



Implication of changing coral communities: do larval traits or habitat features drive variation in density-dependent mortality and recruitment of juvenile reef fish?

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Abstract Many lines of evidence suggest coral communities worldwide are changing rapidly. Responses of coral reef fish populations to such changes will, in part, depend upon how vital demographic rates of fish populations respond to changing coral communities. Our previous work on the reef fish *Thalassoma hardwicke* suggests the strength of density-dependent mortality (a measure of “site quality”) is heterogeneous in space and time. Here we examine environmental features that might account for spatiotemporal variation in quality, to facilitate more accurate predictions of how *T. hardwicke* populations might respond to habitat degradation and/or changing coral communities. Two habitat attributes—density of branching coral *Pocillopora* spp. and presence/absence of territorial damselfish *Stegastes nigricans*—explained >77% of the variation in site quality. The strength of density-dependent mortality experienced by cohorts of *T. hardwicke* was consistently weaker at sites where *S. nigricans* was present, and declined with increasing coverage of *Pocillopora*. However, further sampling suggests that intrinsic quality of juvenile *T. hardwicke* covaries with these same habitat attributes: cohorts collected from sites with relatively high cover of *Pocillopora* had proportionally more lipids and faster otolith growth rates as larvae relative to cohorts collected from reefs with no- or low coverage of *Pocillopora*. We expect that habitat attributes and individual traits both contribute to “site quality”, and suggest that a better understanding of the sources of variation in site quality (i.e., density dependence mediated by habitat- or individual traits) may be necessary to predict the fates of coral reef fish populations with any reasonable accuracy.

Keywords reef fish, cryptic density dependence, habitat quality, fitness, demographic heterogeneity

Introduction

Coral reefs worldwide are severely threatened, with some estimates already classifying >30% of the world's coral reefs as severely degraded (Wilkinson 2000). While changes in composition and structure of coral communities are often the focus of concern, these changes will undoubtedly impact populations of reef fishes that rely upon corals as sites for feeding, reproduction, recruitment, and shelter (e.g., Booth and Beretta 2002; Jones *et al.* 2004). Despite the economic- and ecological importance of reef fishes, there have been relatively few attempts to predict responses of fish populations to changing coral communities.

These responses will, in part, be determined by the relationship between coral community attributes and vital demographic rates of fish populations (i.e., per capita rates of reproduction, recruitment, mortality, or migration). As a further complication, any of these demographic rates may be density-dependent, and the strength of this density dependence may be affected by coral community attributes. We are aware of no predictive models that have attempted to incorporate effects of variation in the strength of density dependence mediated by habitat degradation or disturbance. Because the form and strength of density dependence can determine attributes of population dynamics (and ultimately, persistence), we see this as a major oversight in current research paradigms.

Our previous work on the reef fish *Thalassoma hardwicke* suggests that density dependent mortality shortly after settlement to coral communities is an important determinant of recruitment (Shima 1999; 2001a; 2001b). Importantly, the strength of this density dependence is spatiotemporally heterogeneous (Shima and Osenberg 2003), but the source of this heterogeneity remains unclear. If

heterogeneity in density dependence is determined by attributes of coral communities, then changes to these communities (e.g., projected global decline of coral) may have dramatic effects on the dynamics and structure of *T. hardwicke* populations. Alternatively, heterogeneity in density dependence may arise from intrinsic attributes of fish populations (e.g., spatially structured, among-individual variation in quality). In this alternative scenario, *T. hardwicke* populations may be partially buffered from habitat degradation, provided quality of individuals is independent of coral community attributes.

Here, we address these two alternative hypotheses, with an aim to improve understanding of the mechanisms that underlie heterogeneity in a vital demographic rate that is density-dependent (post-settlement survival), and to facilitate the development of models predicting how fish populations might be expected to respond to widespread disturbance and degradation of coral reefs.

Materials and methods

Heterogeneous “Quality” Among Reefs -

Previously (Shima and Osenberg 2003), we estimated the strength of density dependent post-settlement mortality contributing to 480 recruitment events (i.e., juveniles surviving to 90 days after settlement, for a given reef-date combination) for the six bar wrasse, *Thalassoma hardwicke* on Moorea, French Polynesia (17° 30' S, 149° 50' W). Here, we define site “quality” as $1/\beta$, where β is the strength of density dependence estimated from our empirical data fit by a Beverton-Holt recruitment function (Beverton and Holt 1957). Details of sampling and estimation procedures are given elsewhere (Shima and Osenberg 2003). Our previous results suggest spatiotemporal heterogeneity in site quality: fish settling to some reefs incur stronger density dependence and a greater probability of mortality at a given density, relative to fish settling at similar densities to other reefs (Shima and Osenberg 2003; see also Wilson and Osenberg 2002).

Environmental Correlates with Quality-

For each observation of site quality ($1/\beta$, $n = 480$), we have corresponding estimates of *Pocillopora* spp. density (i.e., branching coral, potential refuges used by *T. hardwicke*) and reef substrate type (either living coral *Porites lobata*, or algal turf associated with territories of the farming damselfish *Stegastes nigricans*). Branching coral density and substrate type are sensitive to disturbance regimes on Moorea (Gleason 1994; *c.f.* Crossland 1928), and both variables are likely to continue to change in response to further environmental degradation. To facilitate predictions of how *T. hardwicke* populations might respond to changing coral communities, we conducted an Analysis of Covariance (PROC GLM, SAS v8.02) to examine the relationship between site quality from a fish’s perspective (i.e., $1/\beta$, a density-

dependent survivorship probability), substrate type (the categorical dependent variable; $n = 192$ for *P. lobata*, $n = 288$ for *S. nigricans*) and *Pocillopora* density (the covariate). *S. nigricans* is known to facilitate *Pocillopora* recruitment and survivorship (Gleason 1994); consequently reefs with *S. nigricans* territories as the predominant substrate type had a greater upper range of densities of *Pocillopora*. We constrained our formal ANCOVA to sites with *Pocillopora* densities less than 1 colony / m² (i.e., a range over which we had observations for both substrate types).

Heterogeneous Quality Among Individuals-

An alternative explanation for spatiotemporal heterogeneity in site quality ($1/\beta$) is that it arises from properties intrinsic to cohorts of fish settling to different sites. Fitness of individuals (and the strength of intra-cohort interactions) may be a function of the quality (e.g., size or physiological condition) of fishes colonizing reefs (Bergenius *et al.* 2002; Shima and Findlay 2002; Vigliola and Meekan 2002; McCormick and Hoey 2004). For this to be a viable explanation of heterogeneous site quality, traits associated with individual quality (e.g., lipid content, larval growth rates) should be positively correlated with site quality.

Because our analyses (see Results) suggested *S. nigricans* territories and *Pocillopora* densities were good predictors of site quality, we collected recently settled *T. hardwicke* (<5d post-settlement) from haphazardly selected reefs with- and without *S. nigricans*, and spanning a gradient of *Pocillopora* cover (cumulative surface area estimated at the time of fish collections) for each substrate category. Following collections, we removed otoliths from fish and freeze-dried them for subsequent lipid extractions.

We estimated total lipids from a spectrophotometric analysis of 143 homogenized, freeze-dried fish; lipids were extracted using a dichromate oxidation assay accessed against a tripalmitin standard (a modification of Parsons *et al.* 1984). We estimated “relative lipid content” for each fish as *total lipids* divided by *sample dry mass*^{0.6} (because preliminary analyses indicated that lipids scaled with dry mass, within groups, to the 0.6 power), and used ANCOVA (PROC GLM, SAS v8.02) to explore variation in relative lipid content (averaged across individuals for a given reef) as a function of presence/absence of *S. nigricans* (dependent variable) and *Pocillopora* cover (covariate). As above, a formal analysis was conducted on a truncated dataset where the range in the covariate was similar among substrate categories (i.e., limited to reefs with *Pocillopora* cover < 7400cm²/reef; $n = 19$ reefs with *S. nigricans* present, $n = 23$ reefs with *S. nigricans* absent).

Because relative lipid content of sampled juveniles may be a *consequence* of site quality rather

than an alternative explanation for site quality, we attempted to hindcast heterogeneity in quality of collected fish at their time of settlement by estimating otolith growth rates during larval development. Studies of other species indicate that larval otolith growth can predict subsequent survival probabilities (Bergenius *et al.* 2002; Shima and Findlay 2002; Vigliola and Meekan 2002; McCormick and Hoey 2004); hence, we estimated individual larval otolith growth rates from image analysis of otolith increments. Otolith radius accrual was an approximately linear function of age during the larval period, and for each fish we estimated larval otolith growth rate as the slope of a linear regression of maximum otolith-radius-at-age vs. age (where “radius-at-age” = cumulative daily increment widths; increments validated in Shima 1999). For each individual, we measured otolith attributes blind on at least two separate occasions. Because some otoliths were difficult to read (reducing our confidence in these samples), we excluded from analysis any samples where slopes were not repeatable at +/- 10 percent. As above, ANCOVA (PROC GLM, SAS v8.02) was used to explore variation in larval otolith growth rate (averaged across individuals for a given reef) as a function of presence/absence of *S. nigricans* (dependent variable) and *Pocillopora* cover (covariate); formal analysis was limited to reefs with *Pocillopora* cover < 7400cm²/reef (; n = 21 reefs with *S. nigricans* present, n= 29 reefs with *S. nigricans* absent).

Results

Environmental Correlates with Quality -

Substrate type (*Stegastes* vs. *Porites* reefs) and *Pocillopora* density predicted 77.4% of the observed variance in quality (Fig 1). Site “quality” for *T. hardwicke* increased with *Pocillopora* density ($F_{1,386} = 148.68$, $P < 0.0001$) and quality was substantially greater for reefs containing *S. nigricans* territories ($F_{1,386} = 1162.59$, $P < 0.0001$), with no significant

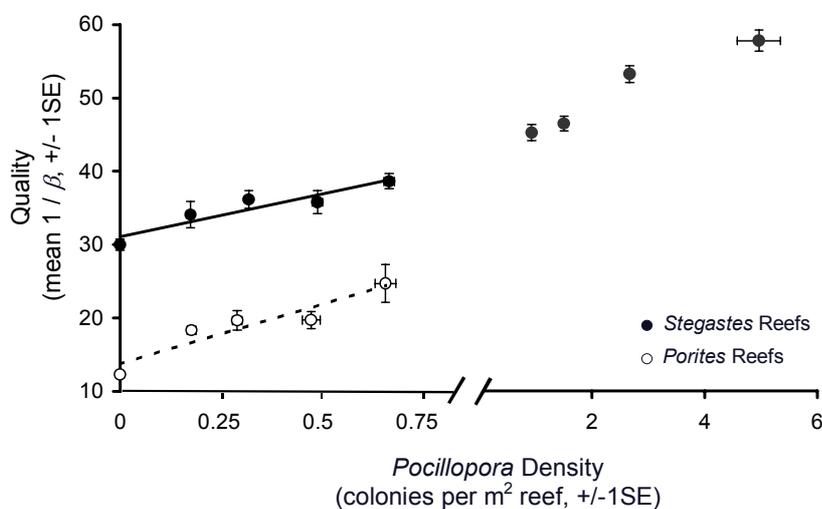


Fig. 1. Environmental correlates with “site quality”. Quality is defined as $1/\beta$, where β is the estimated strength of density-dependent mortality (from Shima and Osenberg 2003). Site quality increases linearly with *Pocillopora* density (branching coral, presumptive shelter), and categorically with presence of territorial damselfish (*Stegastes nigricans*). Note that scale varies on broken X-axis.

interaction between *Pocillopora* density and substrate type ($F_{1,386} = 3.52$, $P = 0.0614$). *T. hardwicke* that settled to sites containing *S. nigricans* and/or *Pocillopora* were likely to experience weaker density dependence and enhanced survivorship at a given density relative to cohorts that settled to sites comprised solely of *Porites lobata*.

Heterogeneous Quality Among Individuals -

Relative lipid content of juvenile *T. hardwicke* increased with cover of *Pocillopora* on reefs from which they were collected (Fig. 2, $F_{1,50} = 11.29$, $P = 0.0016$) but not with presence or absence of *S. nigricans* ($F_{1,50} = 1.25$, $P = 0.2698$; interaction term $F_{1,50} = 0.16$, $P = 0.69$). Similarly, estimates of larval otolith growth rates for these same individuals increased with cover of *Pocillopora* (Fig. 3, $F_{1,49} = 4.12$, $P = 0.048$) but not with presence or absence of *S. nigricans* ($F_{1,49} = 0.66$, $P = 0.42$; interaction term $F_{1,49} = 2.32$, $P = 0.1347$). *T. hardwicke* that settled (and survived to be captured) on sites with higher coverage of *Pocillopora* were likely to have faster growing otoliths as larvae and higher concentrations of lipids as juveniles. Although formal analyses of covariance based on truncated datasets indicated non-significant interaction terms for both tests, Fig 2 (showing complete range of variability in *Pocillopora*) suggests a possible interaction and/or non-linear response of relative lipid content to *Pocillopora* cover when *S. nigricans* is present.

Discussion

The strength of density-dependent post-settlement mortality is heterogeneous in space and time for *T. hardwicke*, and for individual fish this reflects variation in site quality (Shima and Osenberg 2003). Because heterogeneity in a vital demographic rate can influence population dynamics and responses to perturbations (Osenberg *et al.* this volume), we explored our dataset for environmental features that might account for spatiotemporal variation in quality.

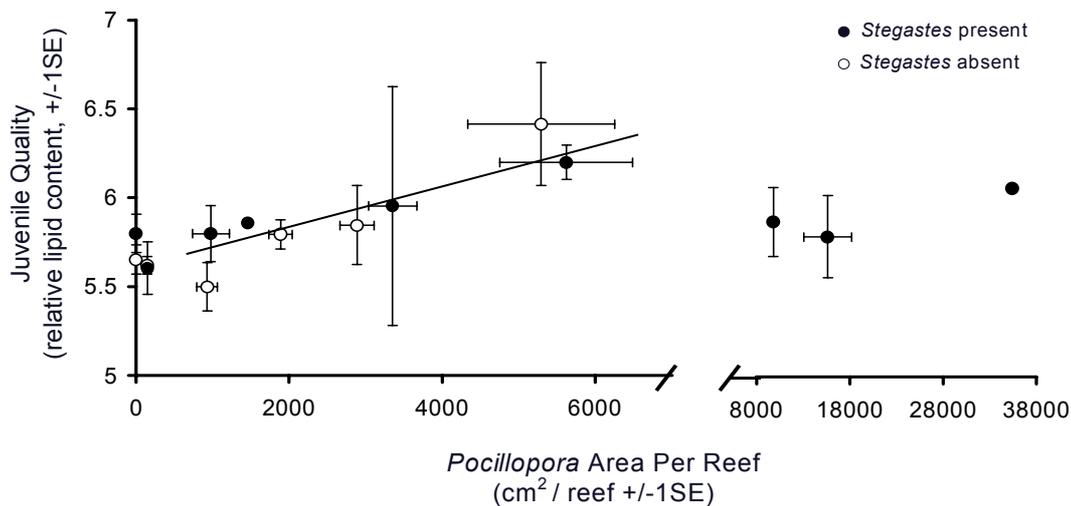


Fig. 2. Variation in “intrinsic quality” of recently settled *T. hardwicke* populating different reef communities. Intrinsic quality is estimated as relative lipid content (averaged across individuals per reef). Reefs with higher coverage of *Pocillopora* were populated by fish with more lipids (possibly of greater “intrinsic” quality). Note that scale varies on broken X-axis. Unequal error bars are the result of binning procedure.

Our aim was to develop a clearer understanding of ecological mechanisms underlying site quality to improve predictions of how *T. hardwicke* populations might respond to habitat degradation and/or changing coral communities.

We found compelling correlations between habitat attributes and previously estimated strengths of density dependence, among observations distributed in space and time. Regardless of substrate type, site quality increased with densities of branching coral colonies (*Pocillopora* spp.) per reef.

T. hardwicke routinely seek shelter in *Pocillopora*, and a pattern of weakening density dependence with increasing *Pocillopora* density is consistent with a relaxation of scramble competition for sheltering sites. In addition, we observed a strong and independent effect of substrate type on site

quality: the strength of density dependence was consistently weaker on reefs comprised primarily of algal turf territories of the farming damselfish *S. nigricans*. Density dependence was ~2.5 times stronger on reefs comprised mainly of living coral *Porites lobata* (i.e., without damselfish territories). This observation is consistent with algal turfs maintained by *S. nigricans* that may provision or enhance food resources (benthic microinvertebrates) for *T. hardwicke*. Alternatively, territorial behavior of *S. nigricans* may afford *T. hardwicke* some protection from predators.

Work by Gleason (1994; 1996) in this same system demonstrates a strong facilitative effect of *S. nigricans* on settlement, growth and survival of *Pocillopora*. Such facilitation (and/or inhibition) almost certainly extends to other species; reefs with

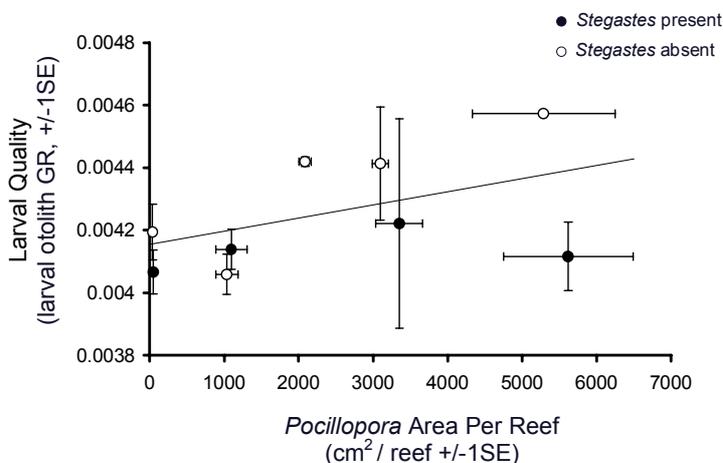


Fig. 3. Estimated larval traits of individuals populating different reef communities. Reefs with more *Pocillopora* were populated by recently settled *T. hardwicke* that exhibited faster growth as larvae, determined from otolith increment analysis. Unequal error bars are the result of binning procedure.

territorial damselfish have a greater diversity of substrate types and resident species than reefs without damselfish (Shima *personal observations*). We expect that any heterogeneity in quality attributable to the territorial damselfish *S. nigricans* is a cumulative consequence of multiple direct- and indirect- effects.

Gleason's (1994; 1996) work is further supported by our observations that *Pocillopora* reaches far greater densities on reefs where *S. nigricans* is present (Fig 1). One important consequence of this may be that *S. nigricans* facilitates sites of "very high quality" for *T. hardwicke*; e.g., where *S. nigricans* was present, maximal site quality was ~4.5-fold greater than for sites with only *P. lobata* substrate. Historic lines of evidence suggest shifting distributions of site quality may have had dramatic consequences for populations of *T. hardwicke*: Island-wide disturbance events on Moorea in the early 1980's (e.g., cyclone damage, *Acanthaster* outbreaks, and bleaching) resulted in reductions of living coral within the lagoons surrounding Moorea (Gleason 1994). Losses of coral colonies (including *Porites lobata*) coincided with increases in *S. nigricans* over this same time (*c.f.* Gleason 1994; Galzin 1987), potentially facilitated by habitat availability following disturbance. Since the early-1980's, *Pocillopora* densities have increased substantially, facilitated in part by *S. nigricans* (Gleason 1994). Perhaps as a consequence of increasing densities of *S. nigricans* and *Pocillopora*, *T. hardwicke* populations at some sites on Moorea have increased by ~168% over this time (Galzin 1987).

Although compelling, inferred contributions of habitat attributes to site quality (and the strength of density dependence) are based entirely upon correlations. An alternative explanation for spatiotemporal heterogeneity in site quality is that it arises from intrinsic properties of individuals, or cohorts of individuals settling to particular sites at particular times. We sampled juvenile *T. hardwicke* from sites with- and without *S. nigricans*, and spanning a range of coverage of *Pocillopora*. Our results suggest that individual quality (as measured by relative lipid content) covaried with the same habitat attributes that predicted much of the variation in site quality. Cohorts collected from sites with relatively high cover of *Pocillopora* had proportionally more lipids relative to cohorts collected from reefs with no- or low coverage of *Pocillopora*. This non-random distribution of cohort quality may be a consequence of increased *Pocillopora* coverage (e.g., because more sheltering sites might result in a net energetic savings, or alternatively, because branching corals might provision a lipid-rich diet). However, this same spatial heterogeneity in cohort quality remains a plausible explanation for variation in site quality: cohorts in better physiological condition may experience weaker density dependence than cohorts in poor physiological condition. Plausibility of this

alternative mechanism underlying site quality is further strengthened by observations that individuals collected from sites with high coverage of *Pocillopora* had faster growth rates *as larvae*. *T. hardwicke* growing rapidly as larvae may settle disproportionately to sites with more *Pocillopora*. Alternatively, fast growing larvae may be differentially successful (e.g., at colonizing, or surviving after settlement) on sites with more *Pocillopora*. Regardless of the mechanism, covariation between individual traits, habitat attributes, and density dependence means that we are unable to rule out the possibility that spatiotemporal heterogeneity in site quality may arise from variability intrinsic to individuals or cohorts. Certainly, both habitat attributes and individual traits may contribute to site quality. Definitive answers require field experiments.

As a further corollary to this story, our previous work (Shima and Osenberg 2003) suggests that intensity of settlement of *T. hardwicke* covaries with site quality—fish settle at higher densities to sites where they ultimately experience weaker density dependence, resulting in greater-than-expected recruitment. This pattern of covariation masks detection of density dependence (Wilson and Osenberg 2002, Shima and Osenberg 2003), and ultimately influences how *T. hardwicke* populations might respond to habitat degradation and/or changing coral communities. As is the case for many species, patterns of recruitment of *T. hardwicke* will depend upon interactions between the strength of density dependence and processes that set initial densities at a site. Habitat degradation or disturbance events can affect demography of *T. hardwicke* by influencing: 1) site quality directly, via effects on "habitat quality" and/or "individual quality"; 2) interactions between habitat- and individual quality that drive the strength of density dependence; and/or 3) patterns of covariance between settlement intensity and site quality (see Osenberg *et al*, this volume).

Predicting responses of reef fish populations to habitat degradation or projected changes to coral communities will not be a straightforward task. At one level, our results suggest that simple indices of "live coral cover" generated by many international coral reef monitoring programs may be insufficient to characterize habitat modification meaningful to fish (e.g., Fig 1 predicts qualitatively different responses of *T. hardwicke* to reductions in "live coral", depending upon whether the coral species in question is *Porites lobata* or *Pocillopora*). At a more mechanistic level, our results indicate several different pathways that may contribute to site quality (and which may affect how fish populations respond to site quality)—each of these pathways is potentially affected by habitat degradation, disturbance, or changes in coral community composition. Our future research in this system is directed at disentangling such relationships, to generate a more complete

understanding of population dynamics and the processes that drive them.

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