

Genetic diversity affects the strength of population regulation in a marine fish

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Abstract. Variation is an essential feature of biological populations, yet much of ecological theory treats individuals as though they are identical. This simplifying assumption is often justified by the perception that variation among individuals does not have significant effects on the dynamics of whole populations. However, this perception may be skewed by a historic focus on studying single populations. A true evaluation of the extent to which among-individual variation affects the dynamics of populations requires the study of multiple populations. In this study, we examined variation in the dynamics of populations of a live-bearing, marine fish (black surfperch; *Embiotoca jacksoni*). In collaboration with an organization of citizen scientists (Reef Check California), we were able to examine the dynamics of eight populations that were distributed throughout ~700 km of coastline, a distance that encompasses much of this species' range. We hypothesized that genetic variation within a local population would be related to the intensity of competition and to the strength of population regulation. To test this hypothesis, we examined whether genetic diversity (measured by the diversity of mitochondrial DNA haplotypes) was related to the strength of population regulation. Low-diversity populations experienced strong density dependence in population growth rates and population sizes were regulated much more tightly than they were in high-diversity populations. Mechanisms that contributed to this pattern include links between genetic diversity, habitat use, and spatial crowding. On average, low-diversity populations used less of the available habitat and exhibited greater spatial clustering (and more intense competition) for a given level of density (measured at the scale of the reef). Although the populations we studied also varied with respect to exogenous characteristics (habitat complexity, densities of predators, and interspecific competitors), none of these characteristics was significantly related to the strength of population regulation. In contrast, an endogenous characteristic of the population (genetic diversity) explained 77% of the variation in the strength of population regulation (95% CI: 27–94%). Our results suggest that the genetic and phenotypic composition of populations can play a major role in their dynamics.

Key words: citizen science; competition; crowding; density dependence; eco-evolutionary dynamics; individual variation; niche width; population fluctuations; resilience; scuba surveys.

INTRODUCTION

The dynamics of a population are largely a reflection of how the population grows when small and shrinks when large. This type of negative feedback, referred to as density-dependent population regulation, is a prominent feature for the vast majority of wild populations (see meta-analyses by Sibly et al. 2005, Brook and Bradshaw 2006). Although regulation is common, our understanding of this process is far from clear. In the wild, density-dependent regulation is often a nonlinear process that may lead to complex dynamics (reviewed by Bjørnstad and Grenfell 2001, Sibly et al. 2005). Additionally, the degree of regulation can vary

widely, resulting in substantial differences in the dynamics of populations (reviewed by Sibly et al. 2007, Herrando-Pérez et al. 2012). Even within a single species, local populations can exhibit considerable variation in their dynamics, with some populations fluctuating extensively while others remain stable (e.g., Den Boer 1981, Fromentin et al. 2001, Gunnarsson et al. 2013).

Population regulation may result from competition and/or predation. In many cases, intraspecific competition is the underlying cause of density dependence in demographic rates. For example, at high densities, a relative shortage of resources can reduce average rates of reproduction, growth, and/or survival (see reviews by Connell 1983, Schoener 1983, Goldberg and Barton 1992). In other cases, predation is the primary cause of density-dependent regulation. This

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may occur if predators consume disproportionately more prey when prey are abundant (Holling 1959, Murdoch and Oaten 1975). Predation can also act in concert with competition, if competition makes prey more susceptible, and predation is the proximate source of mortality (reviewed by Hixon and Jones 2005). Population regulation is itself a dynamic process and the strength of density-dependent regulation may vary if the underlying mechanisms (competition and/or predation) are modified by other factors. For example, the abundance of interspecific competitors can have an effect on the carrying capacity of an environment and thus affect how strongly populations are regulated (e.g., Gilpin and Ayala 1973, Law and Watkinson 1987, Carr et al. 2002). Similarly, variation in food availability can affect the intensity of competition (e.g., Wissinger 1989). Density-dependent predation can be modified by availability of refuge space for prey (Holbrook and Schmitt 2002, Forrester and Steele 2004, Johnson 2007) and/or the local abundance of predators, especially when interactions among predators inhibit or facilitate the consumption of prey (Hixon and Carr 1997, Johnson 2006, Schmitt and Holbrook 2007).

Exogenous factors that modify density-dependent interactions are important and worth accounting for, but *endogenous* factors may also have important effects on dynamics. In particular, the role of genetic/phenotypic variability within a population needs to be considered more carefully. It is well documented that individuals within a population can use different sets of resources consistently and thereby occupy different niches (reviewed by Bolnick et al. 2003, 2007). Moreover, there are many examples where individual niche specialization has a confirmed, genetic basis (e.g., Christensen 1977, Via 1986, Jaenike and Holt 1991, Shine et al. 1998, Svanbäck and Eklöv 2006). If there is link between genotype/phenotype and how individuals use their environment and interact with one another, then this may have important consequences for population dynamics. Mathematical models that describe competition between two individuals as a function of their phenotypic similarity suggest that populations with greater genetic and phenotypic diversity may, on the whole, interact less strongly, leading to weaker population regulation and greater abundance in the long term (e.g., Bjørnstad and Hansen 1994, Doebeli 1996). Recent applications of similar models indicate that phenotypic variation can have a major effect on demographic rates. For example, within-cohort variation in phenotypic traits such as size and growth can be responsible for more than half the observed variation in mortality rates of juvenile fishes (Johnson et al. 2014).

Although theory suggests that the phenotypic/genetic composition of a population can have large effects, understanding the extent to which variation among individuals truly affects the dynamics of populations

requires detailed, empirical study. Particularly needed are large-scale studies that assess the effects of genetic variability by comparing the dynamics of multiple populations within a species' range. In this study, we examined variation in the dynamics of populations of a live-bearing, marine fish (black surfperch; *Embiotoca jacksoni*). In collaboration with an organization of citizen scientists (Reef Check California), we were able to examine the dynamics of populations throughout much of this species' range (i.e., over 4° of latitude and approximately 700 km of coastline). At these spatial scales, the dynamics of populations varied substantially. The purpose of this study was to evaluate how much of that variation could be explained by differences in genetic diversity within local populations. First, we examined the overall evidence of regulation within populations of black surfperch. Next, we tested the hypothesis that genetic variation within a local population would be related to the strength of population regulation in black surfperch. Finally, we examined whether diversity within a population was related to habitat use and spatial clustering: two related mechanisms that may affect the intensity of competition and, ultimately, the strength of population regulation.

METHODS

Study species

Black surfperch (*Embiotoca jacksoni*) are commonly found on nearshore reefs along the west coast of North America, and can be found in high abundance from Central California, USA to Baja California, Mexico (Miller and Lea 1972). Black surfperch tend to stay within 1 m of the seafloor, and feed on benthic invertebrates (e.g., Quast 1968, Alevizon 1975). They give birth to fully developed young and neither the adults nor young are likely to disperse from their home reefs (Hixon 1981, Bernardi 2000, 2005). Black surfperch thus exist within a collection of local populations whose dynamics may be largely independent of one another, even though there may be significant gene flow to nearby sites over long time scales. Moreover, the dynamics of local populations can be dramatically different. For example, from 1982 to 2008, populations on Santa Cruz Island exhibited large swings in abundance, resulting in a coefficient of variation (CV) of 80.6% and abundances that differed by up to a factor of 12.5 (Okamoto et al. 2012). In contrast, during a similar timespan (1975–1999), populations at King Harbor (≈120 km away) remained relatively constant (CV = 19.2%; abundances differed by up to factor of 2.6; Pondella et al. 2002).

The major force that regulates the dynamics of surfperch populations is competition. Individuals compete for a combination of space and food, and intraspecific competition can be very intense, as evidenced

by frequent aggression between conspecifics (Hixon 1980, Schmitt and Holbrook 1986). Males are territorial and defend both mating sites (caves) and food resources (patches of turf algae that harbor their invertebrate prey; Hixon 1981). Black surfperch also compete strongly with their congener, the striped surfperch (*Embiotoca lateralis*; e.g., Alevizon 1975, Hixon 1980, Schmitt and Coyer 1983, Schmitt and Holbrook 1984, 1986, 1990a,b, Holbrook and Schmitt 1989, Holbrook and Schmitt 1995). Although this additional source of competition typically reduces population size, intraspecific competition alone appears to be sufficient to regulate population size (Schmitt and Holbrook 1990a; *this study*).

Data

We used data collected by Reef Check California (hereafter RCCA), an organization of citizen scientists that conducts annual surveys of fish populations throughout the state. RCCA volunteers estimate fish densities using standard, underwater, visual survey methods (Freiwald et al. 2013). This program concentrates on monitoring sites (subtidal reefs that ranged from approximately 27 to 2300 ha in area) on an annual basis. During each survey fish are counted on 18 transects per site (transects are 30 m long by 2 m wide). Exact locations for transects are chosen at random but potential locations are stratified in space and by depth to ensure even coverage of the reef. The RCCA program produces estimates of fish density that are comparable to academic monitoring programs (Gillett et al. 2012), but an organization of citizen scientists with a large number of volunteers can provide far more spatial and temporal coverage than a typical academic program. Data from 45 sites throughout California were used in this study. Many of those sites have been monitored annually from as early as 2006 (Appendix S1). Importantly, black surfperch are large and easily recognizable, making count mistakes less likely than for more cryptic species. Species that are the main predators of black surfperch (kelp bass, lingcod, and rockfishes) are regularly counted as part of the surveys conducted by Reef Check California. The program also provides density estimates for striped surfperch, giant kelp, understory algae, and red algae, as well as estimates of substrate type and vertical relief.

Are black surfperch populations regulated?

To examine the overall evidence of whether black surfperch populations are regulated, we analyzed the relationships between per capita population growth and population density (number of fish per 60 m² transect, averaged across all transects within a site within a census). Population growth was measured as $\ln(N_{t+1}/N_t)$, where N_t is population density in year t and N_{t+1} is

density at the same site in the next year. A negative relationship between growth and density indicates regulation (when the range of growth values encompasses zero), and the steepness of the relationship indicates the strength of regulation (reviewed by Berryman et al. 2002). Because the relationship between growth and density was nonlinear (see Results section), we ln-transformed density before conducting any further analyses.

We used a linear, mixed-effects model to examine the overall relationship between population growth rate and the natural log of density. The data represent variation in densities at a given site, and because surfperch dynamics may vary among different sites, site was treated as a random effect and both the slopes and intercepts of the regression lines were allowed to vary among sites. We used a mixed-effects model to estimate regression parameters, but to test for significance, we used a randomization procedure to correct for bias. When population density (N_t) is estimated with uncertainty, the relationship between $\ln(N_{t+1}/N_t)$ and $\ln(N_t)$ can be biased downward because overestimates of N_t will result in underestimates of population growth (where N_t is in the denominator) and underestimates of N_t result in overestimates of population growth. To generate a null hypothesis that accounts for these biases, we conducted a simulation where we added measurement error to each of our observed densities and calculated the expected relationship between apparent density and apparent population growth when the true instantaneous rate of population growth was zero. We assumed measurement error was lognormally distributed such that 95% of the time, divers would have correctly estimated fish density within a factor of 3. In other words, many of the observed densities in the simulation were the true densities multiplied by a value near 1, but sometimes by a value substantially larger than or smaller than 1. Although it is not possible to know true measurement error in the wild, studies that compare estimates of fish densities from multiple, independent techniques suggest that our margin of error is conservative (Edgar et al. 2004), especially for black surfperch (Gillett et al. 2012). For each of 10 000 iterations, we simulated measurement error at random and then estimated the slope of the relationship between apparent growth and the natural log of apparent density as described above. We used the average slope value from these simulations as our null expectation of slope value, if population growth was truly independent of density. Note that the null expectation of the slope does not change with density. To test whether our observed slope was different than the value expected to be generated from measurement error only, we used a two-sample t test with unequal variances.

Does strength of regulation vary with genetic diversity?

For black surfperch, intraspecific competition is the primary mechanism generating density-dependent

regulation of population size (Hixon 1980, 1981, Schmitt and Holbrook 1986, 1990a, Okamoto et al. 2012). However, throughout the range of this species, the strength of competition is likely to vary among local populations. Given that local populations of black surfperch can vary substantially with respect to the amount of genetic diversity they harbor (Bernardi 2000, 2005), and that in general, genetic diversity may be related to the breadth of resource use within populations (reviewed by Hughes et al. 2008), we hypothesized that genetic variation within a local region would be related to the intensity of competition and to the strength of population regulation in black surfperch. To test this hypothesis, we analyzed regulation within eight regional populations where genetic diversity had been estimated in a previous study (Bernardi 2000) and where there were enough surveys to reliably estimate the strength of population regulation. The eight regions we analyzed included Monterey peninsula, Naples reef, Santa Cruz Island, Anacapa Island, Point Dume, Palos Verdes peninsula, Catalina Island, and Point Loma (Fig. 1). Each of these regions contained multiple sites that Reef Check divers had surveyed consecutively. In all cases, these sites were within 0.5–30 km of each other: close enough that they are likely to experience significant gene flow with each other and can be considered sites within a regional

population (Bernardi 2000, 2005), but isolated from other regional populations by breaks in habitat (e.g., deep water between islands or large expanses of soft-bottom habitat that black surfperch do not use; Fig. 1). The data exhibited a hierarchical structure in which multiple surveys were conducted at each site, and sites were nested within regional populations (see Appendix S1 for more details).

In our analysis, we first estimated the strength of population regulation within each of the eight regions and then tested whether strength of regulation varied with genetic diversity. To estimate the strength of regulation, we used a linear, mixed-effects model to describe the relationship between per capita growth rate and the natural log of population density. We included a random effect of site (nested within region) to account for differences in dynamics among sites within each region. Both the intercept and effect of density were allowed to vary among sites. We also included a random effect for year (nested within region) to account for region-wide variation in growth rate (e.g., among-year variations in temperature, food availability, etc.). Region was treated as a fixed effect, and we tested whether a model in which the strength of density dependence varied among regions (i.e., a model that included an interaction term) provided a significantly better fit than a model in which region affected

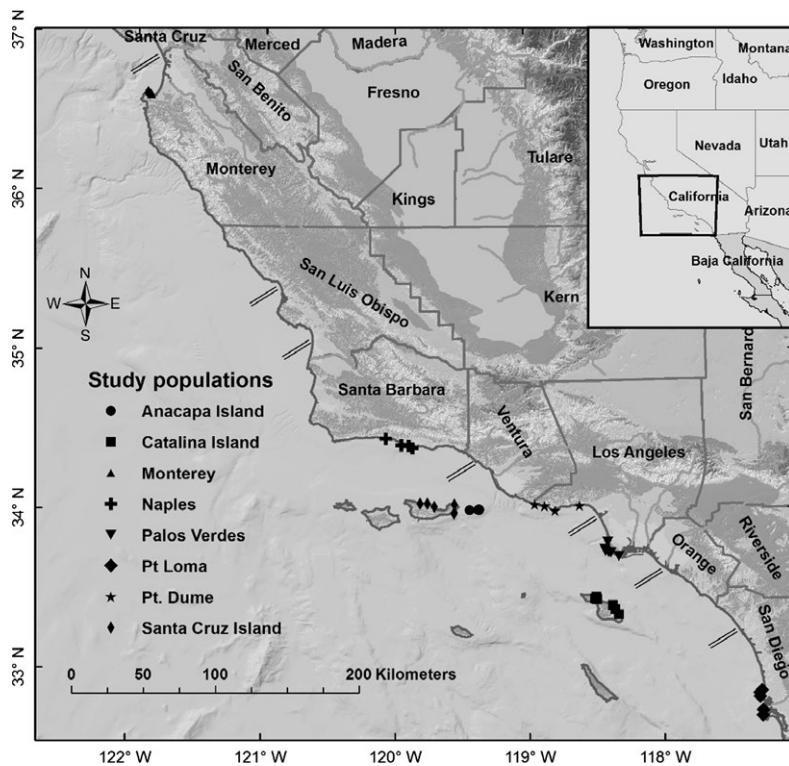


FIG. 1. Map of the study region. Dots indicate sites that are regularly surveyed and sites are grouped within eight regional populations. Double lines indicate locations of major habitat breaks (large expanses of sandy habitat that black surfperch do not use).

overall growth rate (i.e., no interaction included), and a model where the effects of region were omitted altogether. Because the strength of density dependence did vary among regions (see *Results* section), in the second step of this analysis, we used a correlation analysis to evaluate the relationship between genetic diversity at each region and slope of the relationship between population growth rate and density (i.e., our estimate of the strength of regulation). Genetic diversity was measured as the diversity of mitochondrial DNA (mtDNA) haplotypes (haplotype diversity), and was calculated as $h = (1 - \sum x_i^2) / n$, where x_i is the frequency of the i th mtDNA haplotype, and n is sample size within each population (Nei and Tajima 1981). While genetic diversity at neutral sites (such as the mitochondrial control region used here) is not always related to adaptive genetic diversity (Holderegger et al. 2006), variability of neutral sites is constrained when selection is present in other genomic regions (Corbett-Detig et al. 2015), and the two measures of diversity do tend to be positively correlated for many species (see reviews by Reed and Frankham 2001, Väli et al. 2008). This phenomenon is consistent with empirical results obtained for black surfperch based on nuclear markers such as allozymes (Waples 1987) and RAD markers (Longo, G, and Bernardi, G, *unpublished data*) where nuclear genetic diversity mirrored mitochondrial neutral genetic diversity.

Our confidence in any correlation between estimates of genetic diversity and estimates of the strength of density dependence will be affected by the degree of uncertainty in those estimates. To account for the effects of estimation uncertainty in our analyses, we used a resampling procedure to describe the distribution of correlation values that were likely to be produced from the data. For each of 10 000 iterations, haplotypes were resampled from each region, with the resampled number matching the original sample size. Diversity values were then calculated from the resampled data. Estimates of the strength of density dependence were also drawn at random. For each population, we sampled a value from a normal distribution that was specified by our estimates of the mean and standard error of the coefficient of density dependence for that region. We used the distribution of the resampled correlation values to estimate the sample distribution associated with the correlation between genetic diversity and density dependence.

Although our main hypothesis concerned the effects of genetic diversity, other factors may affect the strength of population regulation. For example, for other temperate reef fishes the strength of density dependence may be affected by the abundance of predators, the structural complexity of the habitat, or a combination of both (Nitschke et al. 2002, Johnson 2006, 2007, White and Caselle 2008, Ford and Swearer 2013). In this study, we used correlation analyses to test whether the strength of regulation was related to several factors

including habitat complexity (measured by the densities of both understory and canopy kelp), density of an interspecific competitor (striped surfperch, *Embiotoca lateralis*), and density of predators (see Appendix S2 for details). Similarly, genetic diversity may be related to population size and/or habitat area. Our examination of relationships between diversity, total population size, and the strength of regulation are summarized in Appendix S3.

Crowding, density, and genetic diversity

Measuring population density over time is a natural way of examining population dynamics when counts of the entire population are not practical. However, when densities are summarized as reef-wide averages, it may not be the most accurate way of summarizing the densities perceived by individual fish. Black surfperch commonly form aggregations and at the scales of the entire reef, populations may exhibit a patchy distribution. Because competitive interactions occur among nearby fish (Hixon 1980, 1981, Schmitt and Holbrook 1986), those fish living in high-density patches may experience more competition than fish in low-density patches. Knowing the density experienced by a typical fish, and how this quantity varies across populations and among years can shed light on variation in population dynamics.

In this study, divers counted fish on transects that were 30 m long by 2 m wide (18 transects per survey). To estimate the average density experienced by a typical fish, we calculated the number of neighbors each fish on each transect had and then averaged across all fish observed at each site during a survey (i.e., we calculated mean crowding; Lloyd 1967). If fish were spatially distributed at random, then the average, reef-wide density should match the mean crowding value. If mean crowding exceeds density, this indicates a clustered distribution. On the other hand, if mean crowding is less than density, this indicates that fish are more evenly dispersed in space. The absolute value of crowding will typically change with mean density. For example, as the overall population size increases, so will the density and the average number of fish within each group. It is therefore useful to plot the relationship between mean density (x -axis) and mean crowding (y -axis). If values are consistently above the 1:1 line, this indicates clustering. If they are consistently below, it indicates even dispersion. If the slope deviates from a value of 1, it indicates that the degree of clustering changes with overall density. Note that our sample size for this analysis is slightly larger than for evaluating dynamics because calculating annual growth rate requires two consecutive surveys whereas comparing mean density to mean crowding requires a single survey.

Our analysis proceeded in two phases. First, we evaluated which of three fundamentally different models

provided the best description of the relationship between crowding and density. The first model assumed that crowding remains constant with density (linear model with a slope value of 1 and intercept estimated by the data). The second allowed crowding to change with density, but assumed the pattern was linear (a linear model with both slope and intercept estimated by the data). The third allowed crowding to change with density in a nonlinear fashion (a power function with coefficients estimated by the data). We fit these models using maximum likelihood and compared model fit using AIC values (Burnham and Anderson 2002). In the second phase of the analysis, we tested whether the relationship between mean crowding and density varied among regions with different levels of genetic diversity. Because a power function provided the best overall description of the data (see *Results*), we used a nonlinear mixed-effects model (package nlme in R [Pinheiro et al. 2015]) to fit a power model with both coefficients as random effects. This procedure allowed us to describe the relationship separately for each of the eight regions. We used a correlation analysis to test whether the crowding coefficients were related to genetic diversity.

Genetic diversity and habitat use

For surfperches, the spatial dimensions of habitat use (especially depth) are important components of a population's niche. The availability and type of microhabitat (especially benthic algae and the associated communities of invertebrates that surfperch feed upon) depends strongly on depth (Alevizon 1975, Hixon 1980, Ebeling and Laur 1986, Schmitt and Holbrook 1986, 1990a,b, Holbrook and Schmitt 1995). Although most of the previous investigations of habitat use have focused on understanding how habitat mediates interspecific competition, it is reasonable to believe that all else being equal, populations that use the available habitat more narrowly will experience greater competition among conspecifics. If genetic diversity within a population is related to the breadth of habitat use within that population, it may be one mechanism through which genetic diversity affects the intensity of competition and the strength of local population regulation.

From the survey data, we measured evenness of habitat use by examining the spatial distribution of fish within a reef. For each survey, the 18 transects were separated into three groups of six transects: offshore transects (representing deep habitat; mean transect depth = 10.26 m), mid transects (representing mid depths; mean = 8.77 m), and inshore transects (representing shallow depths; mean = 7.61 m). We counted fish found within each of these three depth categories and calculated evenness as

$$\frac{-\sum_i^3 p_i \log(p_i + 0.001)}{\log(3)},$$

where p_i is the proportion of fish within the i th depth category. A small constant (0.001) was added because sometimes the number of fish with a depth category was zero. This occurred only when densities were very low. Values of evenness of habitat use were averaged for each study location.

The distribution of habitat use always depends on population size. For example, at the lowest of densities (when a single fish was observed in the entire survey), the value of evenness would be zero (the fish could have been observed in only one of the depth categories). As population size increases, evenness values would increase as fish inhabit different areas of the reef. However, the degree to which a population distributes itself among the available habitat at a given population size may vary among local populations, and in turn, this may be related to diversity. To examine this variation, we first plotted the relationship between average density at each site and average evenness of habitat use and modeled the overall relationship as an asymptotic function

$$E = E_{\max}(1 - e^{-kd})$$

where E is evenness of habitat use, d is density, E_{\max} is the maximum evenness observed when values of density are high, and k is a scaling constant describing how quickly that maximum is reached. Note that although E_{\max} is a maximum, we expect the overall relationship to vary among sites and our estimate of this parameter is best thought of as an average of the within-site maximums. After fitting the asymptotic function to the relationship between evenness of habitat use and density, we calculated the residuals for each population and examined whether the average values of these residuals for the eight regions in our study were correlated with genetic diversity (diversity of mtDNA haplotypes). Negative values of the residual would indicate that habitat use (for a given population size) is narrower than average and that a population would use the extent of the available habitat relatively slowly as density increased. Positive values would indicate the opposite.

RESULTS

The relationship between population growth rate and the natural log of density was well described by a linear model (Fig. 2). Even when assuming a substantial amount of measurement error in the estimates of fish densities (i.e., 95% of the time densities of fish are estimated within a factor of 3), the statistical evidence of population regulation was strong. A two-sample t test comparing the observed value of the regression slope (-0.787 ; $SE = 0.070$) to the expected value that could result from a measurement error and subsequent bias (-0.262 ; $SE = 0.02$) yielded a low P value ($P < 1.0 \times 10^{-16}$).

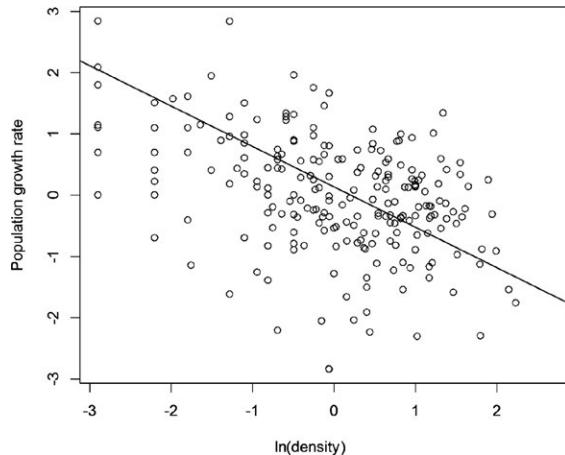


FIG. 2. Overall relationship between density of black surfperch populations (measured as fish/60m²) and annual, per capita growth rate. Regression line was calculated with a mixed-effects model that allowed for variation among sites. Data represent a total of 225 measurements of population growth conducted at 45 sites throughout Central and Southern California, USA.

Consistent with the strong, overall evidence of regulation, each of the eight regions exhibited a negative relationship between density and population growth (Fig. 3). However, the strength of these relationships varied substantially among regions. A mixed-effects model in which the effect of density interacted with the effect of region produced a significantly better fit than a model without the effects of region ($\chi^2 = 69.53$, $df = 14$, $P = 2.35 \times 10^{-9}$) and better than a model in which region affected only the overall level of population growth (i.e., no interaction; $\chi^2 = 18.08$, $df = 7$, $P = 0.011$). For example, Anacapa Island (Fig. 3, top row, middle panel) experienced strong population regulation (indicated by a steep slope), whereas regions such as Palos Verdes (Fig. 3, middle row, right panel) and Catalina Island (Fig. 3 bottom row, left panel) exhibited weaker relationships between population growth rate and density. These patterns suggest that when perturbed, the Anacapa population will return to equilibrium (density at which instantaneous growth = 0) relatively quickly. In contrast, populations at Palos Verdes and Catalina Island are much more likely to experience extended fluctuations in abundance.

Much of the among-region variation in the strength of population regulation was explained by variation in genetic diversity. Regions with low diversity of mtDNA haplotypes experienced strong regulation (i.e., steep relationships between density and growth rate) and regions with high diversity experienced weak regulation (Fig. 4). Values of the magnitude of density dependence (estimated using a linear mixed-effects model) were strongly correlated with values of genetic diversity ($r = -0.88$). This relationship holds up even when allowing for added uncertainty associated with

estimates of genetic diversity and density dependence (95% CI: -0.978 to -0.527). Among these same eight regions, the strength of density dependence was not correlated with any other habitat characteristics, including abundance of interspecific competitors, predators, or structure-forming algae (Appendix S2). In addition, none of these other factors were correlated with genetic diversity, nor was there a clear spatial pattern of variation in diversity (i.e., there were low-diversity sites in both the north and south regions of this study). We found no significant correlations between attributes of population abundance (habitat area and total population size) and either genetic diversity or the strength of density dependence (Appendix S3).

Crowding, density, and genetic diversity

The relationship between mean crowding and density was nonlinear (Fig. 5A). Crowding increased with density, and the vast majority of crowding values were greater than corresponding values for density. These patterns thus indicated a clustered distribution, which is not surprising for reef fish. Because the spread in the data increased at higher densities, we modeled the error distribution to be normal with variance increasing as an exponential function of density. A power function fit the data better than a linear model, which fit the data better than a line with a slope value of 1 ($AIC_{\text{power}} = 1211$, $AIC_{\text{linear}} = 1215$, $AIC_{\text{linear, slope} = 1} = 1260$), confirming that at low densities, a unit gain in density resulted in a proportionally greater increase in crowding (and likely, competition) than a unit increase in density when densities are high. These data are consistent with the observed, nonlinear pattern of density dependence. Because population growth rate declines linearly with the log of density, it implies that growth rate declines sharply with density when densities are low, but changes less dramatically when densities are high. Such patterns are expected if the change in crowding and competition with density is intense at low densities, but relatively relaxed when densities are high (Fig. 5A inset).

The fit of a nonlinear mixed-effects model indicated much greater variation in the exponent of the power function (which describes how crowding scales with density) than the multiplicative coefficient (which describes crowding when density = 1). Standard deviations were 0.04 and 1.8×10^{-6} respectively). These results suggested that among-region variation in how crowding scaled with density could be well summarized by examining differences in the “crowding exponent” – the exponent of the power function. Moreover, predicted values of the crowding exponent were negatively correlated with genetic diversity ($r = -0.79$, $P = 0.02$), indicating that more diverse populations experience less crowding at a given level of density (Fig. 5B).

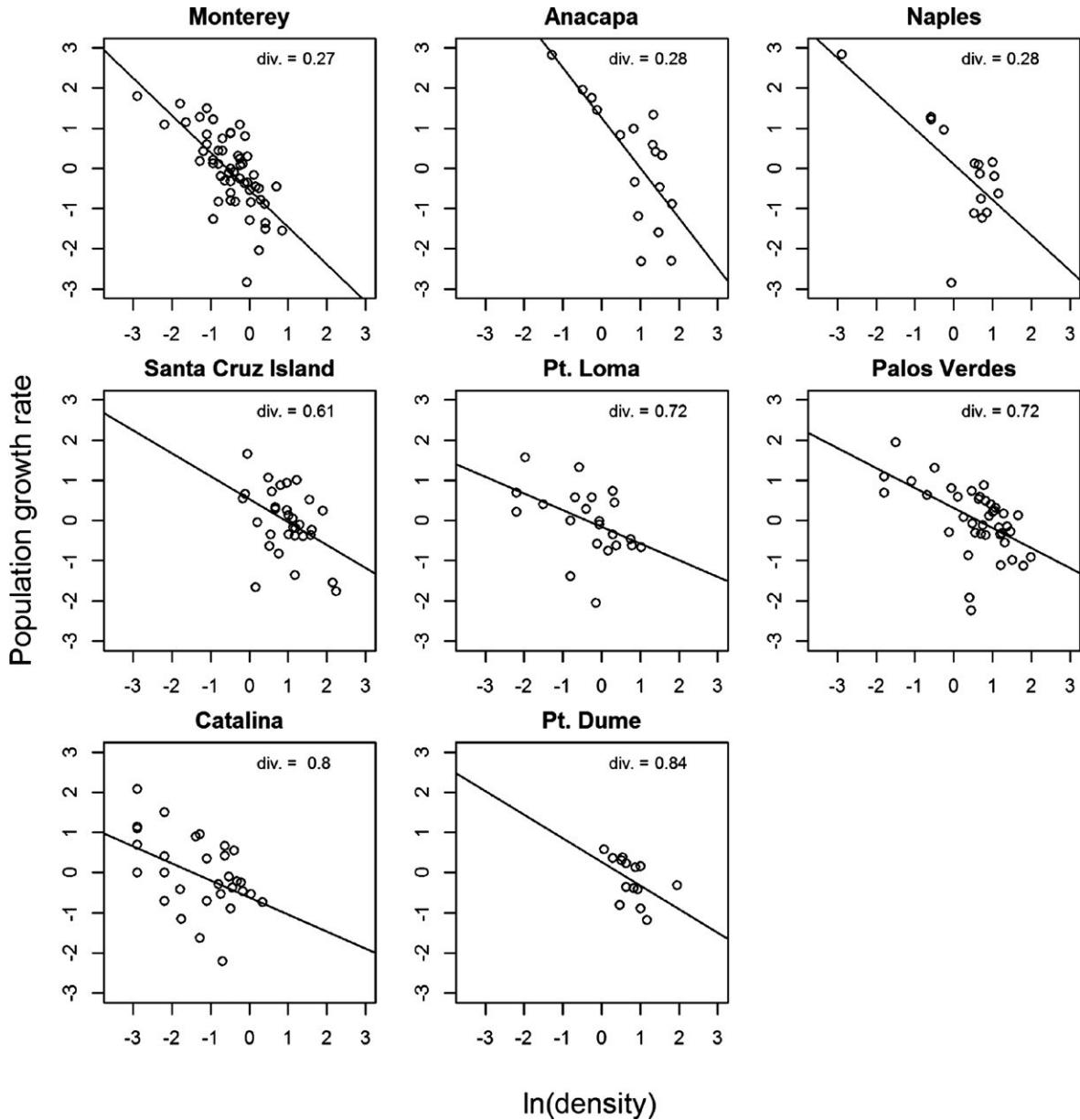


FIG. 3. Relationship between density of black surfperch and annual, per capita growth rate for each of eight populations. Values of genetic diversity (div.) represent Nei and Tajima's (1981) index applied to mitochondrial DNA haplotypes. Regression lines were predicted from coefficients of a mixed-effects model that allowed both the slope and intercept to vary as random effects.

Genetic diversity and habitat use

The evenness of habitat use increased sharply with density before levelling out (on average) at a value of approximately 0.84 (Fig. 6). There was substantial variation in this relationship and much of that variation appears to be related to genetic diversity. Residual values for evenness of habitat use were correlated with values of genetic diversity (Spearman's rank correlation, $\rho = 0.74$, $P = 0.046$, Fig. 6B). These results suggest that fish in low-diversity regions use

the available habitat less evenly than their high-diversity counterparts. There were no obvious patterns in habitat preference. Two of the three low-diversity regions used the shallow habitats the most and the other region preferred the middle depths. A similar mix of habitat preferences were observed for the five regions with high values of diversity. Although striped surfperch can outcompete black surfperch and force black surfperch to marginal habitats (Hixon 1980, Schmitt and Holbrook 1986, 1990a,b, Holbrook and Schmitt 1989, 1995), across the eight regions studied,

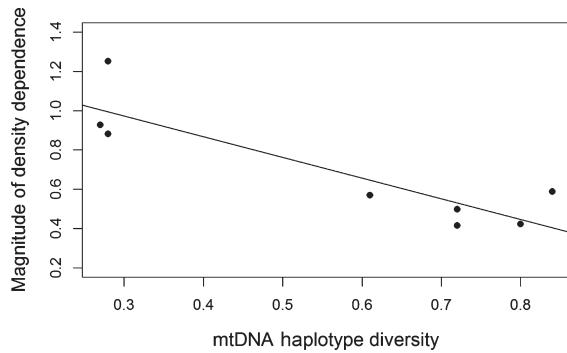


FIG. 4. Relationship between diversity of mitochondrial DNA haplotypes and strength of population regulation (measured as the magnitude of the slope of the relationship between density and growth rate for each of the populations).

residual evenness of habitat use did not correlate significantly with the density of striped surfperch ($r = -0.19$, $P = 0.65$), nor was there a detectable shift in habitat preference along a gradient of striped surfperch densities.

DISCUSSION

Genetic variation within populations is a fundamental source of biodiversity, and despite the growing evidence that genetic diversity can have significant ecological consequences (reviewed by Hughes et al. 2008, Forsman 2014) the role that genetic variation plays in the dynamics of wild populations is often unclear. Here we have shown that genetic diversity within populations may have a strong influence the strength of population regulation. We identified two related mechanisms that link genetic diversity to diversity in resource use, and our results are consistent with the idea that greater genetic variation within a population translates into greater separation of individual niches (e.g., Bolnick et al. 2007). In high-diversity populations, black surfperch were distributed throughout the habitat much more evenly and exhibited a lower amount of crowding at a given density. In low-diversity populations, black surfperch used less of the available habitat and tended to aggregate more. Because competition is expected to be more intense between individuals in close proximity and using the exact same resources, these mechanisms help explain why population regulations was observed to be much weaker in high-diversity populations of black surfperch.

For black surfperch, depth of habitat is an important dimension of their niche. Depth is correlated with light, temperature, substrate type, and availability of prey. Black surfperch show clear preferences for certain depth zones (Alevizon 1975, Hixon 1980), though much of their distribution by depth may be driven by the distribution of microhabitats that they prefer to feed on and/or habitat features that provide cover (Laur and Ebeling 1983,

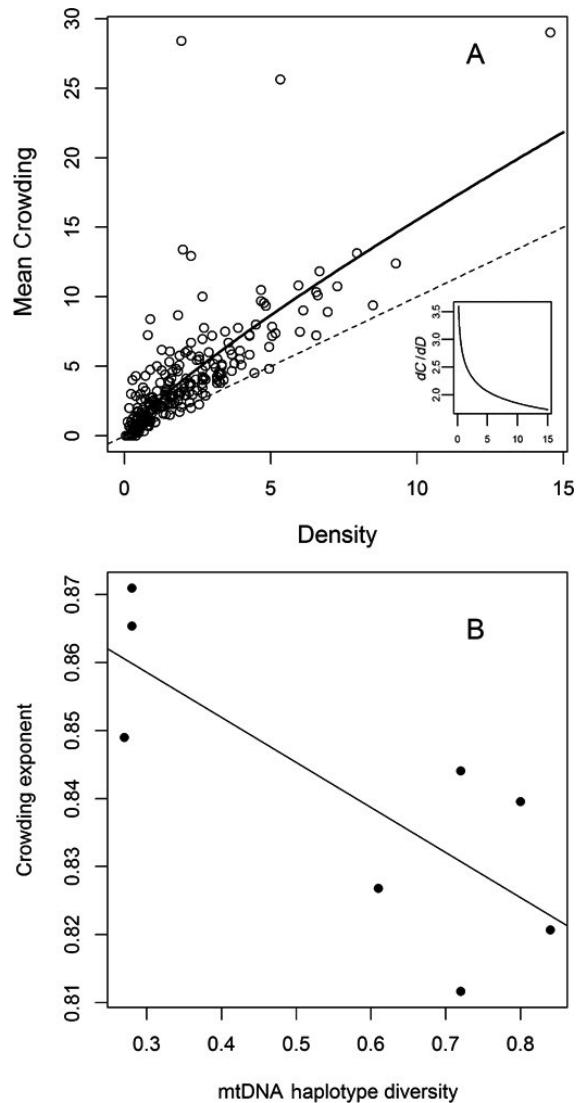


FIG. 5. Variation in the degree of crowding experienced by black surfperch. (A) Relationship between mean crowding (Lloyd 1967) and density. Each dot represents a census of a particular study site (45 sites total, mean number of censuses per site = 6.06). Dashed 1:1 line indicates the expected value of crowding if fish were randomly distributed throughout the habitat. Values above the line indicate a clumped distribution, values below indicate an even distribution. Solid, curved line illustrates the average value of mean crowding, as predicted by a power function of density. The inset describes the rate at which crowding changes with density (dC/dD) and was calculated as the derivative of the curved line in the main plot. (B) Relationship between genetic diversity and estimates of the exponent of the power function relating crowding to density for each of the eight populations.

Ebeling and Laur 1985 Holbrook and Schmitt 1989). Our results suggested that at low densities, fish tended to be concentrated in one of the three depth zones, but that there was no universal preference for depth zone (e.g., some populations preferred shallow depths, others

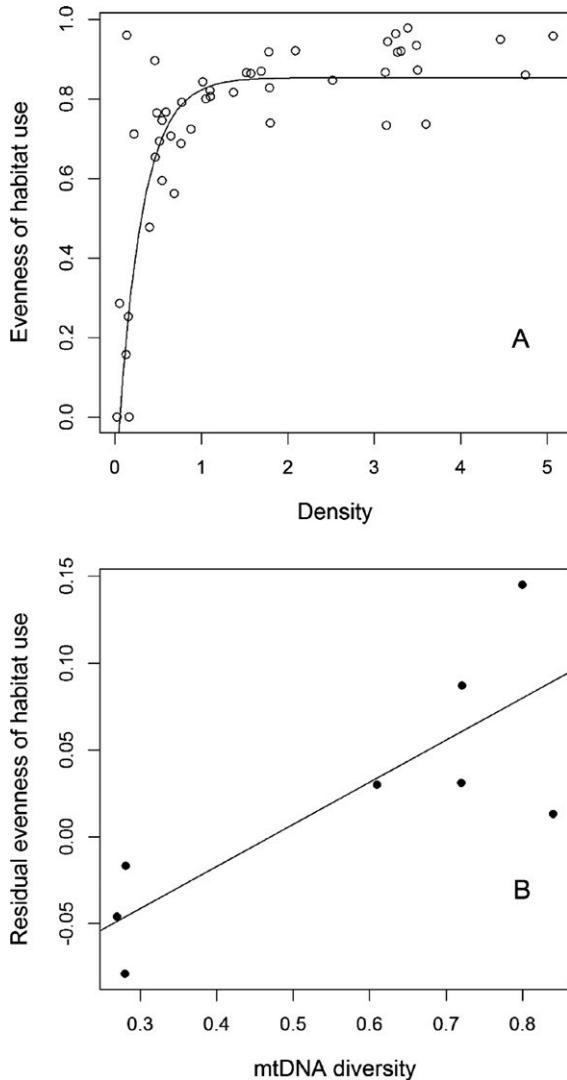


FIG. 6. Variation in the distribution of black surfperch into three habitat zones (deep, mid, and shallow). (A) At the lowest of densities, fish were concentrated in one or two zones, but as density increased habitat use became much more even. (B) Relationship between genetic diversity and residual evenness of habitat use (deviations from the overall pattern in A). Positive values indicate a faster approach toward evenness (i.e., a steeper relationship in part A). Negative values indicate the opposite.

preferred medium depths). When densities were high, fish were more evenly dispersed throughout the reef. At a given density, high-diversity populations tended to be more evenly distributed in space. This suggests that populations with high levels of genetic diversity are made up of individuals with a greater variety of habitat preferences. By distributing themselves more evenly throughout the reef, high-diversity populations may experience lower levels of competition through less crowding and less overlap in diet.

Although black surfperch are not characterized as a strongly schooling species, they do tend to form

aggregations, and our results confirm that they exhibit a clustered distribution at the scale of the reef. The degree of crowding increased sharply at low densities, but then leveled off at high densities. These patterns are consistent with an intermediate optimum for group size. In general, it is thought that fitness increases as singletons and pairs form small groups, but as group size becomes too large, the reduction in resources per individual outstrips the benefits of group living (Clark and Mangel 1986, Booth 1995, Hoare et al. 2004). Our data suggest that individuals form groups more rapidly at low densities (i.e., the relative rate of crowding is high at low densities). However, when densities were high, fish formed a greater number of mid-sized groups (rather than few, large groups), and these groups were more evenly dispersed in space. This nonlinear increase in crowding with density may be one of the reasons for the overall, nonlinear pattern of density dependence. Because population growth rate declined linearly with the natural log of density, density-dependent interactions are expected to be strong at low densities but relatively weak when densities are high. Such patterns of density dependence appear to be the norm in wild populations. In a large meta-analysis, Sibly et al. (2005) found that 78% of 1780 wild populations studied exhibited a non-linear, “convex” pattern of density dependence in which population growth rate declines rapidly as densities increase, but then levels out at high densities. Many species exhibit spatial clustering, and if competition is effected through local interactions rather than depletion of resources throughout the population, then population regulation may be more directly related to crowding, and overall patterns of density-dependent population growth may be convex (see models by Brännström and Sumpter 2005). Our study confirms this theoretical prediction and suggests that spatial clustering may play a large and overlooked role in the dynamics of populations.

The effects of genetic diversity on the relationship between crowding and density help explain why the strength of density dependence varied among populations. In high-diversity populations, crowding increased less rapidly with density, suggesting that in high-diversity populations increases in density had less of an effect on per-capita competition than increases in density in low-diversity populations. Such effects are expected to manifest as differences in the slope of density dependence between high- and low-diversity populations. Moreover, a prior study suggests that the degree of crowding within a population may be related to genetic diversity. In a set of laboratory experiments, Sikkell and Fuller (2010) found that juvenile black surfperch have a very strong preference for schooling with close relatives (broodmates) over unrelated individuals of the same size and age. These results imply that all else equal, populations with lower genetic diversity and greater average relatedness should experience a greater degree

of crowding. An emergent consequence of this behavior would be greater competition and stronger regulation of low-diversity populations.

In this study, we were able to examine how genetic diversity was related to habitat use and crowding. However, we believe that these two mechanisms are only part of the reason why genetic diversity is related to population regulation. In particular, among-individual variation in diet is likely to play a major role in ameliorating competition. Although there is not enough published information on black surfperch diets to conduct a formal analysis, our results can be interpreted in the light of a few prior studies. Schmitt and Coyer (1983) measured dietary niche width as proportional similarity (PS) to a sample of prey in the environment. They found that niche width was relatively high at Santa Catalina Island, one of our high-diversity sites that had relatively weak regulation (PS = 0.75; mtDNA diversity = 0.80), and lower at Santa Cruz Island, one of our medium-diversity sites with moderate regulation (PS = 0.60; diversity = 0.61). In addition, we applied the same measure of proportional similarity (Feinsinger et al. 1981) to data collected at Naples reef (Laur and Ebeling 1983). Naples reef is one of the lowest diversity sites in this study and it had the lowest niche width and strong regulation (PS = 0.55; diversity = 0.28). These data suggest that diet diversity may correlate with genetic diversity, though further studies will be required to evaluate these relationships in sufficient detail.

In this study, we found that genetic diversity of black surfperch populations had a large effect on their dynamics. Based on the relationship between genetic diversity and strength of density dependence in population growth, we expect that high-diversity populations will be 4–6 times more variable and 1.5–2 times more abundant than low-diversity populations, when all other factors (especially density-independent growth rate and environmental variation in population growth) are equal. Moreover, much of the observed variation in the strength of density-dependent regulation was explained by genetic diversity, an endogenous characteristic of populations ($r^2 = 0.77$ for the relationship in Fig. 3; 95% CI: 0.27–0.94). This variation would be missed by traditional models of population dynamics that treat individuals as identical. Our study highlights the importance of understanding how variation among individuals collectively affects the dynamics of populations. Future research within this field, especially studies of population dynamics that explicitly quantify individual variation in phenotypes, will be essential for improving our understanding of community ecology (Bolnick et al. 2011), the ecological effects of biodiversity (Hughes et al. 2008, Forsman 2014), and the reciprocal effects between ecology and evolution (Ezard et al. 2009, Becks et al. 2010, Schoener 2011).

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