Interactive effects of shelter and conspecific density shape mortality, growth, and condition in juvenile reef fish

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Abstract. How landscape context influences density-dependent processes is important, as environmental heterogeneity can confound estimates of density dependence in demographic parameters. Here we evaluate 19 populations in a shoaling temperate reef fish (*Trachinops caudimaculatus*) metapopulation within a heterogeneous seascape (Port Phillip Bay, Australia) to show empirically that shelter availability and population density interact to influence juvenile mortality, growth and condition. Although heterogeneity in shelter availability obscured the underlying patterns of density dependence in different ways, the combination of habitat and its interaction with density were two to six times more important than density alone in explaining variation in demographic parameters for juveniles. These findings contradict many small-scale studies and highlight the need for landscape-scale observations of how density dependence interacts with resource availability and competition to better understand how demographic parameters influence the dynamics of metapopulations in heterogeneous environments.

Key words: cryptic density-dependence; habitat complexity; ideal free distribution; landseape heterogeneity; reef fish; resource limitation.

Introduction

The regulation of populations through feedbacks between population density and demographic rates (i.e., density dependence) is a fundamental principle of ecology (Murdoch 1994, Turchin 1999). Identifying under what circumstances density effects become important is essential for constructing realistic predictions of population fluctuations under different environmental conditions (Hanski et al. 1996). Failure to consider the spatial context of density-dependent processes, however, can lead to biased estimates of its importance (Thorson et al. 2015).

Many organisms use discrete habitat patches that are embedded within a heterogeneous landscape (Levins 1969, Hanski and Gilpin 1991). Patches may vary in resource availability (Moilanen and Hanski 1998, Mortelliti et al. 2010) and/or in their ability to attract colonizers (Brown and Kodric-Brown 1977, Resetarits and Binckley 2013). Variability in patch quality and landscape features is increasingly recognized as an

important source of variation in demographic rates for a variety of organisms such as butterflies (Fleishman et al. 2002), voles (Lin and Batzli 2001), and beavers (Fryxell 2001). However, the effects of a heterogeneous landscape on the patterns and strength of density dependence in multiple demographic parameters (e.g., mortality, growth, condition) remain poorly understood for any system.

Landscape heterogeneity can challenge the detection of density dependence and confound estimates of its strength (Wilson and Osenberg 2002, Shima and Osenberg 2003). For example, if organisms colonize patches of variable quality (i.e., according to an ideal free distribution, sensu Fretwell and Lucas 1970), then density and patch quality will be confounded and this covariance will obscure estimates of density dependence. This phenomenon has been termed "cryptic density dependence" (Shima and Osenberg 2003), where the strength of density dependence varies relative to resource availability (e.g. food or shelter) or abundance and type of predators.

Density-dependent, post-settlement mortality is common in marine reef fish populations (Osenberg et al. 2002), where very high densities often drive intense

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competition for shelter from predators (White et al. 2010). Most of the evidence for density dependence has come from manipulative field experiments observing mortality on small spatial (within patch) and short temporal (days to weeks) scales (Hixon and Carr 1997, Ford and Swearer 2013a), with limited evidence on larger spatial (among patches) and temporal (months to years) scales (but see Forrester and Steele 2004, Johnson 2006). Spatial variability in habitat quality often correlates strongly with the strength of density-dependent mortality among reef fish populations (Shima 2001, Schmitt and Holbrook 2007), and habitat quality in some cases is the strongest predictor of survival (e.g. shelter - Steele 1999, Almany 2004). Samhouri et al. (2009) observed that the ratio of density to shelter was an important determinant of survival within populations, suggesting that an interaction between density and shelter may contribute to variation in demographics at the landscape scale. Similarly, Walters and Korman (1999) used a model to demonstrate that variation in the ratio of predator abundance to food supply can have large effects on recruitment rates. Despite these observations, how the relative importance of local population density versus local resource availability (e.g., shelter, food) varies across a landscape is poorly known, yet this information is a necessary first step to building more realistic spatially-explicit metapopulation models.

Here, we evaluate how density, resource availability, and their possible interaction influence juvenile mortality, growth and condition across 19 populations of a temperate reef fish (*Trachinops caudimaculatus*) metapopulation within a heterogeneous seascape. Specifically, we evaluate whether among-population variation in these demographic parameters is a function of: 1. resource dependence alone, 2. density dependence alone, 3. additive effects of resource- and density dependence or 4. interactive effects of resource- and density dependence.

METHODS

Study species and system

The southern hulafish, *Trachinops caudimaculatus*, is a short-lived (1–5 yr) shoaling zooplanktivorous fish that is widely distributed on temperate rocky reefs in southeastern Australia. It forms large dense shoals over hard reef substrate (Jung and Swearer 2011) and exhibit limited movement among reefs, making it easy to survey on SCUBA (Hunt et al. 2011). Spawning occurs in austral spring and larvae develop in the plankton from late spring to early summer with a pelagic larval duration of 1–1.5 months (Ford 2015). Port Phillip Bay supports the majority of the regional metapopulation, with spawning occurring locally on dozens of reefs (Ford 2015). Larvae settle primarily in December and January (Hunt et al. 2011), and onto any hard substrate deeper than 3 m depth. Newly settled larvae form shoals that are well-separated from adults, and visual size differences

between juveniles and adults persist for up to 3 months post-settlement (Ford 2015).

Hulafish use rocky reef structure as refuge from both pelagic and benthic predators (Ford and Swearer 2013b). Competition for shelter drives density-dependent mortality on small patch reefs (Ford and Swearer 2013a). Given these observations and similar patterns observed for other species (Holbrook and Schmitt 2002, Forrester and Steele 2004, White et al. 2010), we hypothesized that shelter is also a limiting resource at the landscape scale, here defined as the scale of the regional metapopulation (i.e., Port Phillip Bay). If shelter covaries with density, this can confound estimates of density dependence in demographic parameters.

We conducted surveys to quantify mortality, growth, and condition of juvenile fish (<45 mm in length) from the 19 largest hulafish populations distributed across discrete rocky reefs in Port Phillip Bay, Victoria, Australia (Appendix S1: Fig. S1). Reefs were distributed across a wide range of geographical regions and environmental conditions that are representative of this landscape (e.g., varying in depth, complexity, and tidal energy, Appendix S1: Fig. S2).

Fish surveys and collection

To estimate spatial variation in mortality, growth, and condition, we collected juveniles using a combination of barrier nets and hand nets (see Video S1 for video of underwater collection). These collections were made in February 2010 (immediately after larval settlement had ceased for the season), and again 3 months later in May 2010. Most post-settlement mortality and growth occur in this period as predators and food are still abundant, and year class strength is determined by May before shoals break down and fish become less active over winter. Juveniles shoal separately from adults, and collections targeted randomly selected juvenile shoals within each population. At each sampling period, we estimated juvenile abundance on 5 m wide transects using SCUBA. Diver entry and exit locations were marked by GPS to calculate actual transect length, facilitating estimates of fish density. Multiple transects were sampled within each population; these were stratified by depth (constrained to >3 m deep, and subsequent depth bins to capture local bathymetry) and reef structure. Sampling effort was proportional to reef size (ranging from 3 transects for the smallest reef to 16 for the largest, to ensure that at least 5% of the total reef area was sampled). We used known GPS positions and known compass headings to sample the same transects at each reef in each sampling period.

Juvenile mortality

Juvenile densities (number) were averaged across transects within each population for each sampling date. We assumed that our sampling protocols captured a

single annual cohort of recruiting fish shortly after set-tlement and again 3 months later, with equal chance of detecting shoals across sites and densities, and we used these data to estimate instantaneous per capita mortality rates, calculated as the difference between ln(final density) and ln(initial density). One site (PP) was not surveyed in the second period and hence could not be used for mortality analysis.

Juvenile growth and condition

We calculated growth and condition metrics from juveniles collected at 12 of the 19 populations (i.e., where we had collected sufficient numbers of juveniles [$n \geq 15$] at both survey dates). We estimated average daily growth of fish for each population as the difference in mean standard length between survey dates divided by the number of days between surveys. The linear relationship between standard length (SL, in mm) and age in days from otolith increment analysis was strong (SL = $0.306 \cdot$ Age - 2.8, $P < 0.001$, $R^2_{adj} = 0.81$, $n = 503$), indicating this approach provides a robust measure of average fish growth for each population. We used the relative weight (W_{rm}) method (Froese 2006) to compare average condition of fish among populations. This method calculates the deviation of each sample from an overall length-weight relationship for fish collected from all populations ($R^2_{adj} = 0.93$, $P < 0.001$, $n = 238$), using the equation:

$$W_{rm} = 100 \times \frac{W}{aL^b}$$

where W is weight (g) and L is length (mm), a and b are derived from the length-weight relationship for hulafish (0.00016 and 2.96 respectively), and average relative weight is equal to 100. W_{rm} values were averaged at the population level for subsequent statistical analysis.

Resource availability

We defined resource availability as a function of the number of putative sheltering sites and refuges from predators. Based upon prior studies (Hunt et al. 2011, Ford and Swearer 2013a,b) we determined these to be represented by (1) the number of small holes and cracks (<2.5 cm diameter), (2) the number of large holes and cracks (2.5–15 cm diameter) and (3) a measure of reef rugosity. We quantified rugosity following Wilson et al. (2007): we used a 25 m chain (5 mm link diameter, and marked at 5 m intervals) laid out along the reef contour at a randomly selected location and then measured the straight line length between successive marks on the chain, providing five measures of rugosity. At each mark, including 0 m, we placed a 50 × 50 cm quadrat and counted all small (<2.5 cm) and large (2.5–15 cm) holes and cracks, providing six counts for each transect.

Sampling effort (number of transects) was proportional to reef area and ranged from two to six per site. Because fish survey transects were not explicitly paired with resource availability transects, all measures were averaged to obtain reef means.

We used Principal Components Analysis (PCA) to combine the three estimates of shelter availability (rugosity, number of large holes, and number of small holes) on a common scale. Two separate analyses were conducted: one used data from all 18 populations for which we had estimates of mortality, and another used data from the 12 populations for which we had estimates of fish growth and condition. The first principal component explained 67% and 66% of the overall variation, respectively, with more positive scores representing higher densities of holes and cracks, and increased reef rugosity (Appendix S1: Table S1). Consequently, we used these first principal component scores as our estimate of overall shelter availability (hereafter, "shelter") in subsequent analyses.

Statistical analysis

We evaluated the separate and joint effects of shelter and juvenile density on each of three response variables: mortality, growth and condition (at the end of the experiment in May). For each response variable, we evaluated four competing linear regression models (standard least squares model, intercept fit) with the following combinations of predictors: 1) shelter only, 2) initial juvenile density only, 3) shelter and initial juvenile density, and 4) shelter, initial juvenile density and the shelter × density interaction, and then used the lowest corrected Akaike's Information Criteria (AICc), ΔAIC and weight (w_i) to select the best model. We used the "relaimpo" R package (Grömping 2006) which utilizes the LMG method (Lindeman et al. 1980) to calculate the relative importance of regressors in the best-fit model. All statistical tests were performed using R 3.2.1 (R Core Team 2015).

RESULTS

Spatial patterns of abundance and shelter.—We observed positive spatial covariance between shelter and local population densities, as we only observed low densities at the six lowest shelter sites (0.01–1.1 fish/m^2) compared to a wide spread of densities at the six highest shelter sites (0.05–7.2 fish/m^2). Because only 12 of the sites were sampled for growth and condition, this pattern was not reflected in these analyses (see Appendix S1: Table S2 for a complete list of local population densities and shelter by site).

Instantaneous mortality.—The best model (Table 1) incorporated the additive effects of shelter and juvenile density ($R^2 = 0.68$). Mortality increased with density across all shelter levels (Fig. 1a). Shelter was the most

TABLE 1. Comparison of linear models predicting instantaneous mortality, daily growth, and condition in juvenile *Trachinops caudimaculatus* over a 3 month period. The best-fit model (highlighted in bold) was selected using the lowest AICc.

Response	Main effect(s)	Interaction	Parameters	N	R^2	AICc	w_i
Mortality	Shelter	–	1	18	0.33	18.6	0.002
	Density	–	1	18	0.1	23.8	<0.001
	Shelter + Density	**–**	**2**	**18**	**0.68**	**7.2**	**0.72**
	Shelter + Density	Shelter × Density	3	18	0.68	9.2	0.28
Growth	Shelter	–	1	12	0.47	−46.2	0.02
	Density	–	1	12	0.03	−39	0.001
	Shelter + Density	–	2	12	0.66	−49.7	0.12
	Shelter + Density	**Shelter × Density**	**3**	**12**	**0.79**	**−53.6**	**0.86**
Condition	Shelter	–	1	12	0.05	−24	0.01
	Density	–	1	12	0.17	−25.6	0.03
	Shelter + Density	–	2	12	0.17	−23.7	0.01
	Shelter + Density	**Shelter × Density**	**3**	**12**	**0.66**	**−32.4**	**0.94**

important regressor in the selected model, with a partial R contribution of 0.45 or 66% of the full model (Table 2).

Growth.—The best model (Table 1) incorporated the main effects of shelter and juvenile density, and the interaction term ($R^2 = 0.79$). There was no relationship between growth and density at sites with low shelter, and a negative relationship at sites with medium and high shelter (Fig. 1b). Shelter was the most important regressor in the selected model, with a partial R contribution of 0.55 or 70% of the full model (Table 2).

Condition.—The best overall model (Table 1) incorporated the main effects of shelter and juvenile density, and the interaction term ($R^2 = 0.66$). There was a negative relationship between condition and density at sites with low and medium shelter, but a positive relationship for sites with high shelter (Fig. 1b). The interaction of shelter and density was the most important regressor in the selected model, with a partial R contribution of 0.49 or 74% of the full model (Table 2).

DISCUSSION

Our study highlights the importance of the interactive effects of density and habitat in explaining patterns of density dependence in juvenile mortality, growth, and condition of a reef fish ("cryptic density dependence") at landscape scales. Moreover, we found that the patterns of density dependence (and putative mechanisms that underlie them) varied among the three demographic parameters that we evaluated. In all cases, either habitat quality alone, or its interaction with density, was the most important predictor of the demographic parameter. This suggests that the strong, straightforward

density-dependent regulation often observed in small-scale studies (White et al. 2010) may be misleading when considering regional demographic drivers in heterogeneous landscapes. Our results underscore the importance of large-scale empirical observations to complement experiments, as density dependent processes may act independently or interactively with resource availability to influence juvenile life stages in complex and non-intuitive ways.

A number of studies of reef fishes have documented direct density dependence in per capita mortality (Hixon and Carr 1997, Holbrook and Schmitt 2002) and growth (Yeager et al. 2014). In addition, many studies indicate the importance of shelter independent of any density-dependent effect (Almany 2004, Johnson 2007) by providing refuge from predation. We demonstrate that on a landscape scale, habitat quality in the form of shelter was consistently more important than density in explaining demographic rates in the southern hulafish. Shelter explained twice the variation in mortality and four times the variation in growth compared to density alone. Density alone appeared to have no direct effect on fish condition; instead density dependence in condition was mediated through an interaction with shelter. These findings highlight the importance of incorporating habitat heterogeneity when evaluating population dynamics across larger scales, and effectively argue for a need to scale up the "musical chairs" hypothesis (a mortality function dependent on the ratio of prey to refuges) of Samhouri et al. (2009) from single patch reefs to reef networks. Considerable advances in metapopulation modeling and prediction of reef fish population dynamics under future environmental scenarios are likely to be achieved by accounting for the effects of variability in habitat quality and its interaction with density on demographic rates.
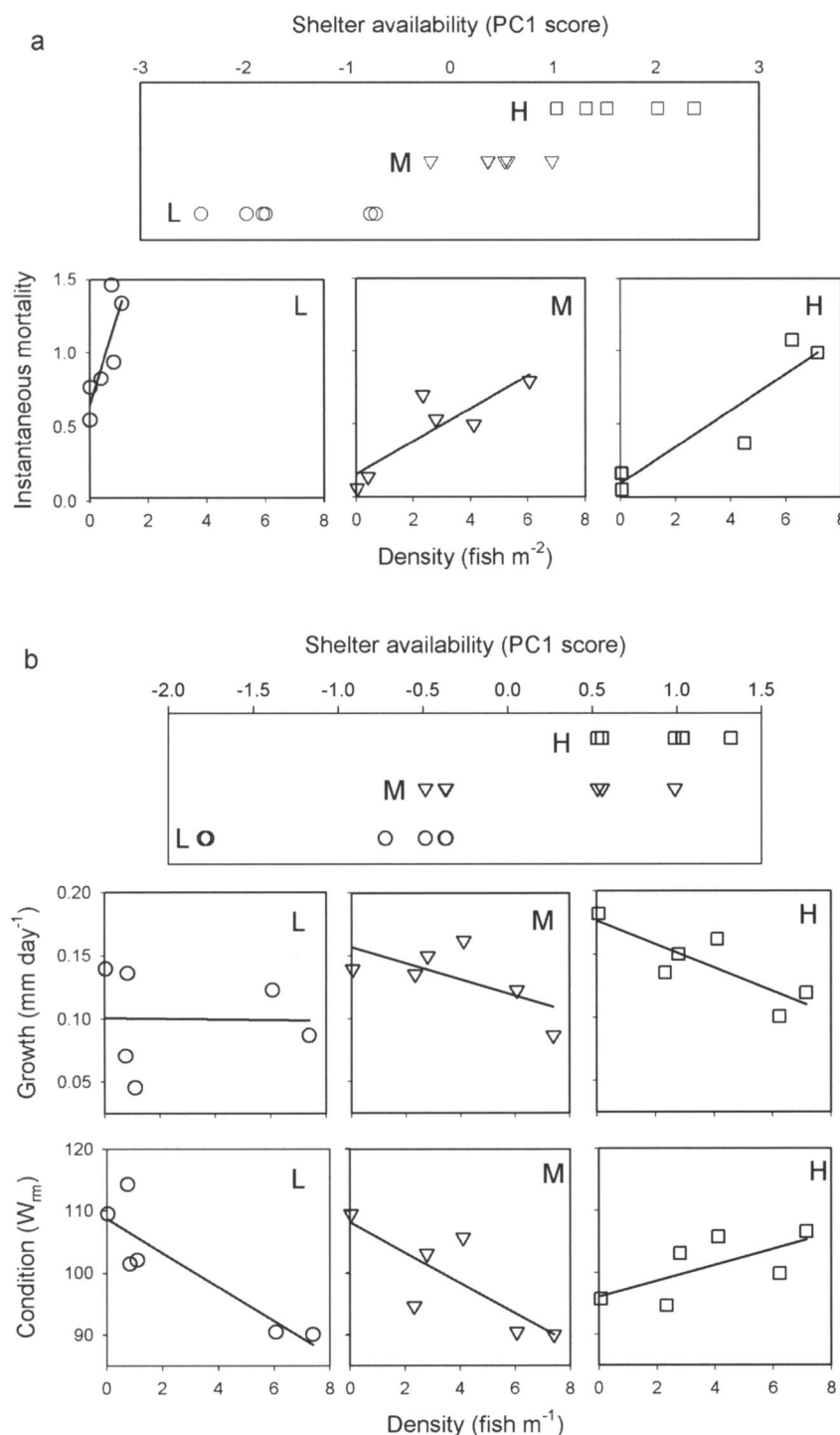
Fig. 1. Co-plots of the effect of density on (a) instantaneous mortality, and (b) individual growth and condition of *Trachinops caudimaculatus*, dependent on shelter availability. The top frame in each figure shows the range of shelter values of sampled sites ($n = 18$ for mortality, $n = 12$ for growth and condition), and the lower frames show the response variable as a function of density under low (L), medium (M) and high (H) shelter availability (circles, triangles and squares, respectively). Shelter ranges overlap to illustrate the continuous nature of the relationship. Hence, in the growth and condition analyses in (b), the three sites with highest scores in the low shelter class are the same as the three lowest score sites in the medium shelter class. Linear regression lines are fit to each frame to demonstrate the change in the relationship with density at different levels of shelter (see ESM Table 1 for full model results). Shelter availability is based on a Principle Component Analysis (PC1 score) incorporating the terms small hole density, large hole density and rugosity, which explained 66% of the variation in shelter across the 18 sites in panel a, and 68% of the variation across the 12 sites in panel b. Note that the shelter classes and linear lines of fit presented here are for illustrative purposes only as the PC1 scores were used as a continuous variable in the regression models.

TABLE 2. Variance partitioning of terms (using the LMG method through "relaimpo" R-package) in the best-fit models predicting mortality, growth, and condition.

Response	Best fit model terms	Partial -R	% contribution
Mortality	Shelter	0.45	66
	Density	0.23	34
Growth	Shelter	0.55	70
	Density	0.11	14
	Shelter × Density	0.13	16
Condition	Shelter	0.03	4
	Density	0.15	22
	Shelter × Density	0.49	74

Instantaneous mortality increased with increasing local densities (direct density dependence), but this effect was dependent on the level of shelter, supporting previous observations of habitat-dependent mortality in reef fish (Shima and Osenberg 2003, Forrester and Steele 2004). However, growth and condition of fish (a putative measure of feeding history and energetic reserves, respectively; Ferron and Leggett 1994) had more complex interactive relationships with local density and shelter availability. Where shelter was in medium to high abundance, growth was (1) higher at low densities and (2) declined with density (direct density dependence); whereas where shelter was rare, growth was comparatively low and exhibited no clear relationship with density. Similarly, fish condition declined with increasing density (direct density dependence), but only when shelter was rare or moderately available. In contrast, when shelter was abundant, this effect was reversed and condition increased with density (inverse density dependence). We cannot discount the possibility of size-selective mortality of larger individuals increasing with density and shelter, which could explain observations of increasing mortality and declining growth at high and medium shelter sites. Larger individuals may be preferred by predators (Li et al. 1985) or act more boldly (Krause et al. 1998) in complex environments, although these effects are unlikely to be strong enough to create the observed patterns.

Consequently, we mostly observed the typical density-habitat relationship, where competition at higher densities reduces survival, growth and condition when shelter is limiting (e.g., Holbrook and Schmitt 2002, Samhouri et al. 2009), and which outweighs any benefits of larger group sizes (in contrast to Sandin and Pacala 2005, White and Warner 2007). However, the non-intuitive observations of no density-dependent growth at low shelter sites, and inverse density-dependent condition at high shelter sites have important implications for what additional mechanisms may contribute to heterogeneity in growth and condition at the landscape scale.

We suggest that these observations are most likely the result of different behavioral strategies occurring at sites that differ in shelter availability. At low shelter sites, densities were typically low, leading to a breakdown in shoaling behavior (Ford 2015) with fish found primarily in groups of less than five individuals and residing much closer to shelter. Therefore, few benefits (food and predator detection) or costs (competition) are likely incurred when fish are in very small groups, leading to lower overall growth rates and the lack of a relationship between growth and density.

In contrast, when shelter is abundant, predation risk is lower and fish can spend more time foraging higher in the water column and less time avoiding predators, facilitating greater energetic resources to allocate to growth or energy stores. As shelter becomes limiting with increasing density, particularly at moderate shelter abundances, fish may have to spend more time jockeying for position and defending their preferred shelters. As a consequence, feeding rates likely decrease and growth and condition are predicted to decline – a pattern also observed in foraging bluehead wrasse (White and Warner 2007). These costs may be less pronounced when shelter is abundant. Consequently, lower levels of wariness with increasing density at high shelter reefs could (1) increase feeding efficiency (leading to concomitant increases in energetic reserves) and/or (2) contribute to greater selective mortality of poor-conditioned individuals. Similar foraging tradeoffs have been hypothesized to occur in response to changes in prey and predator abundance (e.g., Walters and Juanes 1993). Further research that integrates behavioral observations, survival studies, and measures of zooplankton prey and predator abundances could help to identify the underlying drivers of the interactions between density and growth/condition.

The absence of high-density, low-shelter sites suggests that either high early post-settlement mortality was undetected at low shelter sites, or hulafish preferentially colonise sites with more shelter. This result could be attributable to active habitat selection (Montgomery et al. 2001, Lecchini et al. 2005), and/or to hydrodynamic features that deliver more larvae to sites in the south and east (i.e., where structurally complex sandstone reefs are most abundant). Regardless of whether the mechanism of covariance between colonization and shelter is active or passive, the end result is an association between densities and resources that approximates an ideal free distribution (Fretwell and Lucas 1970), a pattern common to many organisms (e.g., songbirds: Haché et al. 2013, and deer: Walhström and Kjellander 1995). In addition to colonization, we also demonstrate that other demographic parameters may respond differently to density × resource gradients. Most strikingly, fish condition was not successfully predicted by either density or shelter, but only by the interaction. The fact that condition differed from growth and mortality in the pattern and direction of its response to density (dependent upon shelter availability) indicates that landscape scale complexity may shape local and regional recruitment dynamics in ways that may be difficult to predict a priori and with empirical approaches alone.

We have demonstrated that demographic rates and the strength of density dependence can vary considerably, and in non-intuitive ways, across a seascape. As many species form spatially-structured populations in heterogeneous environments, this underscores the need for more empirical studies of how spatial heterogeneity in local demographic rates interact with dispersal to influence population dynamics at landscape scales.

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SUPPORTING INFORMATION