



# Geographic variation in demography of black perch (*Embiotoca jacksoni*): Effects of density, food availability, predation, and fishing

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## ABSTRACT

It is well known that demographic rates such as growth and mortality may vary among populations, but the degree of variation in demography is often unknown, especially when considering multiple populations at large spatial scales (e.g., across hundreds of kilometers). Likewise, of the many factors that may affect demography, it is often unknown which are the major factors responsible for spatial variation in demographic rates. In this study, we estimated rates of growth and examined age distributions within nine populations of black perch (*Embiotoca jacksoni*) distributed across ~350 km of coastline. We tested whether spatial variation in demography was associated with several explanatory variables including population density, predator density, food availability, and fishing activity. Our study revealed a substantial amount of spatial variation in demographic rates. Among-population variation in growth accounted for 55% of the total variation, and the coefficient of variation for mean age within a population was 27%, suggesting substantial variation in mortality. Spatial variation in growth was most sensitive to variation in food availability and mean age was lowest at locations with high levels of spearfishing activity. Although the fishery for black perch is not a major one, fishing mortality rates may be very high in some areas. Overall, our results shed light on the ecological forces that shape demographic variation of this species, and suggest that fishing mortality may have a major influence on the dynamics of perch populations.

## 1. Introduction

Demographic rates such as growth and mortality may vary among local populations, but the magnitude of such variation is often unknown. This is especially apparent when considering multiple populations distributed across large geographic regions (Wiens, 1989). Across large spatial ranges, organisms are likely to encounter greater variation in biotic and abiotic factors that may influence demographic rates, and therefore the dynamics of populations (Levin, 1992; Urban, 2005). However, for particular species it is often unclear which factors (e.g., food availability, predation, etc.) are the most important sources of variation in local demography. In order to understand the dynamics of the population at large – and to improve species' management (e.g., Murawski et al., 2001; Hamilton et al., 2011; Scharf et al., 2017) – we need a greater understanding of the degree to which demographic rates vary among populations, and which environmental factors are the most important drivers of variation in demography.

Many ecological and environmental factors may be responsible for variation in growth and mortality rates. One potentially important driver of variation in demography is variation in population density.

The effects of density on population dynamics are widespread, and have been identified as important for the vast majority of species for which the effects of density have been studied in detail (reviews by Sibly et al., 2007; Brook and Bradshaw, 2006). In part, this is because increases in the density of conspecifics can increase competition for resources, which often result in decreases in growth rates (e.g., Lorenzen and Enberg, 2002). Competition may also reduce growth if increases in population density result in more energy being devoted to processes such as competitive interference or territory defense (e.g., Warner and Hoffman, 1980; Moksnes, 2004; Johnson, 2008). Finally, increases in population density may result in an increase in mortality rates, especially if competition results in individuals being relegated to riskier areas of habitat (Holbrook and Schmitt, 2002), or if competition and food shortage results in individuals being smaller than expected and/or undernourished (Hixon, 1980).

Effects of population density on demographic rates may be most apparent when resource levels are constant. However, it is possible that variation in resources such as food may overwhelm the influence of other factors such as variation in population density. Variation in the abundance of food will usually affect growth rates, yet the degree to

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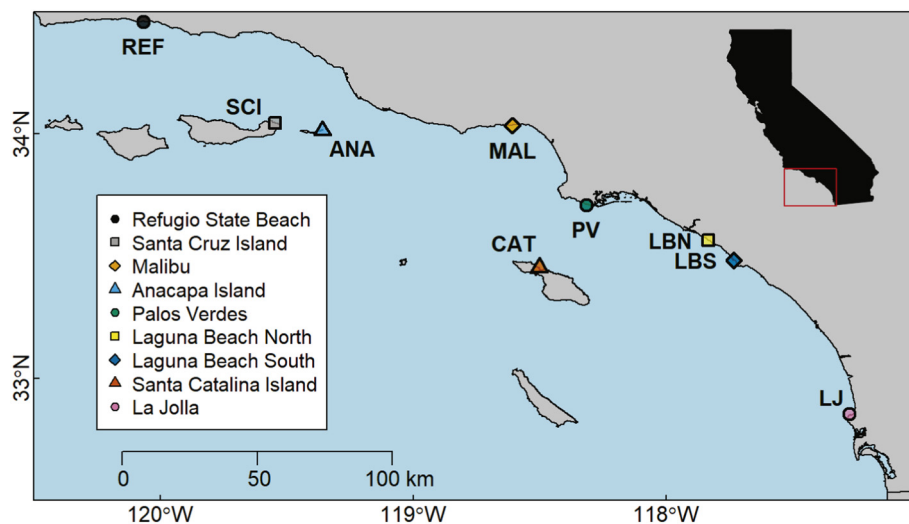


Fig. 1. Map of the study region, and locations of the nine study populations within Southern California, USA.

which food availability varies among populations is rarely known. It is also unclear how sensitive populations are to a change in the availability of food. In some cases, food may be limiting and responses of growth rates may be strong (e.g., Jones, 1986; Anderson and Sabado, 1995; Levin et al., 1997) whereas in other cases growth rates may not be sensitive to changes in food availability (e.g., Barrett, 1999), suggesting that other factors limit growth. Food availability may also affect mortality rates, especially if mortality is size-dependent (reviewed by Sogard, 1997) and if greater food availability leads to greater size for a given age.

The abundance of predators may also affect rates of growth and mortality (review by Hunsicker et al., 2011). Where and when predators are abundant, they may simply consume a greater proportion of the prey population, and thereby increase average rates of mortality. In addition, increases in the number of predators may increase prey vigilance (Lima and Dill, 2011). Such changes in prey behavior can restrict foraging opportunities, and may ultimately result in a reduction in growth rates (Milinski, 1986). Top predators such as piscivorous fishes often exhibit a large degree of spatial variation in their abundance. Piscivorous fishes are often the preferred targets of commercial and recreational fishing (Pauly et al., 1998; Coleman et al., 2004) and spatial variation in fishing pressure can lead to geographic variation in the abundance of predators (e.g., Schroeder and Love, 2002; Friedlander and DeMartini, 2002; Stallings, 2009). Intermediate trophic level species may also be the targets of fishing by humans, and spatial variation in fishing activity may be a direct driver of variation in mortality rates (e.g., Godoy et al., 2010; Frisch et al., 2012).

We studied spatial variation in growth and age distributions of black perch (*Embiotoca jacksoni*). Black perch are a common inhabitant of nearshore reefs along the west coast of North America, and can be found from Central California, USA to Baja California, Mexico (Miller and Lea, 1972). Black perch feed on benthic invertebrates and range from 5 to 25 cm standard length (SL) in our study region. The dynamics of black perch populations are affected strongly by density-dependent competition (Schmitt and Holbrook, 1990; Okamoto et al., 2012, 2016; Johnson et al., 2016; Johnson and Dunk, 2018), though it is not altogether clear which demographic rates are affected by density. There is also evidence that variation in food availability can affect dynamics of black perch. In particular, Okamoto et al. (2012) demonstrated that for a population near Santa Cruz Island, California, increased food availability was associated with increased production and survival of young of the year. Further research at this location also suggested that increased food supply can increase survival of adults (Okamoto et al., 2016). The magnitude of spatial variation in food availability, and its

effects on perch remain unexplored. Black perch risk predation by kelp bass (*Paralabrax clathratus*), a piscivorous serranid that can grow up to 72 cm SL (Eschmeyer et al., 1983). Black perch are also fished to some extent and are often caught by spear (California Department of Fish and Wildlife, 2014). The risk of both forms of predation is variable in space. Kelp bass densities vary both naturally and as a result of spatial variation in fishing history. Spearfishing activity varies primarily with factors such as proximity to urban areas, access from shore, and water clarity. Finally, black perch may compete with striped perch (*Embiotoca lateralis*) for habitat and subsequent access to food (Hixon, 1980; Schmitt and Holbrook, 1986). Field experiments removing striped perch for a period of four years resulted in an increase in the population density of black perch (Schmitt and Holbrook, 1990). However, striped perch are not very abundant in Southern California and even in regions where striped perch are abundant (Northern and Central California) large-scale analyses of population dynamics suggest that interspecific competition is only ~ 25% as strong as intraspecific competition (Johnson and Dunk, 2018).

We measured growth and age distributions of black perch by catching and ageing fish from nine separate populations located within Southern California. Patterns of body size at age were used to measure growth, and age distributions were used to make inferences about relative rates of mortality. In addition, we measured food availability at each of our study populations and obtained concomitant measures of predator density and fishing activity. Our goals were to evaluate the degree to which growth and age distributions varied among our study populations, and to test whether spatial variation in growth and age distributions were associated with the potential explanatory variables of population density, food availability, kelp bass density, and spearfishing activity.

## 2. Methods

### 2.1. Sample collection

Fish were collected from nine separate populations located within Southern California. Study locations ranged along ~350 km of coastline from Refugio State Beach, Santa Barbara County (34°27'39" N, 120°3'58" W), to La Jolla, San Diego County (32°51'11" N, 117°16'36" W; Fig. 1). Study locations were 140 km apart, on average, and the mean distance to the nearest study location was 41 km. Black perch do not have a larval stage, and offspring are born to the same reef as their parents (Behrens, 1977). At these spatial scales, black perch populations exhibit little-to-no connectivity via movement of individuals, and

even over much longer timescales, gene flow is very limited (Waples, 1987; Bernardi, 2000, 2005). The locations in this study thus represent independent, local populations. Within these populations, collections were made by SCUBA divers using spears or hand nets. Fish were collected opportunistically as they were encountered, and effort was made to sample as representatively as possible, especially with respect to characteristics such as fish size and microhabitat location. Collections were made during the summers of 2015, 2016, and 2017, and collections were made between the months of June and October. Approximately 30 fish were collected from each region (total number of samples = 284). The sex of the fish was identified by examining external morphology. Both the left and right sagittal otoliths were extracted from each fish and photographed under a dissecting microscope. Images were archived, and several months later annual growth rings were counted to estimate each individual's age. Otolith images were read blind with respect to fish's size, and counts of growth rings were made by a single observer.

To estimate an individual's age, we used counts of annual rings in the otoliths to estimate birth year and we refined this estimate by adding the difference between the collection date and birth date (assumed to be May 1st – the approximate average time of parturition in our study region; *pers. obs.*). For example, a fish that was collected and measured at the beginning of June and had one annual ring would be estimated to be 1.08 years old (1 year plus one month) whereas a fish collected at the very end of October that had one annual ring would be estimated 1.5 years old (1 year plus 6 months). Although the birthing season is 1–2 months long in our study region (*pers. obs.*) this variation is small relative to the variation in collection dates, and the overall procedure provides a much more accurate description of age and growth than assigning fish to discrete age classes (0+, 1+, 2+, etc.).

In addition to collecting fish, we also estimated the density of prey available at each population. At each collection location, we sampled benthic invertebrates by haphazardly placing 15 cm × 15 cm quadrats on the seafloor then transferring the contents of the quadrat to plastic bags (mean number of samples per site:  $\bar{x} = 9.6 \pm 3.5$  SD). Benthic samples were taken immediately following fish collection and were usually composed of algae and “turf” that black perch forage within for invertebrates. Invertebrate prey included gammarid and caprellid amphipods, gastropods, bivalves, isopods, tanaids, polychaetes, and ophiuroids (order is from most to least frequently observed). Each sample of algae and benthos was washed in fresh water to cause invertebrates to detach and filtered through a sieve to remove large pieces of algae and debris. Invertebrates were counted under a dissecting microscope. Density of prey was expressed as number of invertebrates per m<sup>2</sup> of seafloor sampled.

## 2.2. Analyzing growth

The goal of the following analysis was to first describe the overall pattern of growth of black perch and then examine the influence of factors such as food availability, density, and predator abundance on the relative size of fish at a given age. In the first step of this analysis, we used a power function to describe standard length ( $L_t$ ) as a function of age ( $t$ ):

$$L_t = at^b,$$

where  $a$  is a parameter that describes average size during early life (i.e., when  $t = 1$ ) and  $b$  is a parameter that describes how growth changes as fish get older (if  $b < 1$ , it indicates decelerating growth). Age was expressed in years and reported to two decimal places. Because the growth of fishes is often described by a Von Bertalanffy growth function, we also include estimates of the Von Bertalanffy growth parameters for our data set. We used a three-parameter version of the Von Bertalanffy model:

$$L_t = L_\infty(1 - e^{-k(t-t_0)}),$$

where  $L_\infty$  describes asymptotic size,  $k$  describes how quickly asymptotic size is reached, and  $t_0$  is a parameter that describes age at which length is projected to be zero. The  $t_0$  parameter is useful for describing growth when initial size is not zero. Black perch give birth to large offspring (~5 cm SL), but because our field collections occurred months after parturition, young of the year were typically sampled when they were larger than 7 cm SL. To ensure that our growth curve was representative of fish at the youngest ages, we also included size and age measurements for 115 fish that were born in the lab from mothers that were collected in the field. Lab-born fish were measured at 3 to 17 days old, and our field sample included ages ranging from ~3 weeks to 5.6 years.

Once we described the overall pattern of growth, we conducted a secondary analysis that tested whether spatial variation in size-at-age, and thus growth rate, was associated with several variables including population density, density of natural predators (adult kelp bass), food availability, and spearfishing activity. We also examined competition with striped perch, but because previous analyses suggested that striped perch have a small effect on black perch populations in Southern California (Johnson and Dunk, 2018), our analyses concentrated on density, food availability, and predation. This analysis was a spatial comparison and our nine study populations were the primary units of replication. Explanatory variables with the potential to affect growth were measured using a combination of data we collected and data that are publically available.

Densities of black perch, striped perch, and kelp bass at each of our study locations were obtained from Reef Check California ([www.reefcheck.org/california](http://www.reefcheck.org/california)), an organization of volunteers that conducts annual surveys of population density of fishes on nearshore reefs. To calculate population densities, counts of black perch and striped perch were downloaded for the years 2010 to 2017 – a period that overlaps with the year classes we studied (Table S1). To compare with spatial variation in growth and mortality of black perch, we took the average of the density estimates. This was done to average away any observation error (which may be appreciable in citizen science data), and get a reliable summary of spatial variation in densities. Counts of kelp bass were filtered by size to calculate average densities of large, adult kelp bass (> 26 cm total length). A size threshold of 26 cm was chosen because kelp bass smaller than this size are unlikely to eat black perch. Data on population densities are available in Table S2. Food availability was quantified as described above (see *Sample Collection* subheading). Level of spearfishing activity at our study populations was inferred from the level of activity within online discussion forums related to spearfishing. Specifically, we searched [Spearboard.com](http://Spearboard.com) for postings that contained the names of our study populations. [Spearboard.com](http://Spearboard.com) is a very popular website that contains over 24,000 posts related to California spearfishing with the last year and is the main medium for online communications related to spearfishing in our study region. We summarized relative spearfishing activity at each of our study populations by taking the total number of postings that mentioned the study location during July 2017, to July 2018 (posts on [Spearboard.com](http://Spearboard.com) are searchable for a year). Although this is a proxy measure, the results do align with known variation in dive site popularity. For example, locations with a high number of posts included reefs that have easy access from shore and areas that are known to be popular spearfishing locations (Sheckler and Sheckler, 2008). Black perch are rarely the primary target of experienced spearfishers, but they are taken by many novices, and may be a second-choice catch when other species are unobtainable. Effects of spearfishing are worth considering because recruitment to black perch populations is almost entirely dependent on local reproduction, and even a modest amount of fishing pressure on adults may affect local populations.

The power function provided a better description of size at age (see *Results* section), and a useful feature of the power function is that it can be expressed as a linear relationship between the logarithm of  $X$  and the logarithm of  $Y$ . To evaluate potential causes of spatial variation in growth, we modeled the natural log of size as a function of the natural

log of age, plus the covariates of population density, food availability, kelp bass density, spearfishing activity, and striped perch density. This allowed us to evaluate the independent effects of several potential drivers of spatial variation in growth. We also included population as a random effect in the model, since observations of individual fish were nested within populations, and populations were the primary units of replication. We acknowledge that our explanatory variables may interact to affect demographic rates, but because this secondary analysis focused on variation among populations (which constrained our sample size), we ignored statistical interactions and focused on evaluating each of the main factors independently. Our goal was thus to identify which were the major drivers of spatial variation in demography, rather than to examine the context-specific effects of each factor on demographic rates. In addition, because these are not temporal analyses, the absence of a significant effect does not imply that an explanatory variable is necessarily unimportant. It would merely indicate that a particular variable is not a major source of spatial variation in growth.

To display potential causes of variation in average growth, we calculated the component change in (ln) size-at-age associated with each explanatory variable. These values were calculated as the coefficients from our mixed model analysis multiplied by each explanatory variable. We then plotted each component (plus model residuals) against the explanatory variable to create standard, partial residual plots. Finally, to test for spatial similarities in growth, we conducted a Mantel test to evaluate whether populations that were close to one another in space had similar rates of growth. In this analysis, we calculated the residuals from the overall power function describing size at age, then tested whether the geographic distance between populations was correlated with differences in growth rates (residual size at age values).

### 2.3. Analyzing age distributions

To evaluate potential causes of spatial variation in age distributions, we tested whether variation in mean age sampled was associated with several explanatory variables including population density of black perch, density of natural predators (adult kelp bass), density of a competitor (striped perch), food availability, and spearfishing activity. We note that age distributions may vary among populations because of spatial differences in mortality (which reduces the abundance of older ages), and/or spatial differences in the sequence of relative recruitment strength. For example, a location that experienced a series of low recruitment years followed by high recruitment years will have a greater-than-expected abundance of young age classes relative to old age classes and may appear to have an especially high rate of mortality. Such effects may obscure spatial variation in mortality, but we pooled the data into a single analysis that reduced the sensitivity to spatial variation in recruitment (see below), and our analyses concentrated on spatial variation in *relative* rates of mortality. Importantly, our inferences of mortality are supported by the fact that populations with a relatively low abundance of 1-yr olds also had an appreciable number of older fish (ages  $\geq 3$  yr) whereas populations with a relatively high abundance of 1 yr olds had few if any fish in the 3–6 yr ages (Fig. S1).

Each of the explanatory variables was summarized as described above (see *Analyzing growth* subsection). In this analysis, we used a generalized linear mixed effects model (glmm) to evaluate how the ages of fish sampled within a population was affected by population density, food availability, kelp bass density, and spearfishing activity. We also included population as a random effect in the model because populations were the primary units of replication. We used an inverse link function in this analysis because the inverse of mean age estimates mortality rate if the age distribution follows an exponential distribution. To focus our estimates on mortality rates of adults (fish > 1 yr old), a value of 1 was subtracted from each age. Within this framework, the intercept of the glmm can be used to infer the baseline rate of mortality and the coefficients describe how a unit change in each of the explanatory variables independently affected mortality rates. By

treating population as a random effect, we assumed that the average ages in a population were more similar to other populations than one would conclude if comparing ages on a population-by-population basis. This is the so-called ‘borrowing strength’ feature of mixed models and is useful in this situation because it will reduce the effects of spatial variation in recruitment patterns and/or sampling variability. In essence, this approach uses the entire dataset to inform the general pattern of age distribution and then examines how individual populations deviated from the overall rate of decline. It is much less sensitive to spatial variation in recruitment than an approach that compares the relative abundance of year classes on a population-by-population basis. Our analyses were conducted in R using the function *glmer* in the *lme4* package (Bates et al. 2015). Additional details of the model are described in Appendix 1.

Similar to our analyses of spatial variation in growth, we ignored statistical interactions, and focused our analyses on evaluating each of the main factors independently. We used partial residual plots to illustrate associations between inverse mean age (our estimate of mortality) and our main explanatory variables of interest: population density, kelp bass density, food availability, and fishing activity. Individual ages were displayed as data points in these plots, but the main analyses focused on variation in mean ages among populations. Plots include the expected change in the inverse of mean age, given the model coefficients and values of the explanatory variable and response residuals, which express whether the inverse of an sampled fish's age was greater than expected (if positive) or less than average (if negative). To test for spatial similarities in age distributions (and mortality), we conducted a Mantel test to evaluate whether populations that were close to one another in space had similar values of mean age.

### 3. Results

Our data suggest that black perch grow relatively quickly during their first year of life, and that growth in length gradually decelerates as fish get older (Fig. 2). Within the range of ages sampled, we did not see evidence that standard length levels out, on average. In fact, a commonly-used model of asymptotic growth, the three-parameter Von Bertalanffy function, provided a poorer fit to the data than a simple power function ( $\Delta AIC = 82.69$ ; Table 1). Growth appeared to be

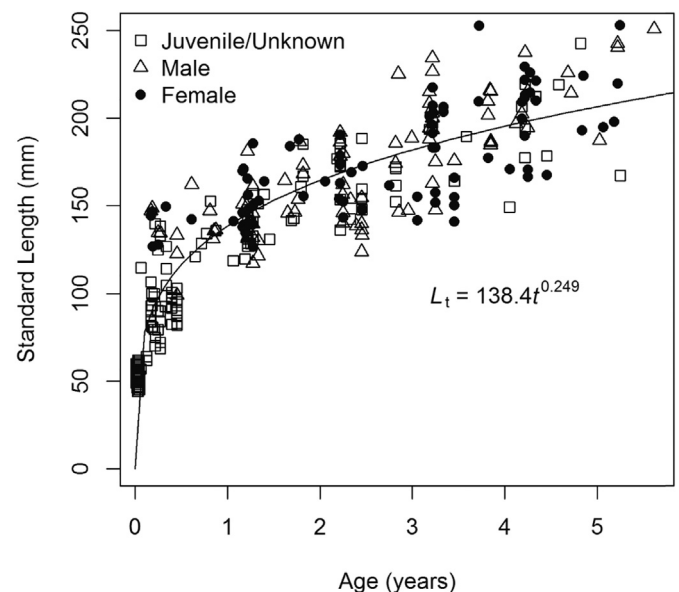
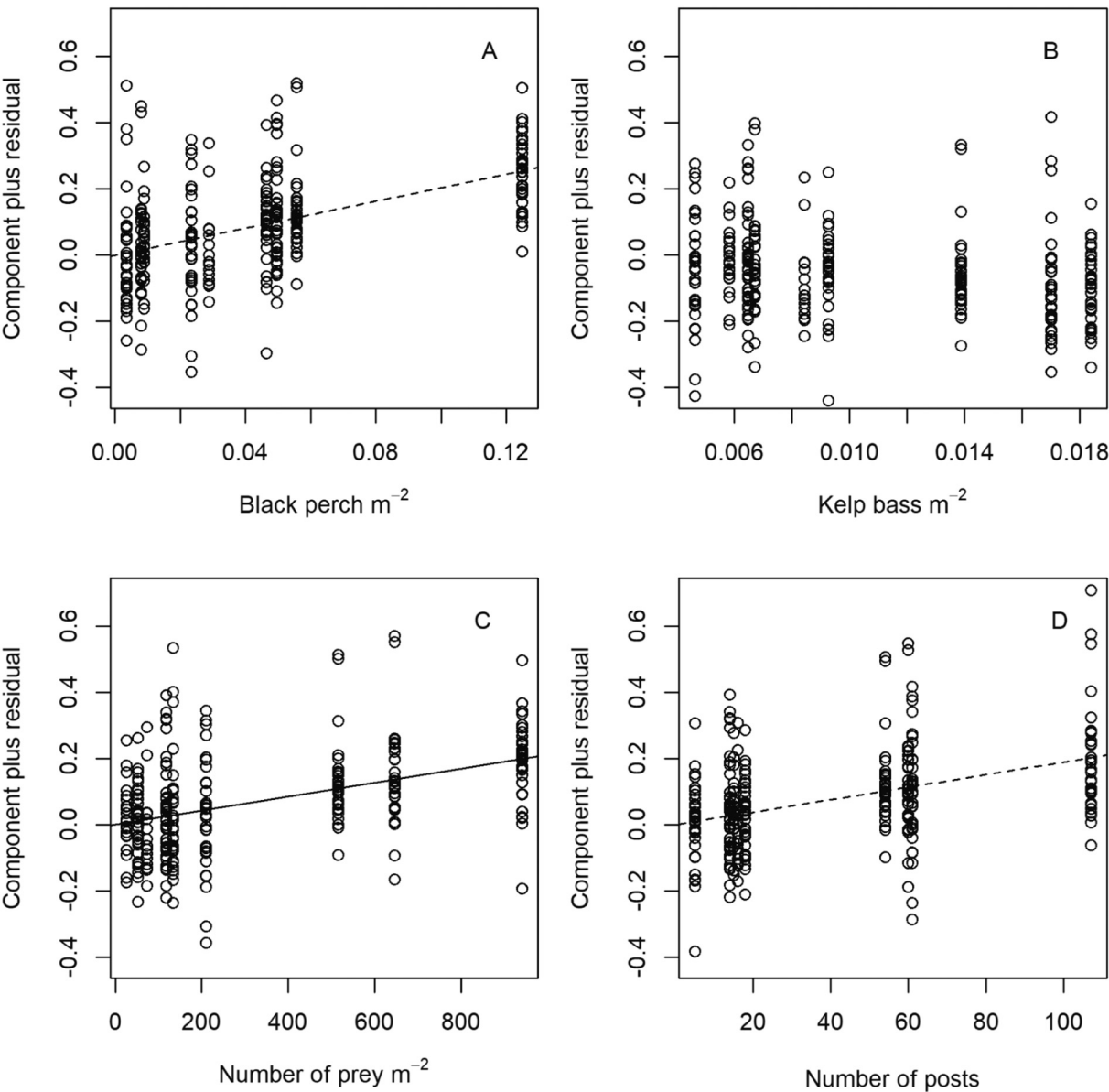


Fig. 2. Relationship between size and age for black perch (*Embiotoca jacksoni*) collected throughout Southern California. Open triangles = males; solid circles = females; open squares indicate juveniles and/or fish whose sex could not be reliably discerned from external morphology.



**Table 1**  
Evaluation of growth models that relate size (SL in cm) of Black perch to their age (in years).

Model	Parameter estimates					AIC	
Power function	$\alpha$	SE	$b$	SE			
Von Bertalanffy	138.400	1.078	0.249	0.00581			2347.4
	$L_{\infty}$	SE	$k$	SE	$t_0$	SE	
	201.878	3.570	0.742	0.054	−0.461	0.038	2422.0



**Fig. 3.** Spatial variation in growth rates of black perch, as summarized by residual size at age. Positive values indicate that a fish was larger than average for its age, negative values indicate a fish was smaller than average. Panels are partial residual plots that display the component of variation associated with each explanatory variable, plus the residuals of the full model. Dashed lines indicate  $P < 0.05$ , solid line indicates  $P < 0.01$ .

indeterminate, and the pattern of growth was similar for males and females (Fig. 2). Residual sizes at age were similar for fish clearly identifiable as males and fish clearly identifiable as females (Tukey's HSD: male – female size = 0.169,  $P = 0.998$ ). Residual sizes at age were smaller for juveniles and fish for which sex was not clearly identifiable from external morphology (Tukey's HSD: unknown/juvenile – female = −6.610,  $P = 0.019$ ; unknown/juvenile – male = −6.78,  $P = 0.014$ ).

Variation in size at age was appreciable. At a given age, most fish ranged from ~73% to 135% of average size (numbers based on 2.5th and 97.5th percentiles; Fig. 2). Much of that variation could be attributed to variation among populations, and variation among mean, residual size at age for our study populations accounted for 54.6% of the total variation in residual size at age. It was unlikely that among-population variation in growth was due a spatial cline in conditions. Populations that were relatively close in space were not any more similar

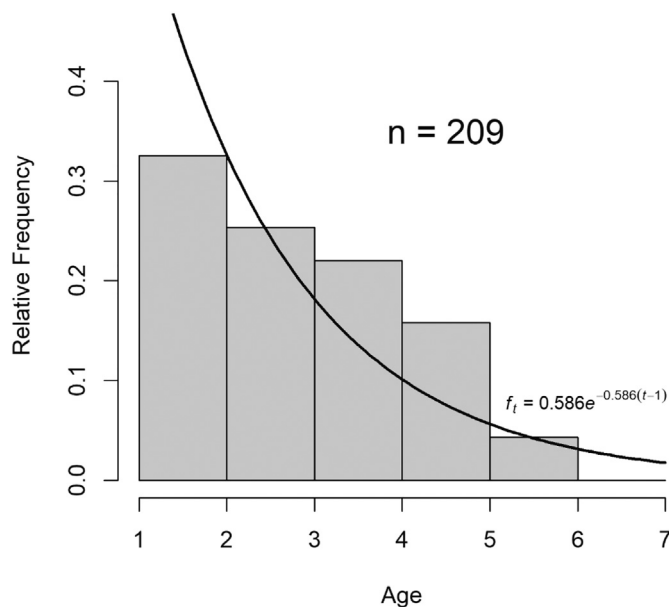


Fig. 4. Histogram displaying the relative frequency of black perch of ages greater than one year old. Solid curve illustrates the probability density function for an exponential distribution fit to the data.

with respect to growth (Mantel test:  $r = 0.020$ ,  $P = 0.340$ ). Further analysis indicated that among populations, there was some evidence of a positive relationship between density of black perch and relative size at age (linear mixed effects model,  $P$ -values calculated with Kenward-Roger approximation:  $t = 3.37$ ,  $df = 3.64$ ,  $P = 0.032$ ), indicating that rates of growth were positively correlated with population density (Fig. 3A). There was no strong relationship between density of kelp bass and growth of black perch ( $t = -1.61$ ,  $df = 3.64$ ,  $P = 0.187$ ; Fig. 3B). There was a strong relationship between prey availability and growth (slope =  $2.12 \times 10^{-4}$ ,  $t = 7.72$ ,  $df = 3.64$ ,  $P = 0.002$ ; Fig. 3C), and our data suggest that growth rate may be moderately sensitive to prey availability. On average, we expect that an increase in prey availability equal to one standard deviation ( $14,363 \text{ prey m}^{-2}$ ) would increase size at age by a factor of 1.07. There was some evidence of a positive relationship between spearfishing activity and growth rate (slope =  $1.89 \times 10^{-3}$ ,  $t = 3.81$ ,  $df = 3.64$ ,  $P = 0.024$ ; Fig. 3D), and no evidence of a relationship between the density of striped perch and growth of black perch ( $P = 0.740$ ).

Older fish were less common than younger fish in our sample, and for adult fish, the overall age distribution was described reasonably well by an exponential model (Fig. 4). With data from all populations pooled, we estimated an overall rate of decline of  $0.586 \text{ yr}^{-1}$  for fish greater than one year of age (95% C.I.:  $0.511 \text{ yr}^{-1}$  to  $0.670 \text{ yr}^{-1}$ ). Among our study populations, adult age distributions varied substantially, with a coefficient of variation of 27.4% for mean age, and a coefficient of variation of 78.2% for the abundance of fish of ages > 3 years old. This variation in the degree of age truncation among populations suggests that mortality rates varied considerably in space. However, populations that were geographically close were not necessarily similar with respect to mean age (Mantel test:  $r = 0.048$ ,  $P = 0.360$ ), suggesting that mortality rates are not necessarily similar for nearby populations.

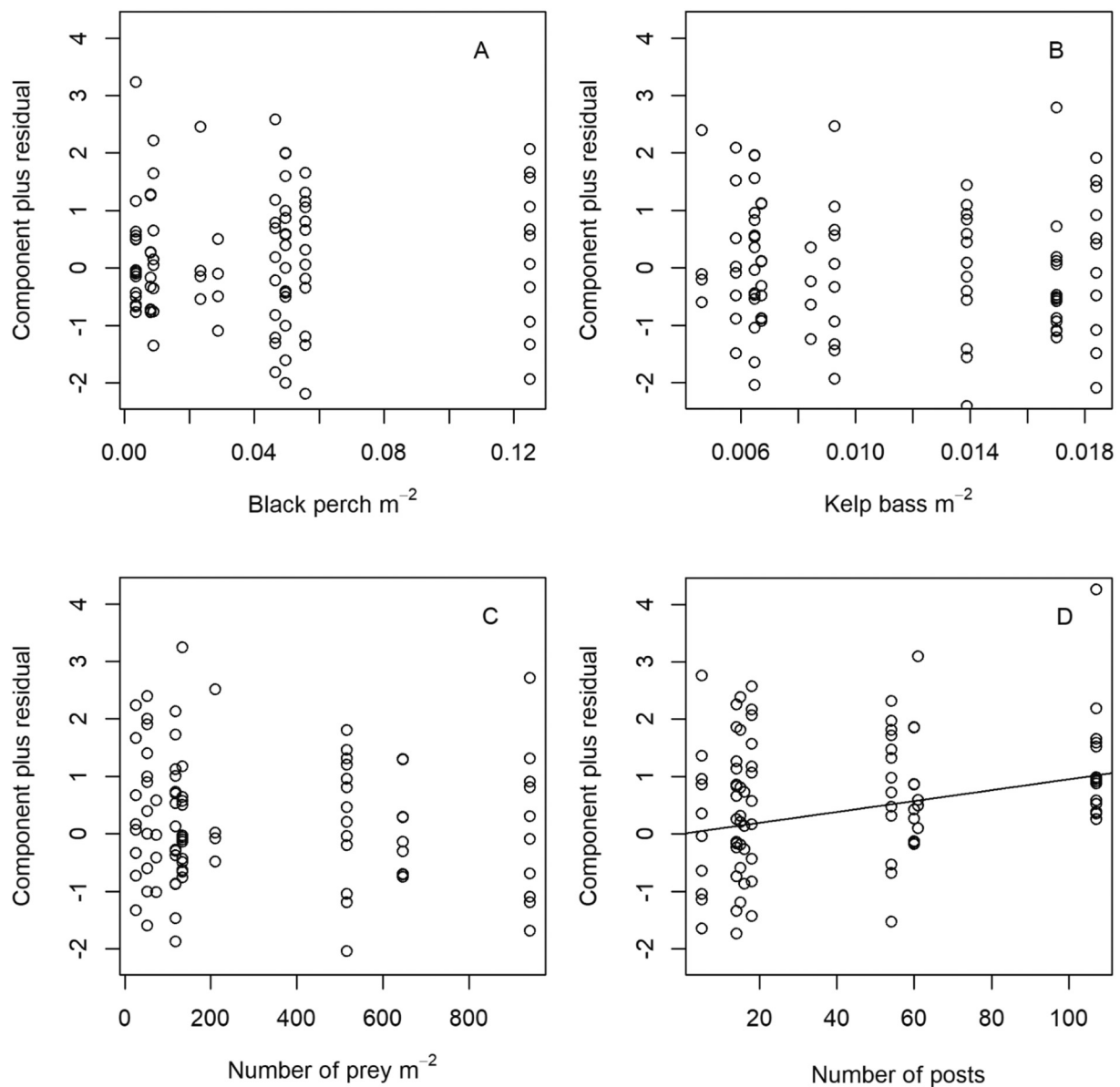
Further analysis indicated that among our study populations, there was no clear relationship between the inverse of mean age – our estimate of mortality – and average population density (glmm with likelihood ratio test:  $P = 0.654$ ; Fig. 5A). There was no relationship between the inverse of mean age and kelp bass density ( $P = 0.326$ ; Fig. 5B), nor was there evidence of a significant relationship with density of invertebrate prey ( $P = 0.962$ ; Fig. 5C). Mean age within the

population decreased significantly with level of activity within online discussion forums related to spearfishing (slope of the inverse mean age with number of posts =  $0.009$ ,  $P = 0.017$ ; Fig. 5D). Populations with low average ages and high rates of spearfishing activity also had low abundances of old fish (fish > 3 years old) whereas populations with relatively high values for average age also had substantial numbers of fish > 3 years old (Fig. S1). There was marginal evidence that inverse mean age also increased with the density of striped perch ( $P = 0.087$ ).

#### 4. Discussion

Black perch grow quickly as juveniles, and growth in length decelerates considerably after about one year of age. These patterns are generally consistent with previous studies of growth and size at age for this species (Isaacson and Isaacson, 1966; Froeschke et al., 2007). In addition to describing the overall pattern of growth, our study revealed a substantial amount of spatial variation in growth rates for a given age. Across the nine study populations, the factor with the greatest influence on growth rates was food availability. Of the factors considered, food availability generally has the most direct effect on growth, so it is perhaps not surprising to detect an association between the two. However, the degree to which food availability varied among our study populations was unknown prior to conducting this study. Food availability was an important driver of spatial variation in the growth rates of black perch both because growth rates were sensitive to changes in prey availability and because the density of benthic invertebrates that black perch eat ranged over an order of magnitude among our study locations. Much of the variation in prey availability appears to be driven by variation in the amount of benthic algae. Biomass of algae per quadrat is correlated with total number of invertebrates ( $r = 0.39$ ) and biomass per quadrat varied substantially among populations (coefficient of variation = 56%). As a result, much of the spatial variation in average growth of black perch was explained by variation in food availability ( $r^2$  for a simple regression was 0.439; also see Fig. 3C). Overall, these results support the idea that variation in food availability is an important driver of spatial variation in the abundance of black perch. Studies of population fluctuations at a single location have demonstrated that food availability affects the production and survival of young of the year (Okamoto et al., 2012), as well as survival of 1 year olds (Okamoto et al., 2016). Because food availability strongly influences relative size at age, and because mortality rates of small fishes often depend on their relative size (Sogard et al. 1997, Perez and Munch, 2010, Johnson et al., 2014), it is possible that the relationship between food availability and population dynamics of black perch is mediated in part by the effects of food availability on growth.

Growth rates varied with population density, but the relationship was positive. Although it is reasonable to expect somatic growth of temperate reef fishes to decrease when densities are increased (e.g., Jones, 1984; Tupper and Boutillier, 1995; Steele, 1998) such effects may be detected more directly when comparing variation in density over time at a single location. In our spatial comparison, the positive relationship between density and growth probably reflects the shared influence of habitat quality. For example, locations with higher quantity and quality of food may have higher growth rates overall, even if growth is density dependent at a particular location. Such effects have been termed “cryptic density dependence” and have been demonstrated for other reef fishes (see Shima and Osenberg, 2003, Johnson, 2006, Ford et al. 2016 for similar effects). An additional complication is that the degree of shoaling and spatial clustering of fish may differ among populations (Johnson et al., 2016). As a result, the density of fish – a property that is measured at the scale of the reef – may not necessarily reflect the amount of spatial crowding and competition that a typical fish experiences. Such effects may make it difficult to detect density-dependent growth in spatial comparisons. The abundance of kelp bass and fishing activity did not appear to have major effects on growth. It is plausible that the reduced feeding opportunities and increased stress



**Fig. 5.** Spatial variation in age distributions of black perch > 1 year of age. Data points represent deviations (response residuals) from a model of the inverse of mean age, a summary that provides an estimate of mortality. For display, data points for individual fish are plotted, but the main analysis focused on populations (see main text). Higher values indicate a lower inverse mean age and higher mortality. Panels are partial residual plots that display the component of variation associated with each explanatory variable, plus the residuals of the full model. Positive values indicate higher than average rates of mortality. Solid line indicates  $P < 0.01$ .

associated with being in a high predation environment will reduce growth rates (Werner et al., 1983). However, when considering spatial variation within our study region, such effects are likely secondary to the effects of variation in food availability. Similarly, growth was higher than average at locations with more spearfishing activity, but these are counter to any mechanistic expectation and may be because popular spearfishing locations also have other attributes that support faster than average growth of black perch. Finally, variation in intraspecific competition with striped perch (*Embiotoca lateralis*) had no appreciable effect on spatial variation in growth of black perch. These results may be due to the fact that densities of striped perch were very low for our study locations (mean density of striped perch was < 1/20th of the density of black perch) and interspecific competition may have much weaker effects than intraspecific competition (Johnson and Dunk, 2018).

A major driver of spatial variation in age distributions of black perch appears to be fishing. Although catch by hook and line is

relatively rare (California Department of Fish and Wildlife, 2014), black perch are regularly taken by spearfishers in Southern California, and have been fished to some extent since at least the early 1960s (Isaacson and Isaacson, 1966). Older fish were very rare at locations that have high spearfishing activity, and the age distributions suggest more age truncation and thus a high mortality rate of adult perch in these locations. Although increases in population density often increase mortality rates of temperate reef fishes (e.g., Steele, 1997; Anderson, 2001, Ford and Swearer 2013), it is possible that any relationship between density and mortality of perch was obscured by spatial variation in fishing activity. Fishing activity is often governed more by proximity to urban centers, accessibility of locations (e.g., mainland vs. islands, travel time), and water clarity than by density of fish (Mann et al., 1997; Lynch, 2006). Locations with low spearfishing activity tended to be offshore locations that are difficult to access, but this was not always the case. For example, Santa Catalina Island is approximately 35 km offshore but is close to Los Angeles and the east side of the island is a

popular location for spearfishing. In our study region, spatial variation in fishing effort was not tightly linked to density of black perch, and idiosyncratic variation in fishing effort may have obscured any density-dependent effects on mortality. Similarly, any effects of food availability on mortality and age distributions are indirect and likely to be minor compared to the direct effects of variation in fishing.

Age distributions did not vary significantly with densities of kelp bass, a large piscivorous fish that is common within our study region. It is possible that variation in fishing mortality of black perch simply overwhelmed any relationship between mortality of black perch and density of kelp bass. However, it worth noting that our focus was on estimating age distributions for perch that were > 1 yr old. Kelp bass readily consume other perches of small to medium size (Anderson, 2001), and may consume juvenile black perch, especially young of the year (Holbrook and Schmitt, 1984; Schmitt and Holbrook, 1985; Ebeling and Laur, 1985). After a year of growth, black perch are around 13 cm SL and may have attained a size refuge from all but the largest kelp bass, which were rare at our study locations (e.g., fewer than 2.9% of the adult kelp bass were > 40 cm SL). Further research will be required to understand the influence of kelp bass on the mortality rates of juvenile perch, but variation in the density of kelp bass did not appear to have strong effects on spatial variation in the mortality of black perch adults. Other top predators such as sea lions and sharks may consume adult perch, but the densities of these top predators are extremely low compared to predatory teleosts. In addition, embiotocids make up an extremely small proportion of the diet of predators such as sea lions (e.g., Lowry et al. 1991), and the effect of these predators on the mortality rates of black perch is likely very small compared to the effects of fishing. Black perch populations may be especially sensitive to spatial variation in mortality because black perch lack a dispersive larval phase and unlike many other fishes, there is little chance that local populations of black perch that are overfished will be rescued by recruitment from external sources.

Overall, this study suggests that growth rate of black perch is indeterminate, even though rates of growth slow considerably after fish are > 1 yr old. Rates of growth varied considerably from location to location, with the among-population variation in growth accounting for 55% of the total variation in size at age. Most of this spatial variation in growth rate appears to be due to differences in the amount of food available within local populations. These results illustrate the plasticity of growth, and emphasize the importance of understanding reasons why the abundance of food varies, as well as the demographic consequences that variation in food supply has for marine populations (e.g., Jones, 1986; Anderson and Sabado, 1995; Okamoto et al., 2012; Goldstein et al., 2016). Age distributions also varied considerably among populations. Our results suggest that spatial variation in mortality of black perch may be strongly influenced by variation in spearfishing activity, as old fish were rare in populations of black perch in locations popular with spearfishers. This study thus contributes to a growing body of literature that examines the effects that spearfishing may have on the demographic rates reef fish populations (e.g., Frisch et al., 2012; Lindfield et al. 2014). Further research should concentrate on understanding how these changes in demographic rates ultimately affect the abundance and long-term health of reef fish populations (Godoy et al., 2010; Pinheiro and Joyeux, 2015).

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jembe.2019.04.008>.

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