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Priority effects and habitat complexity affect the strength of competition

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Abstract Both habitat complexity and priority effects can influence the strength of competitive interactions; however, the independent and synergistic effects of these processes are not well understood. In Moorea, French Polynesia, we conducted a factorial field experiment to quantify the independent and combined effects of priority effects and habitat complexity on the strength of intraspecific competitive interactions among recently settled individuals of a coral reef fish (*Thalassoma quinquevittatum*: Labridae). Simultaneous arrival of focal individuals with competitors resulted in a 2.89-fold increase in survival relative to reefs where focal individuals arrived 5 days later than competitors (i.e., a priority effect). Increasing habitat complexity resulted in a 1.55-fold increase in survivorship when focal individuals arrived simultaneously with or before competitors. However, increasing habitat complexity did not affect the survivorship of focal individuals arriving 5 days later than competitors. Behavior observations showed that survivorship was negatively correlated with aggression. Aggression by prior residents towards focal individuals was significantly greater when focal individuals arrived 5 days later than competitors than when they arrived simultaneously. Increasing habitat complexity did not reduce aggression. Our results suggest that, when competitors arrive simultaneously, competitive interactions are weak and subordinates are not displaced from complex habitat; increasing habitat complexity increases survival by disrupting predation. Conversely, when competitors arrive at different times, aggression intensifies and increasing habitat complexity does not disrupt predation because competitive subordinates are excluded from habitat resources. This study demonstrates that the strength of competition can be context-dependent and may vary with the timing of competitive interactions and habitat complexity.

Keywords Competition · Habitat complexity · Interaction strengths · Priority effects · Reef fish

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Introduction

Historically, empirical and theoretical studies quantifying interaction strengths have been heavily biased towards predatory, competitive and top–down versus bottom–up interactions. Typically, these studies describe interaction strengths by constants or functions that depend on the densities of the interacting individuals, species, functional groups, or cohorts (e.g., Peacor and Werner 2004). More recently, renewed calls have been made for more studies examining how the context within which interactions occur (e.g., disturbance regime: Gallet et al. 2007; higher-order interactions: Peacor and Werner 2004; and environmental attributes: Chase 2007; Crain et al. 2004) shapes interaction strengths (Agrawal et al. 2007). For example, the importance of competition in structuring rocky intertidal communities can vary spatially depending on levels of larval

supply (Connolly and Roughgarden 1999). The magnitude of competition may also vary depending upon the provisioning of structural refuge in complex habitats (e.g., Bonin et al. 2009), or the sequence in which competitors arrive in a community (i.e., priority effects; e.g., Alford and Wilbur 1985). The intensity of priority effects can in turn depend upon the amount of time that separates the arrival of competitors in a community (Geange and Stier 2009), or the presence of predators (Louette and Meester 2007). Here, we examine the potential for variation in habitat complexity and priority effects to create context-dependent competitive outcomes. Understanding the independent and combined effects of priority effects and habitat complexity on the outcome of competitive interactions is of increasing importance as global climate change leads to widespread shifts in breeding phenology and habitat availability (Both et al. 2009; Durant et al. 2007; Hughes 2000; Parmesan and Yohe 2003; Visser and Both 2005; Walther et al. 2002).

Habitat complexity can considerably influence interaction strengths (e.g., competition: Bonin et al. 2009; Buenau et al. 2007; Ladd and Facelli 2008; and predation: Beukers and Jones 1997; Huffaker 1958; Juliano 2009). Increasing habitat complexity is typically expected to mitigate the negative effects of competition for predator free space (e.g., Almany 2004a) or reverse competitive dominance relationships (e.g., Ebersole 1985). More complex habitats often contain a greater diversity of food resources (e.g., Harmon et al. 1986) and refuges from predators (e.g., Beukers and Jones 1997; Finke and Denno 2002), thereby reducing the intensity of competition and predation. Increased structural complexity may also alter encounter rates between predators and prey, increasing predation risk if the structure decreases the visibility of predators to prey, or decreasing predation risk by providing enemy-free structural refuge or interfering with predator maneuvrability and/or the ability to visually detect prey (Andruskiw et al. 2008; Finke and Denno 2006; Janssen et al. 2007; Langellotto and Denno 2004; Persson and Eklov 1995; Rilov et al. 2007; Warfe and Barmuta 2004).

Interaction strengths (e.g., competition and predation) can also be modified by the order (who arrives first) and timing (by how much) of arrival in a community (i.e., "priority effects": e.g., Alford and Wilbur 1985; Dayton and Fitzgerald 2005; Geange and Stier 2009; Lawler and Morin 1993; Price and Morin 2004; Shorrocks and Bingley 1994). Early arrival may confer experience advantages if individuals gain knowledge of the local environment (e.g., greater awareness of established boundaries with neighbors and knowledge of predator-free space), facilitating their ability to acquire resources, defend home ranges, or evade predators. Alternatively, if larger size confers competitive advantages, early-arriving individuals may have a growth advantage over late-arriving individuals. When early

arrival provides a competitive advantage due to differences in experience or size, the competitive effect of the early-arriving individuals on the later-arriving individuals should increase as arrival times diverge (Alford and Wilbur 1985; Geange and Stier 2009). However, many species undergo extensive ontogenetic niche shifts which are often manifested as shifts in habitat use or diet with increasing size (Werner and Gilliam 1984). Such shifts can substantially alter interaction strengths within communities (de Roos et al. 2002; Werner 1992; Werner and Gilliam 1984). For example, individuals arriving at different times may interact less intensely than individuals arriving at the same time because they are, to some degree, acting as separate ecological species (Maiorana 1978). As a result, priority effects will only be important if ontogenetic niche shifts occur slowly, so that late-arriving individuals interact with larger, more experienced early-arriving individuals. Conversely, when rapid ontogenetic niche shifts occur, the optimal strategy for an individual to avoid intracohort priority effects is to either: (1) enter the community before other settlers; or (2) enter the community late enough that prior settlers have undergone ontogenetic niche shifts and no longer pose a competitive threat.

Finally, habitat complexity and priority effects may interact, so that the effects of one process depend upon a second process. For example, although the magnitude of competition may increase as individuals arrive in a community progressively later than their competitors, late-arriving individuals may be released from competition or predation pressure in complex habitats that decrease encounter rates with early-arriving individuals. Understanding how both habitat complexity and priority effects independently and synergistically affect the strength of competitive interactions is essential to estimates and interpretation of the strength of competition.

The few studies that have examined the combined effects of habitat and arrival time on the strength of competition (see Fincke 1999; Sunahara and Mogi 2002) have identified habitat as capable of moderating inhibitory priority effects. In a previous study examining two labrid species that are closely related both genetically and functionally (*Thalassoma hardwicke* and *T. quinquevittatum*), we identified strong intracohort priority effects (Geange and Stier 2009). Aggression toward later-arriving individuals by early-arriving individuals increased as each species entered communities progressively later than its competitor. Additionally, aggression by early-arriving individuals and the survival of late-arriving individuals was negatively correlated, suggesting that the timing of arrival relative to competitors results in context-dependent competitive outcomes. Here, focussing on intraspecific competitive effects, we manipulated habitat complexity and timing of *Thalassoma quinquevittatum* settler arrival to: (1) determine the

independent effects of timing of arrival and habitat complexity on intraspecific competition between *T. quinquevittatum* settlers; and (2) address whether habitat complexity attenuates or enhances intraspecific interaction strengths among settlers arriving at different times. We hypothesized that: (1) when timing of arrival dictates the strength of competition, competitive effects should be weakest when competitors arrive simultaneously and increase in strength as temporal separation among competitor arrival increases; and (2) increasing habitat complexity would disrupt priority effects by releasing late-arriving individuals from competitive interactions with early-arriving individuals.

Materials and methods

Study species

Thalassoma quinquevittatum is a common wrasse throughout much of the Indo-Pacific. *T. quinquevittatum* spawns year round on Pacific coral reefs at latitudes of approximately 15°S (Craig 1998). Planktonic larval development takes 46–68 days (Victor 1986) before competent larvae, 9–11 mm standard length (SL), settle to benthic reef habitat. At our study site, in Moorea, French Polynesia (17°30′S, 149°50′W), settlement occurs around new and full moons. A single *T. quinquevittatum* settlement pulse can last a few days to a week (Geange, personal observation), meaning that, on a given patch reef, individuals in a given pulse often arrive asynchronously. Following settlement, *T. quinquevittatum* juveniles (<25 mm SL) over-associate (relative to availability) with several coral species (e.g., *Porites lobata*, *Pocillopora verrucosa*, and *Porites rus*) and the macroalga *Turbinaria ornata* (Geange and Stier 2009).

Moorea's northern lagoon consists of a matrix of sand and fine coral rubble interspersed with patch reefs. Patch reefs are predominantly massive *Porites* coral colonies, often surmounted by smaller colonies of other coral species (*Pocillopora* spp., *Montipora* spp., and *Acropora* spp.), patches of dead coral skeletons, macroalgae (*Turbinaria* spp., *Dictyota* spp., *Sargassum* spp., and *Halimedia* spp.) and filamentous algae (*Polysiphonia* spp. and *Sphacelaria* spp.). Patch reefs are highly variable in their composition over small spatial scales; thus, interactions between individuals within a settlement pulse are overlaid upon a background of variable habitat complexity. Previous research has demonstrated that variability in habitat complexity within this lagoon does affect post-settlement survival of reef fishes. For example, Shima et al. (2008) demonstrated that when density was held constant, mean post-settlement survival of *T. hardwicke* (a congener of *T. quinquevittatum*) increased

with the abundance of the branching coral *Pocillopora* (a probable refuge from predation).

In this study, we used *T. quinquevittatum* individuals that were approximately 2 weeks post-settlement (13.3 mm SL; SD = 0.8).

Study site

The study was conducted in the northern lagoon of Moorea between April and June 2008. We used an array of 30 isolated live-coral patch reefs separated by ∼10 m in water 2–4 m deep. Reefs were located within a sand-flat, separated from each other, and from nearby natural reefs, by a minimum of 15 m. We constructed reefs to minimize habitat variation by standardizing size, rugosity, and water depth. Each reef consisted of a base of live *Porites lobata* coral with an average area of 2.23 m² (SD = 0.56), and a mean height of 0.59 m (SD = 0.10).

Previous work by Geange and Stier (2009) determined that juvenile *T. hardwicke* exclude *T. quinquevittatum* settlers; we therefore removed all resident *T. hardwicke* from patch reefs. We also removed resident *T. quinquevittatum*, and manipulated the relative abundances of other resident fish species via selective removals and additions, so that the relative abundance of all species was similar among the 30 reefs (see electronic supplementary material, ESM, 1 for background community structure). We used the fish anaesthetic eugenol (clove oil) and hand nets to collect fish.

Experimental design and execution

We examined the effects of habitat complexity and timing of arrival in the context of the survival of focal *T. quinquevittatum* settlers. We controlled habitat complexity by manipulating the availability of the branching coral *Pocillopora verrucosa*. This was achieved by drilling holes into the upper surface of patch reefs. Into these holes, we inserted stainless steel pins attached to *P. verrucosa* colonies with Z-Spar Splash Zone Compound (Kopcoat, Pittsburgh, PA, USA). Mean colony surface area was 0.2 m² (SD = 0.07). We crossed the availability of *P. verrucosa* (two levels: two, or four colonies, which is representative of observed *P. verrucosa* cover within the lagoon (Shima et al. 2008)), with the presence of three tagged *T. quinquevittatum* competitors (three levels: absent, introduced simultaneously with (0 days), or 5 days earlier than the focal individuals). To each reef, we simulated settlement by introducing three tagged *T. quinquevittatum* focal individuals. Thus, our design had six treatments: (1) focal individuals without competitors, with two *P. verrucosa* colonies; (2) focal individuals and competitors introduced simultaneously, with two *P. verrucosa* colonies; (3) focal

individuals with competitors introduced 5 days previously, with two *P. verrucosa* colonies; (4) focal individuals without competitors, with four *P. verrucosa* colonies; (5) focal individuals and competitors introduced simultaneously, with four *P. verrucosa* colonies; and (6) focal individuals with competitors introduced 5 days previously, with four *P. verrucosa* colonies. We ran the experiment in two temporal blocks (17–23 April and 1–7 May 2008), yielding ten replicates (five in each temporal block) for each of the six treatments.

We used *T. quinquevittatum* individuals captured from reefs adjacent to the reef crest, approximately 2 km from the study site. All captured fish were held in aquaria with running seawater for 24 h and then individually tagged with different colors of Visible Implant Elastomer (VIE; Northwest Marine Technology) anterior to the caudal peduncle. VIE tags were readable through the skin of the fish by observers in the field, so it was not necessary to recapture individuals to determine their identity. VIE tags do not have adverse effects on other fishes (Beukers et al. 1995; Imbert et al. 2007; Simon 2007) or on *T. quinquevittatum* (Geange and Stier 2009), and have been used to tag fish as small as 8 mm (Frederick 1997). We therefore assumed that tagging and handling effects were minimal. After tagging, we returned fish to aerated aquaria for 24 h before measuring them to the nearest 0.1 mm SL. For each experimental run, we collected fish twice, once for the 5-day competitors, and once for the 0-day competitors and focal individuals. Each time we collected fish of the same size (see ESM 2). The difference between competitors and focal individuals was therefore their time on the reef and not their size.

Because recently settled fish often experience high rates of mortality (Almany and Webster 2006), we initially introduced six competitors to reefs in the 5-day treatments. At the same time as focal individuals were introduced to these treatments, we haphazardly removed excess competitors when there were more than three competitors (12 instances out of 20 reefs), and added competitors when there were less than three competitors (3 instances out of 20). We used excess individuals removed from other reefs to supplement competitors.

We surveyed reefs twice daily (approximately 0800 and 1600 hours) for 5 days after the introduction of focal individuals. Day 5 was chosen to end the study because previous research found the first 36–48 h after settlement to be most critical (Almany 2003, 2004b; Planes and Lecaillon 2001; Webster 2002; Webster and Almany 2002). In a few instances, individuals not enumerated in one survey were enumerated in the subsequent survey (16 instances out of 570). When this occurred, these individuals were recorded as present at the times they were missed. During surveys, we searched neighboring non-

experimental reefs for tagged immigrants. We found no immigrants or emigrants. Previous research has shown that small reef fish rarely move between reefs separated by as little as 15 m (Caselle 1999; Shima 2001), and previous studies on our experimental array found no migration of similar-sized *T. quinquevittatum* (Geange and Stier 2009). We therefore assume that the disappearance of an experimental fish was due to mortality rather than migration.

Behavioral observations

To help elucidate the mechanisms driving interactions between focal individuals and competitors, we conducted 5-min behavioral observations at the time we added focal individuals to reefs. After allowing fish to acclimate to the observers' presence for approximately 3 min, the observer identified one focal individual that was followed at a distance of approximately 2 m from the reef. The observer recorded three response variables: (1) the number of chases between other fishes and the focal individual (80% of chases were by *T. quinquevittatum* competitors); (2) the number of fin bites inflicted upon the focal individual (all fin bites were inflicted by *T. quinquevittatum* competitors); and (3) time spent inside *Pocillopora* by the focal individual. This was repeated twice on each reef so that behavioral interactions were made for two focal individuals per reef.

Data analysis

Survival analysis

Using generalized linear models (GLM), we conducted an analysis of deviance with binomial error distributions and a logit link function to model proportional survival of focal individuals 5 days after their introduction to reefs. We used an analysis of deviance to evaluate the statistical significance of the main effects and the interaction between the competition and habitat complexity treatments (i.e., the full model). Finding no interaction ($\chi^2 = 0.457$, $df = 2$, $P = 0.796$), we conducted four a priori contrasts: (1) habitat effects without prior residents (absent + 0-day low complexity vs absent + 0-day high complexity); (2) competitive effects (control low and high complexity vs 0-day low and high complexity); (3) habitat effects with competitors (0-day and 5-day low complexity vs 0-day and 5-day high complexity); and (4) timing of arrival effects (0-day low and high complexity vs 5-day low and high complexity). We chose these contrasts to examine main effects of habitat and competition in the absence (contrasts 1 and 2) and presence (contrasts 3 and 4) of timing of arrival effects. Data were not overdispersed (residual

deviance = 46.781, residual $df = 54$). We calculated effect sizes as ratios using mean proportions from the raw data.

Behavior analyses

Because there were strong correlations among behavioral responses (e.g., fin bites only occurred during chases), we used Principal Components Analysis (PCA) to create a single composite aggression score. We transformed data [ln($x + 1$)] prior to analysis to improve normality. PC1 accounted for 73% of the total variation in aggression variables, and was driven by high positive loadings of total chases (64%) and fin bites (60%), and weak negative loadings of time-in-*Pocillopora* (44%). Thus, we interpret this first PC axis as a gradient of overall aggression.

We analyzed overall aggression with a two-way analyses of variance (ANOVA). We transformed data to meet assumptions of normality and equal variance [$1/(X_j + C)$; where C is the largest negative value plus one; see Rummel 1970]. Finding no interaction ($F_{2,54} = 0.012$, $P = 0.987$), we used overall aggression as the response variable to conduct four a priori contrasts equivalent to those described above for survival analysis.

Because our previous work on this genus has shown correlations between aggression and the strength of competition (see Geange and Stier 2009), we used linear least squares regression to correlate survival and aggression across all treatments, treating each reef as an independent replicate and averaging multiple observations conducted within the same reef.

All statistical analysis was conducted in R 2.8.0 (R Development Core Team 2008).

Results

Increasing habitat complexity yielded a 1.50-fold increase in the proportional survival of focal individuals ($P = 0.043$; Table 1; Fig. 1). Relative to reefs where competitors were absent, arriving either simultaneously with or 5 days later than competitors resulted in 1.15- and 3.34-fold decreases in survival, respectively ($P = 0.001$; Table 1; Fig. 1).

Increasing habitat from two to four *P. verrucosa* colonies on reefs where focal individuals arrived simultaneously or before competitors resulted in a 1.55-fold increase in the survival of focal individuals (contrast 1; $P = 0.024$; Table 2). Arriving on reefs where competitors were absent yielded a 1.15-fold increase in survival relative to reefs where focal individuals arrived at the same time as competitors, although this effect was not statistically

Table 1 Analysis of deviance and variance tables testing the significance of low or high habitat complexity, timing of arrival of competitive reef fish and the interaction of these terms on survival of and aggression against focal fish, *Thalassoma quinquevittatum*

	Survival			Aggression		
	df	Deviance	P	df	F	P
Habitat complexity	1	4.090	**0.043**	1,54	0.003	0.959
Timing of arrival	2	19.910	**<0.001**	2,54	18.829	**<0.001**
Habitat: timing of arrival	2	0.457	0.796	2,54	0.012	0.987

Low and high habitat complexity was comprised of two or four *P. verrucosa* colonies, respectively. Timing of arrival treatments for competitors of focal fish were absent (control; no competitors), simultaneous (0 days), or 5 days earlier. Proportional survival of focal individuals was modeled using a GLM with a logit link and assumed binomial error structure. Aggression is a PCA-derived composite of chases, fin bites and time spent inside *P. verrucosa* (see "Behavior analyses") modeled using ANOVA. Significant *P* values (<0.05) are highlighted in bold
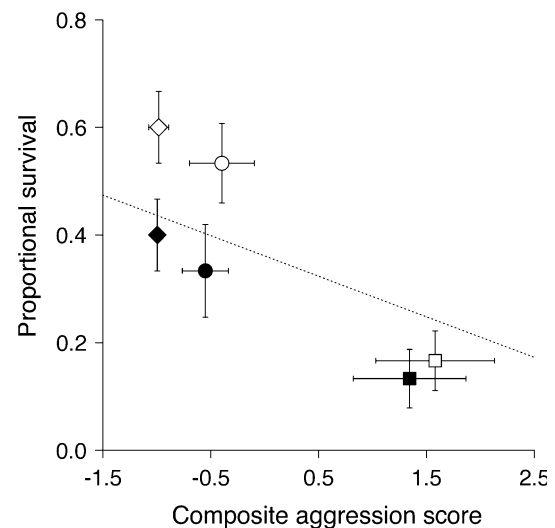
Fig. 1 The effects of habitat complexity and intraspecific competition on survival of focal *Thalassoma quinquevittatum* individuals (mean proportion alive at experiment end ± 1SE) and aggression against focal fish (mean PCA-derived composite score of chases, fin bites, and time spent inside *P. verrucosa* reef ± 1SE). Habitat complexity was either low (two *P. verrucosa* colonies, *closed symbols*) or high (four colonies, *open symbols*). Competition levels are based on the timing of competitor arrival: absent (*diamonds*), simultaneous (0 days, *circles*) or priority effects (5 days before focal fish, *squares*). Linear regression (*dashed line*) is based on the raw data, slope = −0.08, $r^2 = 0.175$, $P = 0.001$

significant (contrast 2; $P = 0.448$; Table 2). When focal individuals arrived simultaneously with or 5 days later than competitors, increasing habitat complexity increased survival, although this effect was not significant (contrast 3; $P = 0.953$; Table 2). Arriving at the same time as competitors yielded a 2.89-fold increase in survival relative to

Table 2 Results from four a priori contrasts testing the effects of low or high habitat complexity and three levels of intraspecific competition (timing of competitor arrival treatments) on survival of and aggression against focal *T. quinquevittatum* individuals (see Table 1 for further explanation)

	Survival			Aggression		
	Estimate	Z value	P	df	F	P
1. Habitat effects without early competitors	−0.441	−2.261	**0.024**	1,58	0.001	0.973
2. Competitive effects	−0.145	−0.760	0.448	1,58	3.004	0.088
3. Habitat effects with early competitors	−0.440	−1.601	0.109	1,58	0.004	0.953
4. Timing of arrival effects	0.636	3.173	**0.001**	1,58	12.331	**<0.001**

The four contrasts presented are: (1) habitat effect without early competitors; (2) competitive effects; (3) habitat effects with early competitors; and (4) timing of arrival effects (see "Survival analysis" for contrast explanations). Z values are from a generalized linear model; F values are from an analysis of variance (see "Methods" for further explanation). Effect sizes are calculated as the ratio of mean proportions from the raw data. Significant P values (<0.05) are highlighted in bold

reefs where focal individuals arrived 5 days later than competitors (contrast 4; $P < 0.001$; Table 2).

Survival of focal individuals decreased with increases in the PCA-derived composite aggression score (slope = −0.08, $r^2 = 0.175$, $P = 0.001$; Fig. 1). Increasing habitat complexity did not significantly affect aggression ($P = 0.959$; Table 1), although timing of arrival did ($P < 0.001$; Table 1). Aggression did not differ significantly between reefs where competitors were either absent or arrived simultaneously as focal individuals (contrast 2; $P = 0.088$; Table 2). Relative to when focal individuals arrived simultaneously as competitors, aggression was significantly greater when focal individuals arrived 5-days later than competitors (contrast 4; $P < 0.001$; Table 2).

Discussion

Intraspecific competitive effects were demonstrably greater when focal individuals arrived after competitors. The large difference in survival and aggression between the treatments in which focal individuals arrived simultaneously with and later than competitors provides direct quantitative evidence that interaction strengths may vary due to the relative timing of arrival of individuals. As with other studies (e.g., Alford and Wilbur 1985), this research suggests historical knowledge is important when estimating interaction strengths.

Increasing habitat complexity increased survivorship of settlers in the control and 0-day treatments. We predicted that increasing habitat complexity would release focal individuals from competitive interactions in 5-day treatments; however, our results did not support this prediction. Increasing habitat complexity did not significantly increase the survival of late-arriving individuals. Similarly, increasing habitat complexity did not affect the level of aggression displayed towards focal individuals by competitors.

To understand the mechanisms driving the relationship between habitat complexity and survival, we need to consider the way in which prior residents affect the survival of late arriving settlers. Based on previous work in coral reef fish communities, predation is likely the ultimate cause of mortality in recently settled reef fishes (Almany 2003; Carr et al. 2002), with competition forcing subordinates into less protective refugia (Holbrook and Schmitt 2002) or displacing them from refuge habitat altogether (Munday et al. 2001). Interactions with more aggressive competitors may also distract subordinates, leading to reduced vigilance and increased conspicuousness to predators (Almany 2003; Carr et al. 2002). In our study, this suggests that when aggression is weak (e.g., when focal individuals arrive before or simultaneously with competitors), subordinates are not displaced from complex habitat, and increasing habitat complexity increases survival by reducing predation pressure (i.e., tight branching morphology of *Pocillopora* excludes the majority of predators we observe on our array); however, when aggression is intense (e.g., when focal individuals arrive later than competitors), increasing habitat complexity does not increase survival because competitive subordinates are displaced from refuge habitat. It therefore seems likely that a combination of the intensity of aggression (arising from the timing of arrival) and habitat complexity underlies observed survivorship of *T. quinquevittatum* engaged in intraspecific interactions.

We add three caveats to these interpretations. First, our experimental design effectively doubled the density of the experimental fish in 0-day and 5-day treatments relative to control treatments. Although we never observed aggregative responses of predators, we acknowledge that this design does not distinguish competitive effects from apparent competition (Holt 1977) because neither *T. quinquevittatum*

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nor predator density were controlled for. However, during our surveys we did not see any evidence of aggregative responses of predators in either this or a previous study (Geange and Stier 2009) that was conducted on the same set of reefs using the same focal species. Second, our study was conducted on small (2.25 m^2) isolated patch reefs. On these reefs, we observed strong aggression towards focal individuals by early-arriving competitors to the point that early-arriving competitors pursued focal individuals across the entire reef. On larger reefs, we may see an effect of increasing habitat complexity on the survival of late-arriving individuals if they are able to avoid contact with aggressive competitors, thereby avoiding exclusion from refuge habitat. Third, larval fish typically undergo rapid morphological and behavioral changes after settlement. Here, we simulated settlement using individuals that were approximately 2 weeks post-settlement. Consequently, the ecological divergence between the fish used in this study is likely to be far less than the ecological divergence between fish that are actually 0 and 5 days post-settlement. Therefore, although this study explores the general concept of how priority effects and habitat complexity interact, the specific relevance to this species and system is limited.

This is one of the first studies to examine the concurrent influence of habitat complexity and the timing of arrival on interaction strengths. Our results suggest that the contexts within which interactions occur are important determinants of the strength of intraspecific competition. Studies encompassing multiple sources of variation are becoming increasingly imperative in the face of large-scale environmental disturbances that simultaneously impact multiple ecological processes. Indeed, simultaneous threats from global climate change, which has already caused shifts in the breeding phenology of many species (Both et al. 2009; Durant et al. 2007; Hughes 2000; Parmesan and Yohe 2003; Visser and Both 2005; Walther et al. 2002) and habitat declines (Barel et al. 1985; Bellwood et al. 2004; Gardner et al. 2003; Silliman et al. 2005; Skole and Tucker 1993), suggest understanding how habitat complexity and priority effects interact could advance models predicting the responses of demographically open populations to global climate change.

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