Spatially correlated recruitment of a marine predator and its prey shapes the large-scale pattern of density-dependent prey mortality

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Abstract
Patterns of predator dispersal can be critical to the dynamics of prey metapopulations. In marine systems, oceanic currents may shape the dispersal of planktonic larvae of both predators and prey, producing spatial correlations in the recruitment of both species and distinctive geographic patterns of prey mortality. I examined the potential for this phenomenon in two fishes, a wrasse and its grouper predator, at a Caribbean island where the near-shore oceanographic regime produces a temporally consistent spatial pattern of fish recruitment. I found that recruitment and adult abundance of groupers were spatially correlated with recruitment of wrasse prey. Furthermore, the local abundance of predators strongly affected the nature of density-dependent prey mortality. At sites with few predators, wrasse mortality was inversely density-dependent, while mortality was positively density-dependent at sites with higher predator densities. This phenomenon could be important to the dynamics of any metacommunity in which physical forces produce correlated dispersal.

Keywords
Cephalopholis fulva, coral reef fish, density dependence, habitat complexity, inverse density dependence, metacommunity, metapopulation, predation, recruitment, Thalassoma bifasciatum.

INTRODUCTION
Ecologists have recently broadened the single-species metapopulation framework to accommodate the concept of metacommunities: assemblages of interacting species occupying a set of spatially distinct habitat patches linked by dispersal (Holyoak et al. 2005). Predator–prey interactions are a key feature of metacommunity dynamics, because spatial variation in the abundance of predators strongly affects the local abundance of their prey, with prey in high-predator patches generally suffering higher mortality than those in patches with fewer predators (Holp 2002). In many cases, the resulting spatial heterogeneity in predation rates can stabilize the metapopulation dynamics of both species (Hoopes et al. 2005). Indeed, the importance of spatial heterogeneity and movement to predator–prey dynamics were recognized long before the metacommunity concept emerged (Hassell & May 1974). Importantly, most theoretical investigations of spatial predator–prey dynamics make the critical assumption that dispersal (usually of the predator) is either random and diffusive (e.g. Hassell et al. 1994) or behaviourally directed, so that predators actively search for prey (e.g. Murdoch et al. 1992). However, neither of these assumptions will hold for most marine systems, in which large-scale movement is driven predominantly by oceanic currents.

Many marine organisms are characterized by a two-phase life-history: demersal adults that are restricted to patches of suitable benthic habitat, and planktonic larvae that may travel between adult habitat patches. Marine larvae are not completely passive particles (Leis & McCormick 2002), but their movement is strongly influenced by oceanographic processes (Shanks 1995). Consequently, attempts to describe marine metapopulation dynamics have commonly involved detailed physical-oceanographic simulations of larval dispersal (Alexander & Roughgarden 1996; James et al. 2002; Cowen et al. 2006). To date, such simulations have focused on single species and assumed that local, within-patch processes, such as predation, are spatially invariant (for a notable exception, see Connolly & Roughgarden 1999).
However, most marine predators also possess planktonic larvae, so the distribution of predators throughout the metacommunity may neither be uniform and diffusive, nor behaviourally directed, but instead influenced by oceanographic delivery of predator larvae.

If the larval trajectories of predators and their prey are affected by oceanographic forces in similar ways, some habitat patches might experience consistently high (or low) recruitment of larvae from both trophic levels. While no study has directly examined the potential for correlated recruitment between predators and prey, there is evidence that oceanographic processes generate spatial correlations in the distribution and delivery of larvae from a broad range of taxa, at least at large spatial scales. Diverse assemblages of fish and invertebrate larvae are concentrated in coastal eddies and retention zones (Wing et al. 1998; Nishimoto & Washburn 2002), and a handful of studies suggest that such temporally persistent oceanographic features can produce consistent patterns of larval delivery for multiple species (Connolly et al. 2001; Mace & Morgan 2006).

The effects of oceanographically driven spatial variability in predator abundance could be especially noticeable in reef fish metacommunities. All fish are small and vulnerable at some point in their life, so predation strongly affects local community structure (Hixon 1991), and reefs with high densities of top predators generally have higher mortality rates of smaller fishes (Holbrook & Schmitt 2003). Reef fish are especially vulnerable to predation immediately after settlement from the plankton, often experiencing spatially density-dependent mortality (Hixon & Webster 2002) as a consequence of competition for shelter space (Holbrook & Schmitt 2002) or aggregation by predators (Anderson 2001). Such mortality can translate into temporal density dependence, in which per capita mortality varies with population density over time at a single location (Steele & Forrester 2005), and thus play an important role in the regulation of population dynamics (Stewart-Oaten & Murdoch 1990). Recent studies indicate that prey at sites with higher predator densities experience stronger density-dependent mortality (Schmitt & Holbrook 2007), so spatial variation in predation may affect both the abundance and dynamics of prey populations.

Because of the importance of predation for within-patch dynamics, spatial covariation in the recruitment of predators and their prey could drastically alter the predictions of existing models of marine metapopulation dynamics, which focus on single species and do not account for the potential consequences of spatial heterogeneity in predator densities or predation rates (James et al. 2002; Croven et al. 2006). Here I present the first empirical evidence for this phenomenon by documenting a spatial correlation in the recruitment of a coral reef fish and one of its predators around an oceanic island and describing the striking pattern of post-settlement prey mortality that develops as a result.

**MATERIALS AND METHODS**

**Study site and species**

I performed all fieldwork at the Caribbean island of St Croix, US Virgin Islands (see Appendix S1). The prevailing surface currents around St Croix are wind-driven and flow westward, but Harlan et al. (2002) observed an area of slow, converging currents off the northwestern edge of the island during the summer of 1997. This oceanographic convergence is likely responsible for the consistent pattern of recruitment observed for many fishes on reefs along the north shore of St Croix: high recruitment on western reefs, declining sharply to the east (Hamilton et al. 2006).

St Croix is surrounded by an irregular network of barrier reef and flat pavement reef habitat. While stretches of this reef habitat are broken up into large ‘patches’ by areas of sand or seagrass (subtidal habitat maps are available at http://ccma.nos.noaa.gov/products/biogeography/benthic/htm/maps/locator.pdf, last accessed 1 Aug 2007), most reef organisms are relatively sedentary, with typical scales of movement far smaller than the extent of a contiguous stretch of reef habitat. Consequently, the composition of fish communities on St Croix differ greatly over the scale of just a few km along physically contiguous reefs (Toller 2002). As such, in this paper I adopt a ‘functional’ metapopulation/metacommunity framework (Kritzer & Sale 2006) in which local sites are not delimited by clear habitat boundaries but are small enough in area (c. 1000 m²) and sampled far enough apart (> 1 km) that over its lifetime, a fish is unlikely to move among sites but very likely to interact with most of the other individuals within its own site. This type of spatial structure is quite common in coral reef systems (Kritzer & Sale 2006) and is increasingly recognized as falling within the broader ‘metacommunity’ rubric (Leibold et al. 2004).

*Thalassoma bifasciatum* Bloch (bluehead wrasse; Labridae), a small-bodied planktivore, is one of the most common reef fishes at St Croix and the primary subject of the recruitment studies noted above. After hatching, *T. bifasciatum* spend approximately 44–50 days in the plankton before settling to coral rubble habitat (Victor 1982). Settlement commonly occurs in monthly pulses following the new moon, and is highest in July–September (Caselle & Warner 1996). New settlers are highly site-attached for c. 7 days, permitting accurate estimation of settler densities and mortality rates during this time window. Predator exclusion experiments indicate that predatory fish are a significant source of mortality for new settlers (White & Warner in press). The most common piscivore on local reefs is the grouper *Céphalopholis fulva* Linnaeus (coney; Serranidae), a territorial
 predator of fishes and crustaceans that grows to a maximum of 40 cm total length (TL) and can live up to 11 year (Potts & Manooch 1999). The high population density and high proportion of small reef fishes (including T. bifasciatum) in the diet of C. fulva relative to other predatory fishes suggest that C. fulva is the major predator of T. bifasciatum on St Croix (Appendix S2).

Spatial patterns of predator and prey recruitment

To estimate the recruitment and abundance of T. bifasciatum and C. fulva, I censused both species on four permanent 25 m transect lines at each of seven sites around St Croix: Butler Bay, Northstar, Green Cay, Jacks Bay, Wood Cottage, Tague Bay and Knight Bay (see Appendix S1). At all sites, transects were parallel to one another, 20–30 m apart on the reef pavement. From June to September 2003, I conducted a visual survey along each transect monthly within 10 days following the new moon. Surveys consisted of one diver swimming slowly over the transect, counting all C. fulva within 3 m of the transect line (a 25 × 6 m transect) and assigning them to 5 cm size bins according to TL. A second diver followed the first, counting all T. bifasciatum within 1 m of the transect line (a 25 × 2 m transect). In the context of these surveys I use the term ‘recruits’ to refer to fish that have recently settled, with the understanding that some mortality may have occurred between settlement and census. For T. bifasciatum, all individuals < 15 mm TL (approximately 4 days post-settlement age) were counted as recruits, based on an otolith-derived age-length relationship (J. W. White, unpublished data). For C. fulva, most spawning occurs between January and July (Shapiro 1988), and young, 5–10 cm TL C. fulva were observed on St Croix reefs well into September 2003. Based on the age and length data presented by Potts & Manooch (1999), I distinguished two classes of C. fulva recruits: those that had settled within the past 0–4 months (< 10 cm TL; hereafter termed ‘recent recruits’) and older fish that had likely settled in 2002 or early 2003 (10–15 cm TL; hereafter termed ‘older recruits’).

Similar surveys of C. fulva population density were made at the same seven sites in June–September 2002 and at Butler Bay, Northstar, Jacks Bay, Wood Cottage, and an additional site, Cane Bay in 2004. To correct for heteroscedasticity in the survey data (sample variance increased with mean density), I applied a log(x + 1) transformation prior to analysis.

Spatiotemporal patterns of prey mortality

To determine the effect of C. fulva abundance on mortality of T. bifasciatum, I monitored the settlement and mortality of T. bifasciatum at five of the sites mentioned above (Butler Bay, Northstar, Jacks Bay, Wood Cottage and Cane Bay) and one additional site (Cane Bay; 2.5 km east of Northstar) in July and September 2005. Detailed methods can be found in White & Warner (in press), where data from the same study were used to examine the effects of group membership on morality at the spatial scale of individual fish; here I use these data to examine patterns of mortality at a larger spatial scale, that of 30–60 m² transects. Briefly, I established three permanent, 30 m transect lines 20 m apart on the reef at each site. I then recorded the initial appearance and subsequent survival of all T. bifasciatum settlers within 1 m of the transect line along one side of the transect (30 m² total; July) or both sides (60 m² total; September) daily during 6 day intervals centred on the monthly settlement pulse. Tagging studies have indicated that settlers are highly site attached for at least the first 7 days post-settlement, remaining within a roughly 20 cm radius of a crevice (or crevices) in the reef where they shelter (White & Warner, in press). As such, settlers can be identified by their unique spatial location and disappearance can be equated with mortality, so I mapped the location of each settler on a coordinate grid and monitored the survival of the settler at each location for the duration of the observation period. Settler density (n m⁻²) was estimated during each day of the observation interval and weighted by the number of settlers present on the transect that day to give a weighted estimate of settler density during the observation period:

\[
\text{Density}_i = \sum_d \left( \frac{n_{i,d}}{\sum_d n_{i,d}} \times \frac{n_{i,d}}{A_i} \right) \tag{1}
\]

where \(n_{i,d}\) is the number of settlers on transect \(i\) on day \(d\), \(A_i\) is the area of transect \(i\) and the sums are taken over all days of the observation window. This weighting ensured that the mean density reflected the effective density experienced by the majority of settlers. For example, if many settlers were present on a transect on the first day of observations but suffered high mortality, leaving only one or two settlers for the remainder of the observation period, eqn 1 would capture the high density experienced by the majority of settlers on that first day better than an unweighted average of the daily densities would. The density of C. fulva at each site was estimated by performing visual surveys of fish within 3 m of each permanent transect before and after each 6 days interval (a 180 m² transect). Data were collected at four sites in July (excluding Wood Cottage) and all five sites in September.

While the focus of this study was the consequences of spatial variability in predator abundance, this is not the only factor that might shape large-scale patterns of prey mortality. In particular, among-site heterogeneity in habitat quality might determine the local strength of density-dependent prey mortality, either independent of or in addition to any effect of predators (Shima & Osenberg 2003). It is well-known that the survival of small coral reef fishes is often a function of the availability and quality of shelter habitat (Hixon & Beets
1993). At St Croix, *T. bifasciatum* settlers primarily shelter in crevices and indentations in the dead coral pavement substrate and associated rubble (JWW, personal observation). To determine whether among-site patterns of settler mortality were a product of differences in shelter habitat, I quantified habitat complexity in terms of substrate rugosity (a common proxy for shelter availability; Luckhurst & Luckhurst 1978). I calculated rugosity as: 1 – (distance covered by chain placed on substrate)/ (actual length of chain) using a 1 m chain with 8 mm links. I estimated the rugosity for each transect used in monitoring settler mortality in 2005 as the mean of four rugosity estimates taken at the 5, 10, 15 and 20 m positions on the transect.

Per-capita mortality on each transect was estimated as

\[
mortality = 1 - \frac{\text{number of settlers remaining on transect at end of interval}}{\text{number of settlers arriving during interval}}. \tag{2}
\]

This measure combines data for fish settling throughout the observation period, so if survivorship increases sharply with age, mortality estimates could be sensitive to the proportion of 1- and 2-day-old fish counted as 'survivors'. However, 235 of the 305 settlers (77%) observed arrived in the first 3 days of observations and only 14 settlers (5% of the total) arrived in the final 2 days, so most settlers were exposed to mortality risk for a similar amount of time, affording a relatively robust comparison of mortality rates among transects.

The denominator in eqn 2 varied greatly among transects, which would prevent error terms in a least-squares statistical model from being normally distributed. I avoided this difficulty by analysing the mortality data using logistic regression with binomial error distribution and a logit link function (Montgomery et al. 2001). To determine whether *C. fulva* abundance or habitat complexity affected either settler mortality or the relationship between settler density and settler mortality, I performed a multivariate regression with terms for settler density, *C. fulva* density, substrate rugosity and all interactions (interaction terms were removed sequentially from the model if they were found to be non-significant at \( P > 0.15 \)). This resulted in a regression model of the form

\[
\ln[\frac{m}{1-m}] = \beta X + \varepsilon,
\]

where \( m \) is the per capita probability of mortality, \( X \) is the matrix of covariates associated with each observation, \( \beta \) is a vector of regression parameters and \( \varepsilon \) is a binomial error term. In this analysis, I considered the mortality estimate for each transect in each site-month to be an independent observation. This confounds temporal and spatial variation somewhat, but I chose covariates (habitat complexity and densities of predators and settlers) that should account for the major sources of spatiotemporal variability in mortality in this dataset. Instead, I examined the two observations of settler density and mortality for each transect at the four sites where data were collected in both months. For six of these transects, settler density was significantly higher in one of the 2 months, and for each of these six transects, I classified mortality as either increasing or decreasing with settler density. Logistic regression (with logit link function and binomial error distribution; Montgomery et al. 2001) was then used to find the relationship between this binary measure of temporal density dependence and the mean *C. fulva* density (taken across the entire summer) at each site. All logistic regressions were performed with the penalized-maximum-likelihood technique for small sample sizes using the *logistf* package (Heinze & Schemper 2002) for R (R Development Core Team 2006). Likelihood ratio tests were used to determine whether regression models were significantly different from a null model.

To visualize multivariate relationships (such as the joint effect of *C. fulva* density and *T. bifasciatum* settler density on settler mortality), I used coplots (Cleveland 1993), which illustrate the conditional relationship between the response variable and each of two predictor variables. Coplots consist of a series of panels, each showing the bivariate relationship between the response (settler mortality, in this case) and the first predictor (e.g. settler density) for a narrow range of values of the second predictor (e.g. *C. fulva* density). To represent the continuous nature of the multivariate relationship, these ranges overlap such that a few points with intermediate values of the secondary predictor are duplicated in each of two adjacent panels. The number of panels and ranges of the secondary predictor were chosen for clarity of presentation and are unrelated to the mechanics of the underlying multivariate analysis.
RESULTS

Spatial patterns of predator and prey recruitment

*Thalassoma bifasciatum* recruit densities ranged from 0.00 to 0.48 fish m$^{-2}$, while *Cephalopholis fulva* densities ranged from 0.00–0.08 fish m$^{-2}$ for recent recruits and from 0.00 to 0.19 fish m$^{-2}$ for older recruits. Densities of both species’ recruits were highest at leeward, northwestern sites (Butler Bay and Northstar), lowest at windward, northeastern sites (Green Cay, Tague Bay and Knight Bay) and intermediate at windward, southeastern sites (Jacks Bay and Wood Cottage).

Across sites, the density of *T. bifasciatum* recruits was positively correlated with the density of both recent (< 10 cm TL; $r = 0.76$, $n = 7$, $P = 0.048$) and older *C. fulva* recruits (10–15 cm TL; $r = 0.87$, $n = 7$, $P = 0.01$; Fig. 1a). The combined density of recent and older *C. fulva* recruits in 2003 was also an excellent predictor of adult *C. fulva* abundance (Fig. 1b), not only in the following years (linear regressions: 2004: $r^2 = 0.99$, $n = 3$, $F_{1,1} = 95.50$, $P = 0.065$; 2005: $r^2 = 0.96$, $n = 4$, $F_{1,2} = 42.99$, $P = 0.023$) but also in 2002 ($r^2 = 0.89$, $n = 7$, $F_{1,5} = 39.77$, $P = 0.0015$) and 2003 ($r^2 = 0.92$, $n = 7$, $F_{1,5} = 54.45$, $P = 0.007$).

![Figure 1](image.jpg)

**Figure 1** Spatial patterns of *Thalassoma bifasciatum* (bluehead wrasse) and *Cephalopholis fulva* (a wrasse predator) recruitment and abundance. (a) Relationship between density of *T. bifasciatum* recruits and density of recent (open symbols, dotted line) and older (filled circles, solid line) recruits of *C. fulva* in visual surveys along permanent transects at seven sites around St Croix in 2003. (b) Relationship between total density of *C. fulva* recruits at each site in 2003 and density of adult *C. fulva* at some of the same sites in 2002–2005. Each point is the mean of 3–12 surveys throughout the summer and across three to four transects within each survey; error bars are one standard error. Points are altered for clarity.

### Spatiotemporal patterns of prey mortality

In 2005, a total of 305 *T. bifasciatum* were observed settling to the transects, and 210 of these disappeared, and were presumed dead, during the observational intervals. Settler mortality was influenced by joint effects of settler density, *C. fulva* density, and habitat rugosity (Table 1). There was a negative relationship between rugosity and settler mortality, and this effect was most pronounced at higher *C. fulva* densities (significant rugosity × *C. fulva* interaction; Table 1, Fig. 2; the curvature present at the bottom of Fig. 2d is an artifact of the logistic nature of the regression model). Furthermore, the local density of *C. fulva* influenced the nature of density-dependent settler mortality: at low *C. fulva* densities, settler mortality decreased with settler density, but as *C. fulva* density increased, settler mortality became positively density-dependent (significant settler density × *C. fulva* interaction; Table 1, Fig. 3).

The spatial pattern of *C. fulva* abundance in 2005 was consistent with that observed in other years: higher at the leeward, western sites (Butler Bay, Northstar, and Cane Bay) and lower at the eastern, windward sites (Jacks Bay and Wood Cottage). Interestingly, the highest *T. bifasciatum* settler densities were observed in September at Jacks Bay, which is usually a low-recruitment, low-*C. fulva* site (although large *T. bifasciatum* recruitment pulses are common there in September; Hamilton et al. 2006). However, there is no indication that the settler density × *C. fulva* interaction is an

### Table 1 Results of logistic regression describing the effect of *Thalassoma bifasciatum* (bluehead wrasse) settler density ($n$ m$^{-2}$), *Cephalopholis fulva* (a wrasse predator) density ($n$ m$^{-2}$) and habitat complexity (dimensionless rugosity index) on per-capita bluehead wrasse settler mortality

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Estimate</th>
<th>SE</th>
<th>$P$-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>1.882</td>
<td>0.960</td>
<td>0.0482</td>
</tr>
<tr>
<td>Settler density</td>
<td>−6.098</td>
<td>1.508</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td><em>C. fulva</em> density</td>
<td>0.635</td>
<td>0.404</td>
<td>0.0965</td>
</tr>
<tr>
<td>Settler × <em>C. fulva</em></td>
<td>2.746</td>
<td>0.994</td>
<td>0.0409</td>
</tr>
<tr>
<td>Rugosity</td>
<td>−0.335</td>
<td>5.524</td>
<td>0.9514</td>
</tr>
<tr>
<td>Rugosity × <em>C. fulva</em></td>
<td>−7.046</td>
<td>3.05</td>
<td>0.0138</td>
</tr>
</tbody>
</table>

Regression parameter estimates, their standard errors (SE), and $P$-values are given for each parameter. For the whole regression model, $n = 305$, likelihood ratio test: $\chi^2 = 33.23$, d.f. = 5, $P < 0.0001$. 

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artifact of those few high-density observations: for the range of settler densities 0.1–0.2 fish m\(^{-2}\), mortality at low-\(C. \text{ fulva}\) sites was already declining sharply with density (Fig. 3a,b) while mortality at high-\(C. \text{ fulva}\) sites was not (Fig. 3c,d).

For the purposes of visualization, curves in Figs 2 and 3 were generated from logistic regression models including only the variables displayed in that figure (e.g. rugosity was not included in the model used for Fig. 2) using the mean value of \(C. \text{ fulva}\) density in each panel. As such, the parameter values given in Table 1, not the curves in Figs 2 and 3, should be considered authoritative.

Predator abundance (but not habitat complexity) also had a significant effect on the temporal pattern of density-dependent \(T. \text{ bifasciatum}\) mortality. Transects at sites with higher \(C. \text{ fulva}\) abundance were more likely to have positively density-dependent mortality (logistic regression: pseudo-\(R^2 = 0.72, \chi^2 = 7.64, P < 0.001\); Fig. 4). Regression models including terms for rugosity alone (\(\chi^2 = 0.34, P = 0.56\)), rugosity and \(C. \text{ fulva}\) density (\(\chi^2 = 3.63, P = 0.16\)), or both factors and their interaction (\(\chi^2 = 3.10, P = 0.38\)) were not statistically significant. This analysis assumes that \(C. \text{ fulva}\) densities were constant at each site over the summer. There was no evidence that this was not the case: a two-way ANOVA on log-transformed \(C. \text{ fulva}\) densities at these four sites across the 2 months of observations found a significant effect of site (\(F_{3,8} = 11.24, P = 0.003\)) but did not reveal a significant effect of month (\(F_{1,8} = 0.06, P = 0.82\)) or a significant site × month interaction (\(F_{3,8} = 1.04, P = 0.43\); this analysis had \(n = 16\) corresponding to two surveys in each month at each of four sites).

**DISCUSSION**

Predators are known to play a strong role in the structure and dynamics of metacommunities (Hoopes et al. 2005), and the exact pattern of predator dispersal can be critical to the

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**Figure 2** Coplot of relationship between habitat rugosity and mortality of *Thalassoma bifasciatum* (bluehead wrasse) settlers, conditional on density of *Cephalopholis fulva* (a wrasse predator). Panels (a–d) show per-capita mortality (independent of density) of *T. bifasciatum* as a function of rugosity (a dimensionless ratio) for the values of *C. fulva* density indicated in the top panel. Each point in (a–d) represents data from a single transect in one site-month combination and each panel displays data from three site-months (all transects in the same site-month had the same *C. fulva* density). To capture the continuous nature of the multivariate relationship, the range of *C. fulva* densities displayed in adjacent panels overlap, such that each panel shares three points (all transects from one site-month) with the panel ahead of it and three points with the panel behind it (indicated by overlapping values of *C. fulva* density in top panel).
dynamics of their prey. For example, the aggregation of predators to patches with high prey density can stabilize prey population dynamics if predators move slowly or have only a weak preference for high-density prey patches, effectively creating temporary low-predator refuges for the prey (Hassell & May 1974; Murdoch et al. 1992; Hassell et al. 1994). Alternatively, rapid predator aggregation to high-density prey patches can destabilize the dynamics of both species (Murdoch et al. 1992). Here I have identified a type of non-aggregative predator dispersal not previously considered in metacommunity systems.

Around the island of St Croix, the dispersal of a common reef fish, *Thalassoma bifasciatum*, and one of its major predators, *Cephalopholis fulva*, appear to be coupled, producing a spatial correlation in the recruitment of the two species. For *C. fulva*, sites with high recruitment also had the highest adult densities. The resulting spatial pattern of predator abundance had a dramatic effect on the post-settlement mortality of *T. bifasciatum*, which was inversely density-dependent at sites with few predators (and thus low mean *T. bifasciatum* recruitment) but directly density-dependent at sites with high predator densities (and thus high mean *T. bifasciatum* recruitment).

The correlation between *T. bifasciatum* and *C. fulva* recruitment was likely a product of near-shore oceanographic processes. A convergence zone off the northwest shore of St Croix may retain and entrain reef fish larvae (Harlan et al. 2002) and appears to be responsible for a consistent pattern of high recruitment of *T. bifasciatum* and other small fishes to reefs in that area (Caselle & Warner 1996; Hamilton et al. 2006). In 2003, the distribution of *C. fulva* recruits largely followed the same pattern, yielding significant correlations between the densities of *T. bifasciatum* recruits and both recent and older *C. fulva* recruits. While larval fish can make behaviourally directed movements over small distances (Leis & McCormick 2002), these correlations almost certainly reflect oceanographic forcing,

![Figure 3](image-url)
not large-scale habitat selection by C. fulva larvae. This conclusion assumes that the distribution of C. fulva recruits has not been substantially altered by spatially variable post-settlement mortality. This assumption is reasonable for the smaller, more recently settled recruits, which had only been exposed to post-settlement mortality for a short time prior to census. The distribution of older recruits may have been altered considerably by several months of mortality exposure, but the close correspondence in the spatial distributions of both recruit age classes suggests that a single process (i.e. oceanographically driven larval delivery) produced both patterns. Careful readers may notice that the density of older C. fulva recruits was greater than that of younger recruits at all sites. This pattern may simply reflect greater total settlement of C. fulva in 2002 and early 2003 (when the 2003 cohort of older recruits settled) than later in 2003 (when the 2003 cohort of recent recruits settled). The nonlinearity of the age-size relationship also means that a wider range of ages comprise the older recruit size class, predisposing it to contain more fish than the recent recruit size class. It is also possible that recent recruits were somewhat undercounted because of their smaller size, but it is unlikely that the spatial distribution I detected was an artifact of undercounting. During the day, C. fulva recruits of this size hover above the reef like their older conspecifics, but smaller fish might be concealed easily by erect gorgonians. However, these potentially concealing structures were far more abundant at the northwestern sites (Butler Bay, Northstar; J. W. White, personal observation) where the highest recruit densities were observed, so any undercounting would have tempered, not amplified, the spatial pattern of C. fulva recruitment.

The spatial pattern of adult C. fulva abundance across four years closely matched the pattern of C. fulva recruitment observed in 2003. One might expect a close correspondence between the 2004 and 2005 adult pattern and the 2003 recruitment pattern, as many of the fish counted in the later censuses may have been recruits in 2003. However, the adult C. fulva population had a similar spatial pattern in 2002 and 2003 (Fig. 1b), suggesting that C. fulva recruitment typically follows the 2003 pattern, generating a consistent spatial distribution of adults. This line of reasoning assumes that post-recruitment migration does not disrupt patterns established at recruitment, which seems reasonable given the large distance between study sites (> 1 km) relative to the scale of movement observed in tagged C. fulva (< 30 m over 3 mo; Chapman & Kramer 2000).

There appears to be a strong relationship between the local abundance of C. fulva and the nature of density-dependent mortality of T. bifasciatum settlers. When C. fulva abundance was low, T. bifasciatum mortality decreased with increased density. This may represent a case of predator ‘swamping’ in which prey abundance greatly exceeds the number that can be consumed by a small number of predators with saturating functional responses, so per capita prey mortality decreases with prey density (Anderson 2001). At higher C. fulva abundances, however, T. bifasciatum
mortality increased with density. Some *T. bifasciatum* settlers form small aggregations (two to six fish) that experience reduced per-capita mortality relative to solitary fish, but there was no among-site variation in the proportion of settlers in such groups during this study (White & Warner, in press), so it does not seem that this phenomenon could explain the occurrence of transect-scale inverse density dependent mortality at low *C. fulva* densities. Instead, the pattern of density dependence likely reflects some aspect of *C. fulva* foraging behaviour, although it is difficult to pinpoint the exact mechanism in the absence of detailed behavioural observations. Within each site, aggregation by *C. fulva* to areas of high *T. bifasciatum* density could produce spatially density-dependent *T. bifasciatum* mortality (Anderson 2001). However, mortality was density-dependent at a spatial scale (reefs separated by kilometres) greater than that over which *C. fulva* could aggregate, which coupled with the evidence for temporal density-dependence at the high-predator sites, suggests that the density-dependent mortality was produced by predator switching (Oaten & Murdoch 1975). *Cephalopholis fulva* are omnivorous and may feed on *T. bifasciatum* recruits at a higher rate when they are more abundant than other prey items.

High local densities of *C. fulva* also appear to amplify the effect of habitat complexity on the survival of *T. bifasciatum* settlers, independent of settler density. When *C. fulva* were abundant, settlers on high-rugosity transects had lower mortality than those on low-rugosity transects, but this effect of rugosity was less pronounced at low *C. fulva* densities. This phenomenon is in accordance with experimental results demonstrating that small reef fishes can utilize crevices in complex (high rugosity) substrata to avoid predation (Hixon & Beets 1993). Because there was not a significant rugosity × settler density interaction in the regression model, there was no evidence for density-dependent competition for enemy-free space as has been found in other reef fishes (Holbrook & Schmitt 2002; Schmitt & Holbrook 2007). Recent *T. bifasciatum* settlers are gregarious and do not appear to compete for shelter spaces (White & Warner, in press), but a more direct experiment would be needed to rule out this possibility.

Two previous studies (Caselle 1999; White & Warner, in press) have described a spatially consistent island-wide pattern of density-dependent mortality for *T. bifasciatum* recruits on St Croix that did not appear to vary with predator densities. However, those studies had less replication than this study and may have been unable to detect a predator effect. They also followed recruits over a much longer time interval than the present study (30–90 vs. 6 days) and began with recruits that were up to several days old (rather than in their first day on the reef, as in the present study), and so may not have captured the early post-settlement processes described here. Many studies reporting density-dependent post-settlement mortality in reef fish have found that the density dependence is most pronounced in the first hours and days on the reef (Hixon & Webster 2002), so the presence of inverse density dependence in recent *T. bifasciatum* settlers during the same timeframe is particularly striking (see also Sandin & Pacala 2005). However, the effects of spatial variation in recruitment intensity (and thus predator density) may not be limited to the first days on the reef: adult *T. bifasciatum* populations at sites identified here as having low recruitment and low predator densities (Jacks Bay and Green Cay) have longer-lived and larger fish than a site with high recruitment and high density of *C. fulva* (Butler Bay; Caselle et al. 2003).

Evidence for a relationship between predator density and the form or intensity of density-dependent mortality is emerging for other reef fish species as well (Johnson 2006; Schmitt & Holbrook 2007). Spatial variation in the form of density dependence, such as that described here, could produce striking differences in the dynamics of subpopulations within a metapopulation. Sites with consistently high recruitment and strong, positive density dependence should experience only small fluctuations around a regulated maximum density (Armsworth 2002), while sites with consistently low recruitment and inversely density-dependent mortality will be more able to ‘store’ occasional pulses of high recruitment (sensu Warner & Chesson 1985), yielding a population with a more variable age structure (even if recruit cohorts later experience some density dependent mortality, as described in the preceding paragraph). As a case in point, the highest *T. bifasciatum* settler densities observed during this study occurred at Jacks Bay, a windward site that generally experiences lower settlement input than leeward sites (Hamilton et al. 2006) and thus has quite low *C. fulva* density. Consequently, these unusually abundant settlers experienced very low mortality (Figs 2 and 3).

Correlated recruitment of predators and prey (and the accompanying effects on prey mortality) may be a common feature of many metacommunities, both marine and terrestrial. Along the coast of California, oceanographic processes supply far more larvae of mussels and their seastar predators to sites north of Pt Conception than to sites south of the point. Consequently, mussel mortality rates are lower in the low-recruitment zone and adult mussel densities there are comparable to those in the high-recruitment zone (Menge et al. 2004). On land, pitcher plants (*Sarracenia purpurea*) harbour predator-dominated aquatic invertebrate metacommunities within their leaves. Larger pitcher plants should receive higher inputs of both wind-dispersed zooplankton prey and their predators, mosquito larvae (Miller & Kneitel 2005), so pitcher plant metacommunities may also be structured by correlated dispersal of predators and their prey. In general, this sort of relationship should
arise whenever certain patches are equally attractive to dispersing propagules of both species, either because of similar habitat preferences, in the case of active dispersers, or similar susceptibility to abiotic forcing, in the case of water- or wind-dispersers. The latter requirement will not be met if predators and prey differ greatly in larval behaviour or the seasonality of dispersal (E. Wieters, S. Gaines, S. Navarrete, C. Blanchette and B. Menge, unpublished manuscript), or if adult movement occurs on a scale large enough to disrupt patterns established at recruitment (Kritzer & Sale 2006).

The existence of correlations in the recruitment of predators and their prey could greatly alter the predictions of existing marine metapopulation models. To date, source and sink populations in marine systems have been identified largely based on connectivity patterns without regard for among-patch differences in demographic rates (James et al. 2002; Cowen et al. 2006). However, if density-dependent mortality is more intense at high-recruitment sites, as our results suggest, patches identified as sources using the connectivity approach may actually be sinks. Similarly, Lipcius et al. (1997) and Figueira (2002) have shown that individual coral reefs can differ greatly in habitat quality, so that poor-quality reefs may be demographic sinks (for lobsters and damselfish, respectively) despite receiving large larval inputs and having high self-recruitment rates. In a sense, this is a large-scale version of the ‘cryptic density-dependence’ phenomenon (Shima & Osenberg 2003), in which spatial covariation between fish settlement and habitat quality affects the intensity of post-settlement mortality. While small-scale cryptic density dependence may lead to weaker-than-expected density dependent mortality when fish settle preferentially in high-quality habitat (Shima & Osenberg 2003), the correlated recruitment effect operating at large spatial scales may intensify the density dependence experienced by prey that settle in large numbers to high-predator reefs. As the theory of marine metapopulation and metacommunity ecology moves beyond the assumption of spatial homogeneity (Guichard et al. 2005), correctly accounting for interspecific correlations in recruitment will become a crucial consideration.

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REFERENCES


**SUPPLEMENTARY MATERIAL**

The following supplementary material is available for this article:

Appendix S1 Description and map of study sites
Appendix S2 Description of predatory fish community on St. Croix reefs

This material is available as part of the online article from: http://www.blackwell-synergy.com/doi/full/10.1111/j.1461-0248.2007.01098.x.

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