A large-scale study of competition of two temperate reef fishes: temperature, functional diversity, and regional differences in dynamics

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ABSTRACT: The dynamics of populations are influenced by competition, both within species and among species. However, the strength of both forms of competition may be modified by environmental factors such as temperature and food availability, and it is not always clear how competition varies throughout a broad geographic range. We examined competition within and between 2 species of temperate reef fish, the black surfperch *Embiotoca jacksoni* and the striped surfperch E. lateralis. Using data collected by an organization of citizen scientists (Reef Check California), we measured competition by analyzing (co)variation in time-series estimates of densities for both species at many locations along the California coast (86 sites spread across ~1050 km). We examined whether competition varied between Northern California (a region characterized by cold water and high food availability) and Southern California (a region characterized by warm water and low food availability). Strength of competition varied between regions, but not as expected. Rather than an intensification of competition with temperature, regional differences in competition resulted from differences in how populations of each species used resources. For black surfperch, intraspecific competition was greater in the north, where populations exhibited greater spatial crowding and ate a narrower variety of prey items than populations in the south. Striped surfperch displayed the opposite pattern. Northern populations experienced weaker intraspecific competition, exhibited less crowding, and ate a greater diversity of prey items than southern populations. Competition and the resulting dynamics of these populations may be more sensitive to functional diversity than to external factors.

KEY WORDS: Density dependence \cdot Citizen science \cdot Lotka-Volterra \cdot Mean crowding \cdot Niche width \cdot Population dynamics \cdot Species coexistence \cdot Stability

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INTRODUCTION

Competition may play an important role in the dynamics of populations. For example, competition among individuals of the same species can be a major reason why populations tend to grow when small and shrink when large (Hassell 1975, Turchin 2003, Royama 2012). This type of density-dependent population growth is a common feature of natural populations and can be a key process that regulates the abundance of a species (reviewed by Fowler 1987, Sibly et al. 2005, Brook & Bradshaw 2006). Competition among individuals of separate species can also be very important for the dynamics of populations (Connell 1983, Schoener 1983, Gurevitch et al. 1992), though the relative magnitudes of withinand between-species competition are not always clear (Inouye 2001, Damgaard 2008). For example, the intensity of competition may be moderated by environmental factors such as temperature (e.g. Taniguchi et al. 1998, Carmona-Catot et al. 2013) and food availability (e.g. Minot 1981, Wissinger 1989, Griffiths et al. 1993, Davis & Wing 2012). Spatial variation in environmental factors can therefore lead to regional variation in the dynamics of competition, and for many species, it is not clear how competition varies throughout a broad geographic range.

When 2 species are known to compete, it is useful to estimate what the long-term outcome of competition will be (i.e. whether coexistence is expected to be unstable or stable), and why. Species that are similar with respect to their resource requirements are expected to compete more intensely (e.g. MacArthur & Levins 1967, Pianka 1974, Bolnick 2001), perhaps to the point where one species can be locally extirpated by its competitor (e.g. Violle et al. 2011). If competition leads to instability, species may coexist because disturbances periodically reset their relative abundances (Connell 1978) or because migration from other populations is enough to sustain a local population that would otherwise go extinct in the long term (e.g. Loreau & Mouquet 1999, Amarasekare & Nisbet 2001). Alternatively, the outcome of competition may be stable. In such cases, detailed analyses of competition may reveal the mechanisms leading to stability (e.g. tradeoffs between the ability to colonize and the ability to compete; Calcagno et al. 2006).

In this study, we examined spatial variation in the intensity of competition between 2 species of temperate reef fish, the black surfperch Embiotoca jacksoni and the striped surfperch Embiotoca lateralis. These 2 species are closely related to each other, have very similar resource requirements (Ebeling & Laur 1986), and exhibit strong competition in the wild. For example, the presence of one species can result in a shift in the other's diet, suggesting that they compete for food (Schmitt & Coyer 1983, Holbrook & Schmitt 1995). In addition, both Hixon (1980) and Schmitt & Holbrook (1986) observed interference competition in the form of aggressive chases between fish foraging in close proximity. Finally, manipulative experiments that removed each of the species from replicate field sites found that these 2 species can compete strongly for space within the habitat. In these experiments, short-term responses (i.e. redistributions of fish that occurred months after the removal of competitors) suggested that striped surfperch may be a superior competitor because striped surfperch affected the distribution of black surfperch, but not vice versa (Hixon 1980, Schmitt & Holbrook 1986). However, in response to a 4 yr manipulation, population densities of both species increased in the absence of competitors, and the responses were nearly equivalent, suggesting that these species may have a similar competitive effect on each other (Schmitt & Holbrook 1990).

Although competition between E. lateralis and E. jacksoni has been studied in detail, these studies have been concentrated in a few locations (e.g. Santa Barbara, Santa Cruz Island). Striped surfperch range from Alaska to northern Baja California, and black surfperch range from Mendocino County, California, to central Baja California (Miller & Lea 1972). These 2 species co-occur within ~1200 km of coastal habitat that ranges from Northern California (~40.0°N) to Baja California (~31.5° N; Miller & Lea 1972). It is possible that the strength and stability of competition between the 2 species varies between regional environments. Within this range, the most notable change in environmental conditions occurs near Point Conception (~34.4° N), an oceanographic breakpoint that divides Northern and Southern California into 2 biogeographic regions (Horn et al. 2006). Nearshore reefs in Northern California experience high upwelling, cold water temperatures, and high productivity. Reefs in Southern California (including most of the Channel Islands) experience less upwelling, warmer waters, and lower productivity (Hickey 1979).

There are several reasons why competition between these 2 species of surfperch may differ between Northern and Southern California. In particular, higher water temperatures in Southern California may raise metabolic rates and create a greater demand for food, thereby increasing the intensity of competition. Such effects have been documented for many other systems (e.g. De Staso & Rahel 1994, Taniguchi et al. 1998, Carmona-Catot et al. 2013), and temperature may affect the long-term outcome of competition between surfperch species. Overall food availability can also affect the outcome of competition (e.g. Wissinger 1989, Griffiths et al. 1993). Nearshore waters in Southern California are generally less productive, and lower availability of surfperch prey (secondary consumers such as amphipods and isopods) may also intensify competition in this region. Population dynamics of black surfperch are sensitive to fluctuations in food supply (Okamoto et al. 2012, 2016), and it is likely that food availability plays a role in mediating competition as well. Finally, competition may be affected by levels of genetic and phenotypic diversity within the interacting populations (e.g. Hughes et al. 2008, Aguirre & Marshall 2012, Johnson et al. 2016). Striped surfperch are generally more abundant and diverse in the north, whereas black surfperch are generally more abundant and diverse in the south (see Fig. 1a, also see Bernardi 2005). It is possible that populations from

northern and southern regions occupy different regions of niche space (e.g. by eating different varieties of prey, and/or using different microhabitats) and that this variation plays a role in modifying competition within and between species.

In this study, we measured competition between striped and black surfperch and evaluated whether competition was expected to be stable in the long term. We measured competition by analyzing annual counts of both species at 86 sites along the California coast and examining whether population growth of each species was negatively related to the abundance of its competitor. We analyzed the joint dynamics of the 2 surfperch species across a large spatial range (~1050 km of coastline), and examined whether the outcome of competition varied between Northern and Southern California. We also gathered information on breadth of diets and average level of spatial clustering—2 factors that may moderate the strength of competition.

MATERIALS AND METHODS

Data collection

This study analyzed data collected by Reef Check California (RCCA) - an organization of citizen scientists that conducts yearly counts of fish at sites throughout the state and posts the data in a publically accessible, online database (www.reefcheck. org). Divers involved with RCCA undergo rigorous training that includes both classroom lectures and ocean dives (Freiwald et al. 2013). Over the course of the training, volunteers are tested in species ID and all survey methods (i.e. separate methods for algae, invertebrates, and fishes). Only after successfully passing the test for the respective survey method are they qualified to collect data for that taxonomic group. This tiered approach of certification allows most volunteers to collect data without compromising the quality of data that are more difficult to collect (e.g. fish surveys). After the initial training, all volunteers have to be re-tested and certified the following year before they can contribute data during that year's survey season. After collection, RCCA data go through a rigorous quality-control procedure including review of datasheets in the field, automated data checks during data entry, and review of entered data by RCCA staff scientists. We acknowledge that volunteers have less training and experience than academic research groups and that data collected by volunteers may have a higher degree of observer variability. However,

observation error can be accounted for statistically, and the influence of observer variability diminishes with sample size. A large organization of volunteers can conduct many surveys, and thus the inferences drawn from such data can be robust, even if observation error is somewhat elevated.

The counts made by RCCA divers are based on standard methods for counting reef fishes. During each survey, divers counted fish on 18 transects site⁻¹; transects were 30 m long \times 2 m wide \times 2 m high. To ensure representative coverage across the entire reef, potential sampling locations were arranged in 6 rows perpendicular to shore and within each row, 3 transect locations were chosen at random. The RCCA program produces estimates of fish density that are comparable to academic monitoring programs (Gillett et al. 2012), and this is particularly true for large and easily identifiable species such as black surfperch and striped surfperch. Each survey may be used to estimate the average density of a species, and yearly averages can provide a time-series that describes changes in population density at a particular location. We analyzed data from 86 sites that ranged from locations in Mendocino County in Northern California (39.451°N, 123.815°W), to locations in San Diego County (32.716°N, 117.161°W) and included many sites through the Channel Islands (Fig. 1, the group of islands off Southern California). The number of annual surveys per site ranged from 2 to 11, with a mean value of 6.9.

Analysis of competition

For every pair of consecutive, yearly surveys at each site, we calculated annual growth rate. Population growth can be represented by an exponential function:

$$N_{t+1} = N_t \mathrm{e}^{rt} \tag{1}$$

where N_t is population density in a given year and N_{t+1} is the population density the following year, r is instantaneous growth rate, and t is time in years. Density was expressed as number per 60 m² transect. Note that even though fish were counted per unit volume, we follow the usual convention of expressing density as number per area. In estimating growth rates from records of density, r was calculated as:

$$r = \ln\left(\frac{N_{t+1} + 0.04}{N_t + 0.04}\right) \tag{2}$$

A small constant (0.04) was added to the density values because there were some instances where the



Fig. 1. (a) Latitudinal gradient of population densities for black and striped surfperch, and (b) map of the study area along the coast of California, USA. Dots indicate locations where reef fish populations have been regularly surveyed by Reef Check California — an organization of citizen scientists. Sites were grouped into northern (n = 40) and southern (n = 46) regions, with the division occurring near Point Conception (marked by the arrow). Densities (no. fish per 60 m² transect) were estimated at each of the 86 sites, and were averaged within latitudinal bins to create the display in (a)

estimated density was zero, even though the true density was unlikely to be zero. For both of these live-bearing, reef-attached species, immigration from other reefs was unlikely, and in the vast majority of cases where a density of zero was recorded, the densities in subsequent surveys were greater than zero. Because the smallest density that could be observed was 0.055 (1 fish observed per 18 transects searched), we used a value of 0.04 for an estimated density that was below the lowest observation possible, but not zero. Surveys occurred in the summer and fall months. When multiple surveys were conducted at a site, densities were averaged for that year. Calculation of annual growth rates required consecutive surveys. In this analysis, we examined relationships between density and growth from 179 observations in Northern California, and 240 observations in Southern California.

We used linear mixed effects models to analyze the degree to which average growth rate of each species declined with the density of its own species and the density of its competitor. Because overall rates of growth may differ among sites and years, we fit models in which the intercept was allowed to vary by site and year. Although these components turned out to be minor sources of variation, including site and year as random factors allowed us to account for variation in population growth that was unrelated to density, but could be attributable to factors that differ by site (e.g. predation rates) and year (e.g. region-wide variation in productivity and food supply). From the fixed effect components of the model, population growth rate of black surfperch (\hat{r}_{BP} ; black surfperch designated as species 1) was modeled as:

$$\hat{r}_{\rm BP} = r_{\rm MAX1} - \beta_{1,1}BP - \beta_{2,1}SP$$
 (3a)

and population growth rate of striped surfperch ($\hat{r}_{\rm SPi}$ striped surfperch designated as species 2) was modeled as:

$$\hat{r}_{SP} = r_{MAX2} - \beta_{1,2}BP - \beta_{2,2}SP \tag{3b}$$

where r_{MAX} is the intercept (estimated value of r when *BP* and *SP* both approach zero), $\beta_{1,1}$ and $\beta_{2,2}$ are the fixed effect coefficients for intraspecific competition (e.g. the effect of species 1 on itself) and $\beta_{2,1}$, $\beta_{1,2}$ are the fixed effect coefficients for interspecific competition (e.g. the effect of species 2 on species 1). Random effects of site and year were included in the estimation procedure, but because random effects affect the variability of coefficients and not the means, for simplicity, they are not included in Eq. (3). BP is the density of black surfperch and SP is the density of striped surfperch. Note that Eq. (3) is a basic Lotka-Volterra model of competition. We acknowledge that mechanisms other than competition may result in densities being correlated. For example, predator attraction or increases in predator consumption may cause density-dependent population growth. Similarly, temporal fluctuations in environmental conditions that support the growth of one population but retard the growth of another may give the appearance of competition. However, competition is the simplest explanation for the patterns in the data, and many studies have demonstrated the importance of inter- and intraspecific competition within this system (e.g. Hixon 1980, Schmitt & Coyer 1983, Ebeling & Laur 1986, Schmitt & Holbrook 1986, 1990, Holbrook & Schmitt 1995).

We conducted our analyses of competition for 2 separate regions (Northern and Southern California) based of the existence of an important biogeographic break at Point Conception (reviewed by Horn et al. 2006). Waters to the north of Point Conception are colder than waters to the south. A comparison of population dynamics between Northern and Southern California is thus a comparison between competition in cold and warm conditions. However, because our results were not consistent with the a priori expectation that competition would be more intense in warmer conditions, we followed up with a more direct evaluation of the effect of water temperature on competition (see Supplement 1 at www.int-res.com/ articles/suppl/m593p097_supp.pdf). Because this analysis revealed no significant effect of temperature itself on competition, we continued with our regional comparison.

We also note that within our analyses, estimates of intraspecific competition will be biased by observation error. For example, when N_t is overestimated,

then per capita growth $(\ln[N_{t+1} / N_t])$ will be underestimated. This phenomenon will inflate the estimated magnitude of intraspecific competition. In this study, we corrected for bias in a 2-stage procedure. First, we estimated observation error from field data. Next, we calculated the degree to which observation error would bias the parameters describing the relationship between per capita growth and N_t . The expected bias was then subtracted from the coefficients that were estimated from the raw data. This procedure yielded unbiased estimates of the parameters in Eq. (3) (see Supplement 2 for details).

Does competition result in stable coexistence?

Once the competition coefficients had been estimated, we calculated the zero growth isocline for each species. Growth rates (\hat{r}) were set to zero and Eq. (3) was rearranged to express the combination of species densities that would result in no population growth. For example, Eq. (4) gives the combinations of black surfperch and striped surfperch densities for which growth of black surfperch is zero:

$$SP = \frac{r_{\text{MAX1}} - \beta_{1,1}BP}{\beta_{2,1}}$$
(4)

The parameters of this equation are defined by the competition coefficients that were estimated by the mixed model analysis. We also calculated the zero growth isocline for striped surfperch, and used the combined properties of these isoclines to evaluate whether the outcome of competition was stable. Competitive equilibrium points were calculated as the intersection between the zero growth isoclines for each species. Variation of the equilibrium point estimates was estimated by a resampling procedure. For each of 1000 iterations, we resampled the data with replacement, and estimated competition coefficients with mixed models (as described above). The resampled competition coefficients were used to calculate equilibrium points, and the resampled distribution of 1000 equilibrium points was used to describe a 95% confidence region.

We applied these analyses to data from both Northern and Southern California. We were interested in whether there were differences in competition between these 2 regions, and if so, what those differences were. For example, if both regions were stable, then differences in the intensity of competition may lead to differences in properties such as equilibrium densities. In contrast, if competition was stable in one region but not the other, this would represent fundamental differences in the long-term dynamics of these species. Striped surfperch are absent from some areas of Southern California (where waters are relatively warm), but present further south in Baja California (where waters are colder because of coastal upwelling). Bernardi (2005) suggested that this discontinuity in range may be because black surfperch have excluded striped surfperch from warmer habitats.

Mechanisms affecting strength of competition

Because our main analyses indicated that the intensity of competition was different between Northern and Southern California (see below), we followed up on these results by evaluating spatial crowding and diet variation—2 mechanisms that may affect the strength of competition (e.g. Svanbäck & Persson 2004, Brännström & Sumpter 2005). These are not the only mechanisms that can be responsible for differences in competition, but they are 2 mechanisms that likely play an important role, and could be evaluated with available data.

We measured spatial crowding because there may not necessarily be a direct relationship between population density (which is measured at the scale of the entire reef), and the density that an average fish experiences. Surfperches can have home ranges on the order of meters to 10s of m (Hixon 1981, Holbrook & Schmitt 1995), and at the scale of entire reefs (100s of ha) the distribution of surfperches can be patchy (Ebeling & Laur 1986, Johnson et al. 2016). Because competitive interactions occur among nearby fishes (Hixon 1980, 1981, Schmitt & Holbrook 1986), and because spatial clustering may depend on population density (Johnson et al. 2016), we examined how population density corresponded to mean crowding (the average number of neighbors each fish had; Lloyd 1967).

The goal of this analysis was to calculate a crowding coefficient — a quantity that describes the degree to which a unit increase in population density increases the average amount of spatial crowding. Crowding coefficients were calculated in 2 steps. First, we calculated crowding by counting the number of neighbors each fish on each transect had. For example, if there were 6 fish on a transect, each fish had 5 neighbors. If there was only one fish on a transect, that fish had no neighbors. For each survey (18 transects total), we calculated the number of neighbors each fish had and averaged across all fish observed on that survey. This provided a measure of mean crowding (Lloyd 1967). Second, we examined the relationship between mean density and mean crowding. If fish are distributed randomly in space, we expect a 1:1 relationship. If they are clustered together, we expect the slope to be >1 and if they are uniformly dispersed in space, we expect the slope to be <1. To calculate crowding coefficients from our data, we used a linear model to estimate the slope between mean crowding and mean density. Note that because the line has to pass through zero (crowding is zero when there are no fish present), we fit a model with no intercept. We calculated crowding coefficients for both Northern and Southern regions. To describe the different types of crowding, we calculated crowding coefficients for each of the 4 species combinations: black surfperch crowding black surfperch (BP \rightarrow BP), black surfperch crowding striped surfperch (BP \rightarrow SP), striped surfperch crowding black surfperch (SP \rightarrow BP), and striped surfperch crowding striped surfperch (SP \rightarrow SP).

Dietary niche width and diet overlap may moderate competition. Populations that consume a greater diversity of prey typically do so because of greater specialization among individuals (reviewed by Bolnick et al. 2007), and diet breadth within a population may affect intraspecific competition in the same way that diet overlap between species may affect interspecific competition. Diets of both black and striped surfperch have been studied in both Northern and Southern California (Ellison et al. 1979, Haldorson & Moser 1979, Schmitt & Coyer 1983, Schmitt & Holbrook 1984, Laur & Ebeling 1983, Toews 2012). We compiled and analyzed these data to examine whether patterns of diet breadth and diet overlap differed between the 2 regions. However, because many of the diet studies are comparatively old, and because the number of diet studies that are available is small, we regard this analysis as being suggestive, rather than confirmatory. Our major conclusions are drawn from our analyses of competition and spatial crowding, but because a reasonable number of diet studies have been conducted for these species, we believe that a comparison of diets can still be informative. We examined whether diet diversity for each species differed between Northern and Southern California. Diet diversity was measured by the Shannon-Wiener index: $H' = -\sum_{k} p_k \ln (p_k)$, where p_k is the proportion of prey type k in the species' diet. We also compared whether diet overlap for the 2 species differed between Northern and Southern California. Diet overlap was measured as proportional similarity of diets (PS):

$$PS = \sum_{k} \min(p_{ik}, p_{jk})$$
(5)

where the p_{ik} and p_{jk} are the proportions of the k^{th}



Fig. 2. Component-residual plots illustrating the average effect of black and striped surfperch densities on population growth in Northern California. (a,d) Intraspecific competition; (b,c) interspecific competition. Dashed lines: 95% confidence region

prey type in species i and j's diets, respectively (Schoener 1968).

RESULTS

In Northern California, population growth rates of black surfperch declined in response to increases in the densities of both black surfperch and striped surfperch (Fig. 2a,b). Similarly, population growth rates of striped surfperch decreased when the densities of black surfperch increased (Fig. 2c), and when densities of striped surfperch increased (Fig. 2d). Intraspecific competition (Fig. 2a,d) was stronger than interspecific competition (Fig. 2b,c), and there was a slight asymmetry in interspecific competition. Striped surfperch decreased the population growth rates of black surfperch more than black surfperch decreased the population growth rates of striped surfperch. Populations in Southern California exhib-



Fig. 3. Component-residual plots illustrating the average effect of black and striped surfperch densities on population growth in Southern California. (a,d) Intraspecific competition; (b,c) interspecific competition. Dashed lines: 95% confidence region

ited qualitatively similar results. Again, intraspecific competition (Fig. 3a,d) was stronger than interspecific competition (Fig. 3b,c).

The strength of competition differed between southern and northern regions. Specifically, our results suggest that for black surfperch, there was stronger intraspecific competition in the north than in the south (-0.611 vs. -0.035; Table 1). For striped surfperch, the pattern was opposite. Intraspecific competition was stronger in the south than in the north (-0.969 vs. -0.280; Table 1). We observed smaller differences in the magnitude of interspecific competition. Interspecific competition was moderate in the north, but weak in the south. In Northern California, growth capacities (r_{MAX} values) were estimated to be similar between the 2 species (Table 1). However, in Southern California, growth capacity of black surfperch was estimated to be slightly lower than growth capacity of striped surfperch (Table 1). The random effects of site and year accounted for little of the variation in per capita growth rates that was unexplained by competition. Including a random ef-

Table 1. Estimated coefficients of competition between black surfperch *Embiotoca jacksoni* and striped surfperch *E. lateralis.* Coefficients of intra- and interspecific competition describe how population growth rate (yr^{-1}) responded to a unit increase in the density of its own species or the density of its competitor. r_{MAX} represents the estimated population growth as the density of both conspecifics and competitors approaches zero

Region	Population	r _{MAX} Coef95 % CI Lower Upper		Intraspecific competition Coef. — 95 % CI — Lower Upper			Interspecific competition Coef. — 95 % CI — Lower Upper			Random effects % variation in <i>r</i> Site Year		
North	Black perch Striped perch	$0.499 \\ 0.444$	0.193 0.230	0.805 0.657	-0.611 -0.280	-0.879 -0.406	-0.342 -0.153	-0.131 -0.240	-0.319 -0.463	0.057 -0.017	4.82 0.00	7.94 4.04
South	Black perch Striped perch	0.072 0.230	-0.157 -0.009	0.301 0.469	-0.035 -0.969	-0.084 -1.343	-0.014 -0.594	-0.028 -0.046	-0.352 -0.107	0.295 0.015	$0.00 \\ 0.00$	7.05 0.00

fect of site accounted for 0 to 4.82% of the variation, and including a random effect for year accounted for 0 to 7.94% of the variation (Table 1).

Analyses of the zero growth isoclines suggest that the dynamic of competition between these 2 species was fairly straightforward (Fig. 4). Each species responded much more strongly to densities of its own species that to its competitor. In Northern California, the equilibrium point occurred at relatively low densities of black surfperch and relatively high densities of striped surfperch (Fig. 4a). Analyses of expected growth tendencies indicated that this equilibrium was stable in the long term. For example, if the system started out in the lower right quadrant, the population of the striped surfperch would increase toward the dashed line and the population of the black surfperch would decrease toward the solid line. The net movement of these 2 population densities (represented by the arrows in Fig. 4) would be toward the point of intersection. Similarly, if the system started in the top left quadrant, the population of striped surfperch would decrease and the population of black surfperch would increase. Again, the system would gravitate toward the intersection (equilibrium

Fig. 4. Analyses of population growth and competitive stability showing growth of surfperch populations in (a) Northern and (b) Southern California. Solid lines: zero-growth isocline for black surfperch (i.e. the combination of species densities for which average growth of the black surfperch population is zero). Dashed lines: zero growth isocline for striped surfperch. Arrows: expected change in densities for various regions of state space; large symbols: equilibrium points. (c) Observed densities of black and striped surfperch in Northern California (blue triangles) and Southern California (red circles). Large symbols indicate the estimated equilibrium points; lines indicate the 95% confidence region (dashed line: Northern California; dot-and-dashed: Southern California). Densities are expressed as number of fish per 60 m²



point), indicating stability. In Southern California, competition was also estimated to be stable, though the equilibrium point occurred in a different location (Fig. 4b). When comparing the equilibrium densities between Northern and Southern California, we found that black surfperch densities were ~3.3 times higher in the south and striped surfperch densities were ~7 times higher in Northern California. The 95% confidence regions for the estimated equilibrium points showed no overlap between Northern and Southern California, and the estimated equilibrium points were near the center of the observed densities, suggesting that average densities are near those that are expected at competitive equilibrium (Fig. 4c).

Analyses of crowding coefficients revealed significant differences in habitat use and spatial crowding between Northern and Southern California. In particular, black surfperch exhibited much greater increases in crowding with density in Northern California (Fig. 5). In contrast, striped surfperch exhibited much greater increases in crowding with density in Southern California (Fig. 5). These results are in agreement with our estimates of competition coefficients. Where spatial crowding was relatively strong, overall competition coefficients were also relatively high. Striped surfperch crowded black surfperch in proportion to population density in both Northern and Southern California (i.e. crowding coefficients were near 1; Fig. 5). However, striped surfperch experienced crowding by black surfperch in rates that increased faster than population density (i.e. crowding coefficients >1; Fig. 5). Black surfperch crowded striped surfperch slightly more in northern regions.

Patterns of diet breadth and overlap also differed between Northern and Southern California (Fig. 6). Black surfperch ate a more diverse assemblage of prey items in southern populations, and striped surfperch ate a more diverse assemblage of prey in the north. The overlap in these species' diets was greater in southern populations, although because sample sizes were low, statistical evidence of these differences was marginal in all cases (p-values for 2-sample, unequal variance *t*-tests were 0.088, 0.078, and 0.076, respectively).

DISCUSSION

We found that competition between striped and black surfperch differed between Northern and Southern California. However, the differences we

2.5 2 1.5 1.5 0.5 0 $BP \rightarrow BP$ $BP \rightarrow SP$ $SP \rightarrow SP$ $SP \rightarrow BP$ $SP \rightarrow BP$

Fig. 5. Regional variation in spatial crowding of black and striped surfperch. Crowding coefficients (mean \pm 95% CI) measure the degree to which a unit increase in population density increases mean crowding experienced by fish. BP \rightarrow BP: black surfperch crowding black surfperch; BP \rightarrow SP: black surfperch crowding striped surfperch; SP \rightarrow SP: striped surfperch crowding striped surfperch; SP \rightarrow BP: striped surfperch crowding black surfperch



Fig. 6. Regional variation (mean ± 95% CI) in black and striped surfperch dietary niche width and dietary overlap. For populations of a single species, dietary niche width was measured using the Shannon-Wiener index of diversity. Dietary overlap between the 2 species was measured using proportional similarity (see 'Mechanisms affecting strength of competition', Eq. 5 for details)

observed were not as expected. In the south, where waters are warmer and food is generally less abundant, we expected that competition would be more intense overall (e.g. Persson 1986, Vasseur & Mc-Cann 2005, Nakayama et al. 2016). Instead, the major difference we found was that intraspecific competition varied strongly between northern and southern regions, and for each species, intraspecific competition was weaker near the center of its range. Striped surfperch (the species with the more northern distribution) competed with members of its own species much more strongly in the south than it did in the north. Black surfperch (the species with the more southern distribution) competed with members of its own species more strongly in the north. Interspecific competition did not vary much between northern and southern regions.

Regional differences in the magnitude of competition were consistent with regional differences in habitat use and diet variation. Intraspecific crowding coefficients were higher for black surfperch in the north than in the south, suggesting that in northern populations, black surfperch exhibit greater shoaling and are more tightly concentrated in certain areas of the habitat. These patterns could reflect the grouping of black surfperch within favored depth zones and microhabitats (see Laur & Ebeling 1983 and Johnson et al. 2016, for detailed examples of how surfperch may cluster in space). For striped surfperch, the opposite was true, and intraspecific crowding coefficients were higher in the south. Black and striped surfperch have similar habitat preferences (Ebeling & Laur 1986) and if regional differences in crowding were driven by regional differences in habitat composition and configuration, we would expect that the 2 surfperch species respond in the same way. That the 2 species exhibited opposite patterns suggests that something else is causing this pattern. The dietary niche width of black surfperch was higher in the south, and the dietary niche width of striped surfperch was higher in the north, even though the statistical support of these trends was modest. Taken together, these results suggest that regional differences in competition were not driven by temperature or food availability. Rather, regional differences in competition may have resulted from differences in functional diversity (i.e. how populations of each species used resources). Populations with wider niches (at least with respect to habitat use and diet) experienced weaker intraspecific competition. Such effects are expected based on theory (e.g. Roughgarden 1972, Taper & Case 1985), and an interesting result of this study was that niches for each species were wider near the center of their geographic ranges. It is possible that a longer history of competition within the center of the range has resulted in greater specialization of individuals, and therefore wider niches overall (Van Valen 1965, Bolnick et al. 2007). Such

effects would explain why intraspecific competition was weaker for striped surfperch in the north, and weaker for black surfperch in the south.

Even though the magnitude of intraspecific competition varied among regions, overall we found that intraspecific competition was stronger than interspecific competition. These results are consistent with previous studies of these 2 species. Both Hixon (1980) and Schmitt & Holbrook (1986) studied interference competition within and between black and striped surfperch populations. These studies found that interspecific chases occurred less often than intraspecific chases (interspecific chases were 0.4 to 0.5 times as frequent). Similarly, the average, proportional similarity in diet was within the 0.3 to 0.5 range (data gathered from Ellison et al. 1979, Haldorson & Moser 1979, Schmitt & Coyer 1983, Ebeling & Laur 1986, Schmitt & Holbrook 1984, Toews 2012). By comparison, the average values of the interspecific competition coefficients estimated by this study were ~0.45 times the magnitude of their intraspecific counterparts. Overall, these results suggest that competition coefficients estimated from time series of densities are consistent with detailed, mechanistic studies of competition. The results also suggest that competition for food and foraging space (processes that were elucidated by intensive, small-scale field studies; e.g. Hixon 1980, Laur & Ebeling 1983, Schmitt & Holbrook 1986, 1990) do scale up to play major roles in the dynamics of these populations.

The fact that intraspecific competition was stronger than interspecific competition is also a major reason why competition between the 2 surfperch species is expected to be stable in the long term. In addition to indicating whether competition is stable, analyses of growth isoclines can reveal reasons leading to stability. For example, comparisons of growth isoclines often reveal a trade-off between colonization or reproductive capacity and competitive ability (Chesson 2000, Calcagno et al. 2006). When growth rates are modeled following Eq. (3), species 1 may invade if $r_{MAX1}/r_{MAX2} > \beta_{2,1}/\beta_{2,2}$ and species 2 may invade if $r_{\text{MAX2}}/r_{\text{MAX1}} > \beta_{1,2}/\beta_{1,1}$. Stable coexistence therefore depends on whether a species' relative capacity for population growth outstrips the relative /competitive effect of its competitor. In this study, estimated values of $r_{\rm MAX}$ were similar for the 2 species, and the ratio of population growth capacities was near 1. This is consistent with observed similarities in life history traits of these 2 species (including similarities in age at maturation and number of offspring; Baltz 1984). In contrast, the magnitudes of inter- and intraspecific competition were quite different, and the relative

competitive effects were much below 1 (i.e. a unit increase in density of a species decreased the growth of its own population much more than the population of its competitor). As a result, each species could invade at low densities. Because intraspecific competition was stronger than interspecific competition, when a species was abundant, it was more effective at driving down the numbers of its own population, thereby promoting coexistence. Although our results suggested that coexistence is stable, in Southern California the equilibrium point occurred at very low densities of striped perch (0.15 fish per 60 m²). These results are somewhat consistent with Bernardi's (2005) suggestion that striped surfperch may have been competitively excluded by black surfperch in some parts of Southern California. Competition keeps the density of striped surfperch at a consistently low level in Southern California, but the main driver appears to be intraspecific competition, rather than interspecific competition.

By analyzing the joint dynamics of the 2 surfperch species across 1050 km of coastline, we were able to measure competition throughout most of the spatial range within which these species co-occur. Such large-scale comparisons are critical for revealing how the dynamics of competition vary, and how such variation in species interactions may affect the structure and functioning of communities (e.g. Wiens 1989, Urban 2005, Hunsicker et al. 2011). This study was possible because of the efforts of RCCA—an organization of citizen scientists that monitors populations of nearshore fishes and invertebrates. Monitoring programs such as these are especially valuable because of the spatial and temporal coverage that an organization with a large number of volunteers can provide (Dickinson et al. 2010). Continued monitoring of nearshore species and thoughtful analyses of the data, including methods that account for the additional observer variability (e.g. Hochachka et al. 2012, Bird et al. 2014) will be essential for understanding the large-scale dynamics of marine species. Because such efforts are particularly useful for guiding conservation and management, we hope these programs receive support and continue to flourish.

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