptation to light conditions at different depths, as eye size relative to body size often increases with depth in marine fishes (Warrant et al. 2003, Warrant and Locket 2004).

Having identified PC2 and PC3 as predominantly α and β traits, respectively, we predicted that PC2 would mediate resource competition and show a signal of limiting similarity, while PC3 would be subject to environmental filtering. PC1 (body size) showed weaker associations with the niche axes, and as size is related to many aspects of both resource use and habitat we did not have strong reason to treat PC1 as either an α or β trait. We performed tests for trait evenness and trait clustering for all three PC traits, but did not make a priori predictions for PC1.

Community data

We reviewed academic and technical literature to compile community data from studies that documented the identity and abundance of all rockfish species in a well-defined geographic area. We identified 30 assemblages from a wide range of depths and latitudes in the northeast Pacific (Appendix B). Some assemblages were different regions or depth strata from the same study, including 15 from a recently published U.S. National Oceanographic and Atmospheric Administration (NOAA) trawl survey. As different assemblages overlapped in area surveyed or used similar research protocols it is difficult to determine to what extent they are statistically independent units. However, as all surveys were separated in space or time (or both), we treat the 30 studies as independent while bearing in mind that some pseudoreplication may be unavoidable. As well, we cannot rule out the possibility of some detection bias due to differences in methods (e.g., longline fishing vs. bottom trawling) and sampling effort, but as all studies were intended to identify all rockfish species present we expect that any such bias would be small. As well as species presence and absence we recorded the midpoint latitude and the midpoint and range of depths surveyed.

Analysis of community structure

To test for nonrandom trait distributions and phylogenetic structure in the 30 rockfish assemblages, we compared observed patterns to a simple null model in which species' traits do not influence community membership. For each community with species richness N, we simulated 999 null communities by sampling N species without replacement from a species pool. For this null model (null model 1) we sampled from the pool of all 59 species in our morphological data set, which includes all common species in the northeast Pacific. To account for potential dispersal limitation we repeated our analyses with a second null model (null model 2), in which only species with latitudinal distributions (from Love et al. 2002) overlapping the latitude surveyed were candidate community members. For example, null model 2 accounts for the possibility that species that recently originated in southern California are absent from higher latitude communities because they have had insufficient time to disperse there, not because they are unsuitable community members. Few of our results were affected by the choice of null model, so we present only the results from null model 1 unless otherwise noted. Both of our null models give species equal weights when sampling from the species pool, consistent with most previous work. Hardy (2008) recently showed that null models accounting for species' overall abundances can allow improved tests of community structure; while appropriate data are not presently available for all species in our study, incorporating species abundances would be a desirable addition to future tests for community structure in *Sebastes*.

We used simple metrics to quantify trait distributions within communities. To test for limiting similarity we focus on the evenness of spacing between adjacent species on a trait axis. While competition may not produce perfectly even trait spacing, on average we can expect traits in a community structured by competition to be more evenly spaced than in a randomly assembled community (Ricklefs and Travis 1980, Weiher et al. 1998, Stubbs and Wilson 2004). We first sorted trait values and calculated all neighbor distances (ND) as the differences between adjacent species. We then quantified the evenness of trait spacing as the standard deviation of neighbor distances divided by the range of traits present (sdND/R). This value will be low if species' traits are evenly spread across the trait space occupied. This metric has the advantage that, unlike measures such as mean ND or sdND, it is not strongly affected if a habitat filter excludes extreme trait values from the community but not from the null model (Stubbs and Wilson 2004). To test for environmental filtering we asked if the range of traits present in a community (RANGE) was less than expected for a randomly assembled community (Cornwell et al. 2006). For each community we calculated sdND/R and RANGE for PC1, PC2, and PC3 in the observed species as well as for the 999 simulated communities.

We used two metrics of phylogenetic community structure to test whether coexisting rockfish species tend to be more or less related than expected by chance. Mean pairwise distance (MPD) measures the average relatedness of all species in a community, while mean nearest taxon distance (MNTD) measures the average relatedness between each species and its closest relative (Webb 2000, Kraft et al. 2007). A recent simulation study found that MNTD is more powerful for detecting limiting similarity, while both metrics have high power

to detect environmental filtering on conserved traits (Kraft et al. 2007). The predictions of community phylogenetics can depend on the amount of phylogenetic signal in traits subject to assembly rules (Cavender-Bares et al. 2004, Kraft et al. 2007). We quantified the phylogenetic signal (K) of each PC trait using the program PHYSIG (Blomberg et al. 2003). K will be close to 1.0 if species' trait similarity is proportional to their common evolutionary history (shared branch lengths on the phylogeny), as occurs under a model of evolution by Brownian motion. $K < 1$ indicates a weaker phylogenetic signal than expected under Brownian motion, while $K > 1$ indicates stronger signal.

We used two statistical approaches to test for nonrandom patterns of trait and phylogenetic dispersion: significance testing within each community and meta-analysis of all 30 communities. For each metric (sdND/R, RANGE, MPD, and MNTD), we calculated P values as the proportion of the 999 null communities with a value more extreme than the observed value. For a two-tailed test with $\alpha = 0.05$, an observed metric is therefore significant if it is larger or smaller than 97.5% of metrics calculated from the null model. Measures of phylogenetic and trait dispersion in single communities often have low power to detect nonrandom patterns against null models (Stubbs and Wilson 2004, Kraft et al. 2007). To increase our power to detect overall trends and to alleviate the issue of multiple comparisons (eight tests in each of 30 communities), we used a meta-analysis on standardized indices of trait and phylogenetic dispersion. Webb et al. (2002) introduced a method to standardize observed values of MPD and MNTD to the null model for this purpose. The net relatedness index (NRI) is calculated from MPD, and the nearest taxon index (NTI) is calculated from MNTD, as

$$\text{NRI} = -(\text{MPD}_{\text{observed}} - \overline{\text{MPD}_{\text{null}}})/\text{sd}(\text{MPD}_{\text{null}}) \quad (1)$$

$$\text{NTI} = -(\text{MNTD}_{\text{observed}} - \overline{\text{MNTD}_{\text{null}}})/\text{sd}(\text{MNTD}_{\text{null}}). \quad (2)$$

NRI and NTI will be positive if species in a community are more closely related than expected under the null model and negative if they are more distantly related (Webb et al. 2002, Kembel and Hubbell 2006, Kraft et al. 2007). We extended this approach to calculate a trait evenness index (TEI) from sdND/R and a trait clustering index (TCI) from RANGE:

$$\text{TEI} = -\left\{ \frac{(\text{sdND/R})_{\text{observed}} - \overline{(\text{sdND/R})_{\text{null}}}}{\text{sd}\left[(\text{sdND/R})_{\text{null}}\right]} \right\} \quad (3)$$

$$\text{TCI} = -\left[\frac{\text{RANGE}_{\text{observed}} - \overline{\text{RANGE}_{\text{null}}}}{\text{sd}(\text{RANGE}_{\text{null}})} \right]. \quad (4)$$

Positive values of TEI indicate more even trait spacing than expected under the null, while positive values of TCI indicate a lower range of trait values present than

expected. We used one-sample t tests to determine whether NRI, NTI, TEI, or TCI were significantly different from zero across all 30 communities, indicating overall tendencies toward clustering or evenness in relatedness or traits. We also used correlation tests to assess whether any of the indices varied with depth, latitude, or the number of species in the assemblages.

RESULTS

Few values of the metrics of trait dispersion were significantly different from a null expectation within individual assemblages (Appendix B: Table B2). sdND/R and RANGE were each significant for only one to two of 30 assemblages for each trait, as would be expected by chance alone. Of the phylogenetic metrics, MPD was significant in seven of 30 assemblages (six of which showed lower phylogenetic relatedness than expected) and MNTD was significant in eight assemblages (seven of which showed greater nearest taxon distances than expected).

Some overall trends emerged when we used meta-analysis on the standardized indices of trait (Fig. 2) and phylogenetic (Fig. 3) dispersion. As predicted, our trait evenness index (TEI) showed a tendency toward even trait spacing for PC2 ($P = 0.007$) but not for PC3 ($P > 0.80$). Additionally, PC1 (reflecting overall body size) showed a weak tendency toward even spacing ($P = 0.026$). Our trait clustering index (TCI) showed that PC3 tended to have a lower range than expected ($P < 0.001$), as did PC2 ($P = 0.003$) but not PC1 ($P > 0.15$). With regard to phylogenetic community structure, NTI was significantly higher than expected by ($P < 0.001$), while NRI was not different from zero ($P > 0.4$). All of these results were qualitatively unchanged when we used Null Model 2 or when we used nonparametric Wilcoxon signed-rank tests instead of t tests.

Phylogenetic signal (K) was estimated as 0.54 (PC1), 0.79 (PC2), and 0.67 (PC3). These values are typical for body size and other morphological traits in a wide range of species (Blomberg et al. 2003).

A number of our indices were correlated with the latitude, depth, or number of species in the assemblages (Table 3). TEI decreased with latitude for both PC1 and PC2, indicating more even trait spacing in southern assemblages. TEI decreased with assemblage species richness for PC1 but increased with richness for PC2. TCI increased with depth and decreased with latitude for PC2, showing that deeper, lower-latitude assemblages tended to exhibit a restricted range of gill raker morphologies. None of these relationships changed substantially when the second null model was used. NRI and NTI both decreased with depth and with the number of species in an assemblage, indicating a tendency toward lower phylogenetic relatedness in deeper and more diverse assemblages. NRI also decreased with latitude, but this relationship did not occur when we used null model 2.
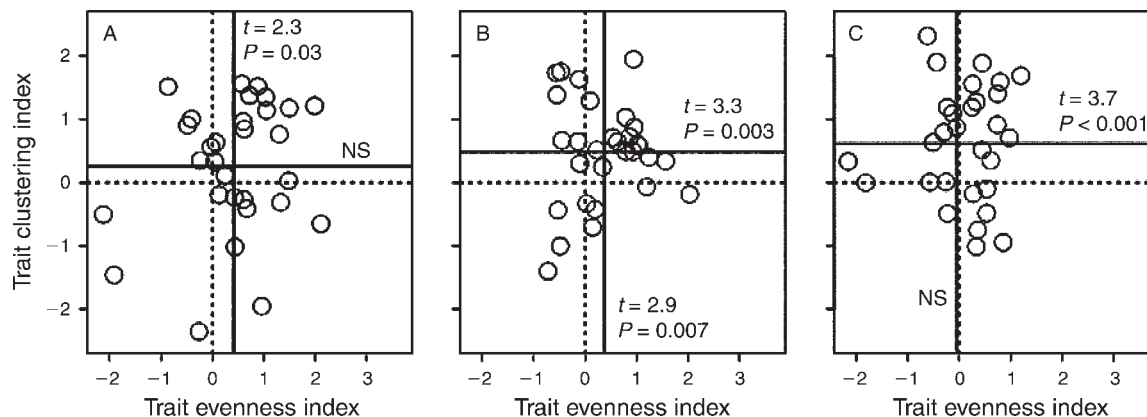
FIG. 2. Standardized indices of trait dispersion for (A) PC1, (B) PC2, and (C) PC3 in 30 rockfish assemblages. Values of trait evenness index (TEI) > 0 indicate more even trait spacing (lower sdND/R [standard deviation of neighbor distances divided by the range of traits present]) than expected under the null model, while values of trait clustering index (TCI) > 0 indicate a lower observed range of trait values than expected. Dotted lines indicate the null expectation for each index (zero) and solid lines indicate mean observed index values.

DISCUSSION

We found patterns in the trait distributions of rockfish that were consistent with both competition and environmental filtering influencing the species composition of assemblages. Gill raker morphology, a trait associated primarily with the α-niche, showed tendencies toward even spacing as expected if competition drives species assortment or character displacement. For relative eye size, a trait related to the β-niche, we detected clustering within communities as expected under environmental filtering. These results provide evidence for trait-based assembly of *Sebastes* communities in the northeast Pacific. This is the first study to demonstrate such patterns in a widely dispersed group of marine fish. The parallels between our results and recent conclusions derived largely from terrestrial plants (Stubbs and Wilson 2004, Ackerly and Cornwell 2007, Cornwell and Ackerly 2009) suggest that common mechanisms are involved in structuring these widely disparate types of communities.

Body size and two size-independent axes of variation (defined mainly by gill raker morphology and by eye size) accounted for most of the interspecific variation in morphology in our data set. We suggest that these can be treated as three orthogonal axes of functional variation with distinct ecological implications. These traits have both α and β components (also shown in Ackerly and Cornwell 2007), as indicated by relationships with both $\delta^{15}N$ and depth distribution. However, we were able to identify PC2 as most strongly associated with the α-niche and PC3 as most strongly associated with the β-niche using both statistical approaches (Fig. 1; Table 2) and functional considerations. PC1 showed weaker relationships with niche axes, though it was more associated with depth than with $\delta^{15}N$. However, our finding of a weak tendency toward overdispersion in

PC1 suggests a possible role for body size in mediating species interactions.

Body size has a long history in the study of limiting similarity in communities (Hutchinson 1959). As size influences many aspects of species biology (Peters 1983), there may be multiple explanations for patterns of overdispersion in body size. Body size is certain to affect some aspects of diet (even if it is not strongly related to trophic position) in gape-limited fishes, but size may also influence competition for space. Rockfish compete for territories (Larson 1980), so the tendency toward even spacing could be explained if similar-sized species exhibit aggressive interference (Oksanen et al. 1979), or if species with different sizes occupy distinct microhabitats.
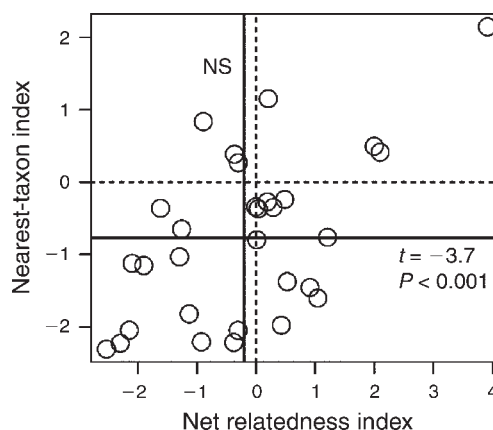

FIG. 3. Standardized measures of the phylogenetic structure of 30 rockfish assemblages. Values of nearest-taxon index (NTI) > 0 indicate greater relatedness between closest relatives than expected under the null model, while values of net relatedness index (NRI) > 0 indicate a lower total phylogenetic diversity than expected. Dotted lines indicate the null expectation for each index (zero), and solid lines indicate mean observed index values.

TABLE 3. Results of correlation tests for relationships between standardized indices of community structure and midpoint survey depth, latitude, and number of species in the assemblage (N sp.).

		Null model 1			Null model 2			
Index	Trait	log(depth)	Latitude	N sp.	log(depth)	Latitude	N sp.	% Pool
TEI	PC1	−0.03	−0.37*	−0.39*	−0.04	−0.25	−0.34	−0.39*
	PC2	−0.08	−0.38*	0.44*	−0.02	−0.26	0.54**	0.41*
	PC3	0.31	−0.27	0.21	0.28	−0.26	0.17	−0.01
TCI	PC1	0.35	−0.25	0.08	0.38*	−0.15	0.15	0.06
	PC2	0.70***	−0.48**	0.18	0.65***	−0.62***	0.27	0.03
	PC3	0.31	−0.03	0.24	0.33	−0.03	0.14	0.12
NRI		−0.64***	−0.46**	−0.32	−0.77***	−0.02	−0.43*	−0.38*
NTI		−0.59***	0.19	−0.56**	−0.58***	0.25	−0.54**	−0.39*

Notes: Correlation coefficients are shown for indices from both null models. "% Pool" is the percentage of species in the regional pool that are present in each community (not shown for null model 1, which uses the same regional pool for all communities, making % Pool and N sp. equivalent). Abbreviations are: TEI, trait evenness index; TCI, trait clustering index; NRI, net relatedness index; NTI, nearest-taxon index.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Gill rakers are a well-studied ecomorphological trait due to their important role in prey capture in many groups of fishes. Gill raker morphology frequently diverges during ecological character displacement (Schluter 2000) and in the development of resource polymorphism (Skúlason and Smith 1995). The strong correlation between PC2 and $\delta^{15}N$ (Fig. 1B) shows that gill rakers are consistently associated with trophic position. $\delta^{15}N$ does not perfectly indicate the potential for competition between species (as isotopically similar species may consume different prey), but the use of stable nitrogen isotopes allowed us to quantify trophic position for many species and provided an objective and integrated measure of potential dietary overlap. Similarly, gill raker morphology is not an unambiguous predictor of diet: numerous long gill rakers are predominantly associated with planktivory, but species with fewer short rakers may feed on a wide variety of larger prey such as fishes, cephalopods, and benthic molluscs and crustaceans. While PC2 similarity will therefore not always indicate high diet overlap, our analyses suggest that this trait is nonetheless subject to limiting similarity. We found that PC2 also showed a signature of environmental filtering: some of the lowest values of this trait occur in derived inshore species that are absent from the deeper assemblages, driving an overall tendency toward clustering in this trait even though most communities include a fairly broad range of trait values.

Our results indicate that PC3, associated mainly with eye size, is subject to environmental filtering across a depth gradient. Increased eye size relative to body size is a common adaptation to decreased light availability within the depth range occupied by *Sebastes* (less than 1000 m; Warrant et al. 2003, Warrant and Locket 2004). Mean PC3 was strongly correlated with survey depth ($r = 0.86$) and the range of PC3 values present was reduced across the depth gradient. We do not expect that eye size is the only trait, or even necessarily the most important trait involved in depth adaptation in rockfish. However, PC3 is an easily measured feature of species that is likely to be a useful surrogate for multiple traits involving gas-exchange physiology (J. L. Rummer, *personal communication*) and vision (Warrant et al. 2003). Environmental filters can operate simultaneously on many characteristics of species (Cornwell et al. 2006), but if a suite of traits is associated with depth adaptation it is likely that multiple traits related to the β-niche covary in response to this key environmental gradient (see also Ackerly and Cornwell 2007).

We detected nonrandom phylogenetic community structure, but it is difficult to confirm whether these patterns reflect assembly processes. NTI showed that closest relatives were more distantly related than expected, a pattern that is often interpreted as limiting similarity. However, the relatively low phylogenetic conservatism of the traits considered in this study should result in low power of phylogenetic tests to detect limiting similarity (Kraft et al. 2007). Phylogenetic overdispersion can also reflect environmental filtering on highly convergent traits (K approaching 0), but within the range of phylogenetic signal of traits in this study ($K = 0.54$–0.79) no simple assembly process is expected to produce detectable phylogenetic overdispersion (Kraft et al. 2007). The tendency toward phylogenetic evenness that we detected using NTI suggests one of two explanations. First, assembly processes might act on unmeasured traits that are either more conserved (if subject to limiting similarity) or convergent (environmental filtering). Second, phylogenetic patterns in rockfish assemblages might reflect the biogeographic history of the genus rather than trait-based assembly processes.

The relationships among NTI, NRI, depth, and latitude suggest a role for biogeographic history in generating phylogenetic community structure. Deeper and higher latitude assemblages tend to contain species that are less related to one another than shallow southern assemblages, although the NRI–latitude relationship disappears when we use the second, latitude-restricted null model. It is possible that NTI and NRI vary with latitude and depth because of shifts in the relative

importance of limiting similarity and environmental filters across these gradients. In this case, we should expect stronger evidence for environmental filtering in shallow, southern assemblages (where NTI and NRI tend to be negative) and stronger evidence for limiting similarity in deeper, northern assemblages. TEI is unrelated to depth for both PC1 and PC2, and while there are correlations between TEI and latitude for both traits, they are opposite to the direction expected if assembly processes vary with latitude (i.e., less trait evenness in northern assemblages). Environmental filtering on our primary depth-related trait (PC3) appears to be equally strong across depths and latitudes, while the relationship between TCI for PC2 and depth is also inconsistent with stronger filtering in shallow water (although the latitude relationship is consistent with stronger filtering on this trait in southern assemblages; Table 3).

In the absence of evidence for shifts in assembly processes consistent with the patterns in phylogenetic community structure, it seems likely that the biogeographic history of *Sebastes* is responsible for these patterns. Historical events can impact aspects of community structure (e.g., Wiens et al. 2006), and it is possible that the geographic mode of speciation (sympatric vs. allopatric) can produce nonrandom phylogenetic community structure (D. I. Bolnick, *personal communication*). *Sebastes* species in the northeast Pacific are thought to be descended from a deep-dwelling ancestor that dispersed from the genus' area of origin in the northwest Pacific (Hyde and Vetter 2007). Subsequent expansion southward and inshore followed by repeated speciation likely explains the tendency toward phylogenetic clustering in nearshore communities in southern California. Phylogenetic evenness in the ancestral deep and high-latitude habitats may result from replicate radiations as lineages moved south and inshore, leaving more distantly related species in these ancestral habitats. It remains possible that geographically variable assembly processes contribute to the phylogenetic structure we detected in *Sebastes*; however, due to low phylogenetic signal in ecologically important traits and conflicting patterns of trait and phylogenetic structure across depth and latitudinal gradients, we feel it is premature to interpret this phylogenetic structure as additional evidence for assembly rules in rockfish.

We have presented patterns consistent with trait-based assembly in *Sebastes*, supporting the idea that competition and environmental filtering act on traits associated with different components of the niche. As we analyzed communities of mobile marine organisms using community data collected for other purposes, there was inevitable variation in methodology, scale and the assignment of community boundaries. However, rockfish tend to occur in fairly consistent assemblages (Love et al. 2002), and we expect that most of the communities we analyzed are true collections of species that coexist and potentially compete for food and space. It is noteworthy that we detected these patterns even though our morphological data did not come from individuals from the survey sites. Intraspecific morphological variation in *Sebastes* has not been investigated in any detail, but it is possible that character displacement and adaptation to local conditions could produce even stronger signals in species' traits within communities. Finally, we considered only species of *Sebastes* in our tests for trait overdispersion, but the genus is variable enough that some species very likely show greater niche overlap with distant relatives than with some congeners. The survey data did not contain enough information on fish species other than *Sebastes* to examine this possibility, but interactions with more distant relatives may also influence adaptive radiation and community assembly in rockfish.

Our findings show that a priori identification of traits associated with the α- and β-niche can allow powerful tests for assembly rules. The continued integration of community phylogenetics with the study of functional morphology, trait evolution and adaptive radiation promises to allow increasingly thorough analyses of the factors influencing the assembly of ecological communities.

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APPENDIX A

Summary information on *Sebastes* specimens used in analyses of community structure (*Ecological Archives* E090-172-A1).

APPENDIX B

Information on community data and results of tests for community structure (*Ecological Archives* E090-172-A2).