

Order of arrival affects competition in two reef fishes

SHANE W. GEANGE^{1,3} AND ADRIAN C. STIER²

¹*School of Biological Sciences, P.O. Box 600, Victoria University, Wellington, New Zealand*

²*Department of Zoology, University of Florida, Gainesville, Florida 32611-8525 USA*

Abstract. Many communities experience repeated periods of colonization due to seasonally regenerating habitats or pulsed arrival of young-of-year. When an individual's persistence in a community depends upon the strength of competitive interactions, changes in the timing of arrival relative to the arrival of a competitor can modify competitive strength and, ultimately, establishment in the community. We investigated whether the strength of intracohort competitive interactions between recent settlers of the reef fishes *Thalassoma hardwicke* and *T. quinquevittatum* are dependent on the sequence and temporal separation of their arrival into communities. To achieve this, we manipulated the sequence and timing of arrival of each species onto experimental patch reefs by simulating settlement pulses and monitoring survival and aggressive interactions. Both species survived best in the absence of competitors, but when competitors were present, they did best when they arrived at the same time. Survival declined as each species entered the community progressively later than its competitor and as aggression by its competitor increased. Intraspecific effects of resident *T. hardwicke* were similar to interspecific effects. This study shows that the strength of competition depends not only on the identity of competitors, but also on the sequence and timing of their interactions, suggesting that when examining interaction strengths, it is important to identify temporal variability in the direction and magnitude of their effects. Furthermore, our findings provide empirical evidence for the importance of competitive lotteries in the maintenance of species diversity in demographically open marine systems.

Key words: community dynamics; competition; competitive lotteries; coral reef fish; intracohort competitive interactions; Moorea, French Polynesia; priority effect; recruitment; settlement; *Thalassoma* spp.

INTRODUCTION

Many communities undergo repeated periods of development due to regenerating resources or pulsed arrival of young-of-year (e.g., Gibbs and Grant 1987, Schauber et al. 2002). Because numerous species are highly fecund (e.g., many insects, plants, fishes, and marine invertebrates), with females producing thousands of offspring, individuals often enter communities in large pulses. Further, species often enter communities asynchronously due to interspecific differences in phenology, with the competitive pressures faced by early-arriving individuals differing markedly from late-arriving individuals. In such instances, the degree to which one individual affects the success of another depends, in part, on both the sequence (who arrives first) and timing (by how much) of arrival of each individual into the community (i.e., "priority effects"). Priority effects may reflect interspecific differences in breeding phenology, which can be adaptive to, among other things, interspecific interactions. For example, competitive intensity may be less when a subordinate competitor

breeds before or simultaneously with a superior competitor. In such cases, priority effects simply refer to interspecific interactions whose outcomes depend on the relative or absolute timing of arrival, breeding, or activity of the interacting species (Lawler and Morin 1993).

There are at least two general types of priority effects: one in which per capita competitive effects are constant but long-term dynamics are dependent on initial conditions and the other in which timing of arrival alters the strength of per capita competitive effects. The Lotka-Volterra competition model exemplifies the first type. When each species suffers more from inter- than from intraspecific competition, the equilibrium outcome of competition is dependent upon initial conditions, with the species with a sufficiently large initial abundance having the advantage and excluding the other species. In this scenario, an early-arriving species can build up to sufficiently high numbers that it excludes the invasion of the other species. Reversals in sequence of arrival can reverse the competitive outcome.

In the other type, the strength of competition varies according to conditions under which competition is occurring, i.e., the per capita strength of competition is not constant. For example, if early arrival provides a competitive advantage due to differences in experience or size, then the competitive effect of the early-arriving

Manuscript received 3 April 2008; revised 18 November 2008; accepted 7 January 2009. Corresponding Editor: M. H. Carr.

³ E-mail: Shane.Geange@vuw.ac.nz

species on the later-arriving species should increase as the arrival times diverge. In either case, knowledge of such temporal effects is critical to estimates and interpretation of realized interaction strengths of competitors in a community.

In this study, we are concerned with the second type of priority effect, how sequencing and timing of arrival change the strength of competition. The direction and magnitude of priority effects will depend on the underlying processes that give rise to the effect. For example, if initial size differences or the time available for resource preemption confers an advantage upon a competitor arriving in a community early, performance of late-arriving competitors should decline as they arrive progressively later than the early-arriving competitor (e.g., Lawler and Morin 1993). Alternatively, when species are of similar size, differences in arrival time can affect the duration of head-to-head competition, in which case performance of late-arriving competitors should increase as they arrive progressively later than the early-arriving competitor (Lawler and Morin 1993).

Intracohort priority effects, which we define here as occurring within the same settlement season, have previously been shown to affect community dynamics, having been documented in protist (Price and Morin 2004), zooplankton (Louette and Meester 2007), insect (Benke 1978, Shorrock and Bingley 1994), and amphibian communities (Lawler and Morin 1993, Blaustein and Margali 1996, Dayton and Fitzgerald 2005). In marine systems, work on intracohort order of arrival has predominantly focused on sessile invertebrates (e.g., Sutherland and Karlson 1977). However, reef fish communities are also a good platform for testing the influence of (1) changes in the timing of arrival and (2) reversals in the sequence of arrival, because they conform to repeated periods of development driven by pulsed arrival of young-of-the-year.

The majority of reef fishes have two-phase life histories, consisting of a dispersive planktonic larval phase and benthic, reef-associated juvenile and adult phases. Given the dispersive nature of the planktonic larval phase, most reef fish communities are relatively open, relying on spatially and temporally unpredictable larval supply from external populations for colonizing juveniles. At high latitudes ($>10^\circ$ N/S), recruitment patterns are typically seasonal, producing strong cohorts (Doherty 1988, 1991, Srinivasan and Jones 2006). Conversely, at low latitudes, longer breeding seasons are usually associated with lower fecundities (Wine-miller and Rose 1992), reducing the potential for strong cohorts. As individuals within a cohort make the transition from planktonic to benthic habitat, they encounter individuals that have settled in previous cohorts (i.e., established residents) and other recently settled individuals from the same cohort, with both intra- and intercohort interactions capable of determining the success of a newly arrived individual. To date, the majority of research examining priority effects in reef

fishes has focused on intercohort effects of established residents on the success of later-arriving individuals (for examples, see Shulman et al. 1983, Sweatman 1985, Almany 2003, 2004, Munday 2004). These studies have demonstrated that the recruitment success of newly arrived juveniles is strongly influenced by interactions with established residents and for the most part have concluded that strong interaction strengths add a degree of determinism to future community structure when the influence of prior residents on later-arriving individuals is species specific.

A fundamental endeavor of ecologists is evaluating interaction strengths among species and the consequences for community structure and dynamics and how communities will respond to changes in the biotic environment. However, this type of information is only useful if we can identify the variability of interaction strengths across space and time. Here, we expand on previous research into the effects of established residents on new arrivals (i.e., intercohort effects) by examining the effect subtle differences in timing and order of arrival have on the recruitment success of individuals within the same cohort. Specifically, we examine intracohort priority effects between two competing reef fishes (*Thalassoma hardwicke* and *T. quinquevittatum*). Using experimental manipulations, we tested whether the strength of competitive interactions depends on the sequence and temporal separation of arrival of competing individuals. We predicted that: (1) when symmetrical intracohort priority effects occur (and not generic competitive effects), reversing the order of arrival should reverse the observed effects (i.e., effects should be a function of order of arrival and not species identity); and (2) when priority effects (rather than species effects) are most important, competitive effects should be weakest when competitors arrive simultaneously and increase in strength as temporal separation between competitor arrival increases.

METHODS

Study species

The wrasses (labridae) *Thalassoma hardwicke* (see Plate 1) and *T. quinquevittatum* co-occur on reefs throughout the Indo-Pacific (Myers 1999). At tropical latitudes ($\sim 14^\circ$ S), *T. hardwicke* and *T. quinquevittatum* spawn year round (Craig 1998), with planktonic larval durations of ~ 47 and ~ 56 d, respectively (Victor 1986). Both species settle in pulses around the new moon in the austral summer, at a standard length (SL) of 9–11 mm (S. W. Geange, *personal observation*). At our study site in Moorea, French Polynesia, a single pulse of reef fish settlement can last up to 14 d (Dufour and Galzin 1993). We determined habitat association for individuals of *T. hardwicke* and *T. quinquevittatum* <25 mm by calculating mean Manly's alpha values (Manly et al. 1972, Chesson 1978) for 13 habitat categories across 240 patch reefs (surface area = 7.98 ± 3.79 m² [mean \pm SD]). Manly's alpha measures the proportion of fish at a given

reef on a given habitat type, relative to the probability of the fish associating with that habitat type under conditions of random assortment. *Thalassoma hardwicke* and *T. quinquevittatum* were highly similar in habitat use, strongly associating with massive *Porites* corals, *Pocillopora verrucosa*, *Porites rus*, and the macroalgae *Turbinaria ornata* (Fig. 1). Both species also have similar diets, feeding predominantly on planktonic and benthic crustaceans (Randall 2005). Intra- and interspecific aggression, consisting of chases and fin bites, presumably for habitat, is common within and between these species (S. W. Geange, unpublished data). Given that settlement of *T. hardwicke* and *T. quinquevittatum* occurs in irregular pulses around the new moon, in which *T. hardwicke* and *T. quinquevittatum* settle asynchronously (S. W. Geange, personal observation), we hypothesize that competitive dominance between individuals within a cohort will be determined by order of arrival.

Study site

The study was conducted in the northern lagoon of Moorea, French Polynesia (17°30' S, 149°50' W) between February and August 2007, using a grid of 28 live-coral patch reefs in water 2–4 m deep. Reefs were located within a sand-flat, separated from one another and 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 area of $2.25 \pm 0.57 \text{ m}^2$ (mean \pm SD) and a height of 0.60 ± 0.10 m. We added two colonies of *Pocillopora verrucosa*, with an average area projected downward onto a 2-D surface of $0.191 \pm 0.057 \text{ m}^2$, onto the upper surface of each reef using Z-spar epoxy (Kopcoat, Pittsburgh, Pennsylvania, USA). Reef quality for *T. hardwicke* increases as a function of *Pocillopora* cover (Osenberg et al. 2006, Shima et al. 2008). We removed all resident *T. hardwicke* and *T. quinquevittatum* and manipulated the absolute and relative abundances of other resident fish species via selective removals and additions, so that the relative abundance of all species was similar among the 28 reefs (see Appendices A and B for background community structure). We used the fish anaesthetic eugenol (clove oil) and hand nets to collect fish.

Experimental design and execution

To test for priority effects, we experimentally manipulated the sequence and timing of arrival of *T. hardwicke* and *T. quinquevittatum* onto reefs. We used recent settlers (13.8 ± 2.3 mm SL [mean \pm SD]; approximately two weeks post-settlement) captured from reefs roughly 4 km from the study site. All captured fish were held in tanks with running seawater for 6–12 h, then individually tagged with different colors of visible implant elastomer (VIE; Northwest Marine Technology, Shaw Island, Washington, USA) forward of the caudal

peduncle. 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. The VIE tags do not have adverse effects on other fishes (Beukers et al. 1995, Imbert et al. 2007, Simon 2007) and have been used to tag fish as small as 8 mm (Frederick 1997), and a preliminary study we conducted showed no mortality of 12 tagged *T. hardwicke* and *T. quinquevittatum* held in aquaria for 48 h. We therefore assumed that tagging and handling effects were small. After tagging, we returned fish to aerated aquaria for 6–12 h before measuring them to the nearest 0.1 mm SL and deploying them in the field. We used newly collected and tagged fish in two experiments. Experiment 1 examined interspecific priority effects between *T. hardwicke* and *T. quinquevittatum*. Experiment 2 examined intraspecific priority effects within *T. hardwicke*.

Experiment 1: interspecific priority effects between T. hardwicke and T. quinquevittatum.—We experimentally manipulated the sequence and timing of the arrival of *T. hardwicke* and *T. quinquevittatum* settlers; one portion of this experiment was designed to quantify effects of *T. hardwicke* (as the prior resident) on *T. quinquevittatum* (as the focal species); the other was designed to test the effects of *T. quinquevittatum* (as the prior resident) on *T. hardwicke* (as the focal species). For both cases, we simulated settlement pulses by introducing three fish of the focal species onto reefs where three tagged fish of the prior resident were either absent, had been introduced 12 d earlier than, 5 d earlier than, or simultaneously with (0 d) the focal species. Simulated settlement pulses of three fish are representative of natural settlement rates to reefs of the size used in this study. All fish were collected and tagged in the 24 h preceding their deployment in the field. We ran the experiment in two temporal blocks (11–30 April and 2–21 May), randomly assigning treatments to reefs and fish to treatments, yielding eight replicates (four in each temporal block) for each of our seven treatments: (1) *T. hardwicke* without *T. quinquevittatum*; (2) *T. hardwicke* and *T. quinquevittatum* introduced simultaneously; (3) *T. hardwicke* with *T. quinquevittatum* introduced 5 d previously; (4) *T. hardwicke* with *T. quinquevittatum* introduced 12 d previously; (5) *T. quinquevittatum* without *T. hardwicke*; (6) *T. quinquevittatum* with *T. hardwicke* introduced 5 d previously; and (7) *T. quinquevittatum* with *T. hardwicke* introduced 12 d previously (Table 1). Note that treatment 2 served as the simultaneous arrival treatment for both species. For each experimental run, we size matched focal individuals and prior residents, so that all fish were the same size at the time they were added to reefs (see Appendix C). Size differences between prior residents and focal individuals were then a function of the length of prior residency (e.g., growth advantage conferred upon 12-d prior residents relative to 0-d prior residents was 12 d). Fish on a given reef were not size matched, but sampled randomly from the pool of available sizes for that treatment.

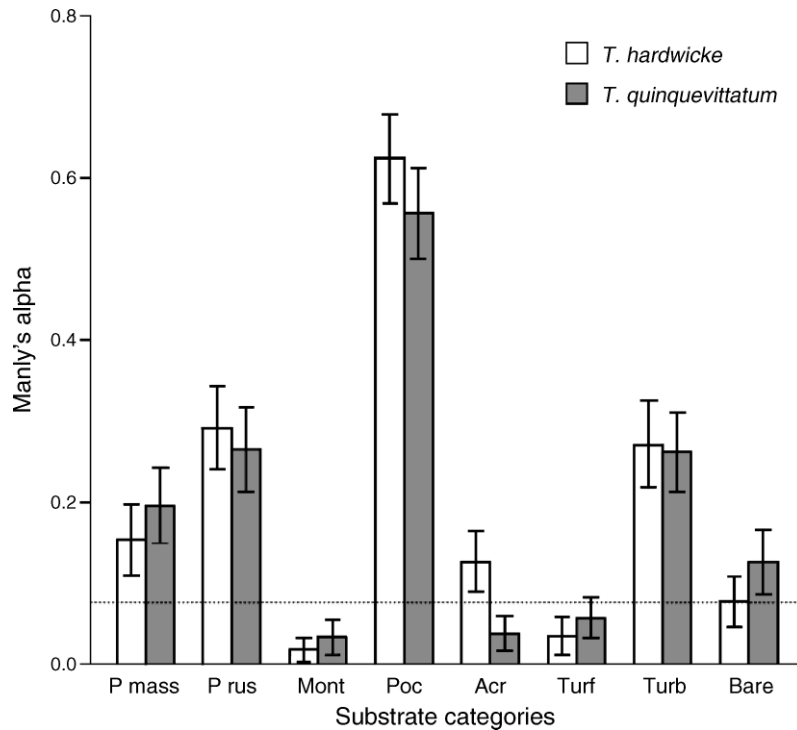


FIG. 1. Patterns of habitat association for the reef fishes *Thalassoma hardwicke* and *T. quinquevittatum* presented as Manly's alpha values (means with 95% CI), which range from 0 (least associated) to 1 (most associated). The study was conducted on a coral reef off Moorea, French Polynesia. Results are presented for the eight (of 13) habitat categories with which fish associated. Abbreviations are: P mass, *Porites* massive; P rus, *Porites rus*; Mont, *Montipora*; Poc, *Pocillopora* spp.; Acr, *Acropora* spp.; Turf, a mixed filamentous red algal assemblage consisting predominately of *Polysiphonia* spp.; Turb, *Turbinaria ornata*; and Bare, reef substrate that did not comprise a significant biological component. Substrate categories that *T. hardwicke* and *T. quinquevittatum* did not associate with were other coral, *Dictyota*, *Halimeda*, and sponge. The broken line represents expectations of random habitat association; values with error bars crossing this line are not statistically different from this expectation; values with error bars above or below this line indicate over- or underuse (relative to availability), respectively.

Because recently settled fish often experience high rates of mortality (Almany and Webster 2006), we initially introduced six prior residents to reefs in the 12-d and 5-d treatments. Prior to introducing focal fish to these treatments, we haphazardly removed excess residents when there were more than three residents (18 instances out of 32 reefs) and pressed residents at the

same time as focal individuals were added when there were less than three residents (six instances out of 32). Pressed residents were disproportionately distributed amongst treatments: *T. hardwicke* residents were pressed on four reefs (two individuals on two 12-d treatments, one individual on one 12-d treatment, and two individuals on one 5-d treatment) and *T. quinquevitta-*

TABLE 1. Summary of experiment 1 showing timing of neighbor introductions relative to focal introductions of reef fishes, where H represents *Thalassoma hardwicke* individuals and Q represents *T. quinquevittatum* individuals.

Timing	Treatment						
	1	2	3	4	5	6	7
12 d	Q (H)	H ...
5 d	Q (H)	H
0 d	...	H	Q (H)	H	...	Q	... Q

Notes: Focal individuals for each treatment are in boldface. Each of our seven treatments were as follows: (1) *T. hardwicke* without *T. quinquevittatum*; (2) *T. hardwicke* and *T. quinquevittatum* introduced simultaneously (0 d); (3) *T. hardwicke* with *T. quinquevittatum* introduced 5 d previously; (4) *T. hardwicke* with *T. quinquevittatum* introduced 12 d previously; (5) *T. quinquevittatum* without *T. hardwicke*; (6) *T. quinquevittatum* with *T. hardwicke* introduced 5 d previously; and (7) *T. quinquevittatum* with *T. hardwicke* introduced 12 d previously. Note that treatment 2 served as the simultaneous arrival treatment for both species. Treatments 1–4 examine effects of prior *T. quinquevittatum* residency on *T. hardwicke* settlement. Treatments 2 and 5–7 examine effects of prior *T. hardwicke* residency on *T. quinquevittatum* settlement. Treatments 1–4 with “(H)” indicate experimental design for experiment 2, where neighbor and focal individuals were both *T. hardwicke*. The study was conducted on a coral reef off Moorea, French Polynesia.

tum were pressed on two reefs (two individuals each on one 12-d and one 5-d treatment). We used excess individuals removed from other experimental reefs to press residents.

We surveyed reefs twice daily (at approximately 08:00 and 16:00) for seven days after we introduced focal individuals. We also searched neighboring nonexperimental reefs for tagged immigrants. We found no immigrants or emigrants, and previous research has shown that small reef fish rarely move between reefs separated by as little as 15 m (Caselle 1999, Shima 2001). We therefore assumed that the disappearance of an experimental fish was due to mortality rather than migration.

Experiment 2: intraspecific priority effects between T. hardwicke individuals.—We used a similar experimental design to examine intraspecific priority effects for *T. hardwicke* (i.e., *T. hardwicke* recruits served as both the focal and resident individuals; Table 1). Because the intraspecific design had four instead of seven treatments, all seven replicates of the four treatments were conducted together once (6–25 July). We removed excess residents from six of 14 reefs and added residents to three of 14 reefs (one 5-d treatment and two 12-d treatments) prior to adding focal individuals to reefs. All other aspects of experiment 2 were identical to experiment 1.

Behavioral observations

To help elucidate the mechanisms driving priority effects 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 ~3 min, behavioral observations were conducted at a distance of ~2 m from the reef. Observers remained stationary or moved slowly while conducting behavioral observations. This reduces the likelihood of "herding" or frightening fish onto or off reefs, or between substrates within reefs. We recorded three response variables: (1) the number of chases between focal individuals and both prior residents and the background community (in experiment 1, 96% and 89% of chases were inflicted by prior residents upon *T. hardwicke* and *T. quinquevittatum*, respectively; in experiment 2, 98% of chases were inflicted by prior residents); (2) the number of fin bites inflicted during chases (all fin bites were inflicted by prior residents on focal individuals in both experiments); and (3) the time spent inside *Pocillopora* by focal individuals.

Data analysis

Survival analysis.—We modeled time-to-disappearance for each treatment using Cox proportional hazard regression (Cox 1972, Cox and Oakes 1984). We modeled the underlying distribution of focal individual mortality against time of resident arrival. The probability distribution of mortality is specified as a hazard

function, $h(t)$, the conditional or instantaneous mortality, expressed as a function of time, t :

$$h(t) = h_0(t) \exp(\beta_1 x_1 + \beta_2 x_2 + \dots + \beta_p x_p) \quad (1)$$

where $h_0(t)$ is the time-dependent baseline hazard function that is dependent upon a set of p covariates (x_1, x_2, \dots, x_p), whose impact is measured by the size of the respective coefficients ($\beta_1, \beta_2, \dots, \beta_p$). The density of residents slowly decreased through time after we added focal individuals. For resident-present treatments, we controlled for decreasing resident densities through time by including density of residents as a time-dependent covariate in our model. For experiment 1 we also included a strata term in the model to account for experimental run, which is similar to effects of blocks in ANOVA (Therneau and Grambsch 2000). We right-censored the data (i.e., analyzed data on minimal survival times), used the Efron approximation to handle tied data, used partial likelihood to derive regression coefficients (β_i), converted these coefficients to a hazard ratio as e^{β_i} , and converted the hazard ratios into estimated percentage of changes in mortality rate (CMR) by subtracting 1 from the hazard ratio and multiplying by 100. We conducted model reduction using ANOVA.

We determined whether the fitted Cox regression model adequately described the data using Schoenfeld residuals scaled by the Kaplan Meier estimate to test the assumption of proportional hazards, and df-beta values (the relative differences between the least squares and deleted estimates of the coefficients [Freund and Wilson 1998]) to test for influential data. Cox regressions were conducted using the survival package in R 2.5.1 (R Development Core Team 2007).

We ran three orthogonal survival analyses. (1) We tested competitive effects by contrasting survival of focal individuals between resident-absent and resident-present treatments (i.e., absent vs. 0 d, 5 d, 12 d). (2) We tested the effects of arriving later than residents by contrasting survival of focal individuals with simultaneous vs. later arrival (i.e., 0 d vs. 5 d, 12 d). (3) We tested the effects of arriving progressively later than residents by contrasting survival of focal individuals arriving 5 d vs. 12 d later than residents.

Behavior analysis.—Because there were strong correlations among behavioral responses (e.g., fin bites only occurred during chases), we analyzed behavior data using principal components analysis (PCA) to create a composite aggression score. We transformed data ($\log[x + 1]$) prior to analysis to improve normality. We conducted separate analyses for each of the three sub-studies (*T. hardwicke* with *T. quinquevittatum*, *T. quinquevittatum* with *T. hardwicke*, and *T. hardwicke* with *T. hardwicke*). Results were very similar for all three analyses. Principal components axis 1 (PCA 1) accounted for 63–68% of the total variation in aggression variables and was driven by high positive

TABLE 2. Hazard ratios from the Cox proportional hazard assessment for: (A) interspecific competition between *Thalassoma hardwicke* and *T. quinquevittatum* and (B) intraspecific competition between *T. hardwicke* individuals.

Orthogonal contrast	Coefficient (b_i)	HR ($\exp(b_i)$)	CMR (%)	95% CI	<i>P</i>
A) Interspecific effects					
<i>T. hardwicke</i> focal individuals					
Absent vs. (0 d, 5 d, 12 d)	1.090	2.96	196	(1.61–5.45)	<0.001
0 d vs. (5 d, 12 d)	0.506	1.66	66	(0.94–2.93)	0.082
5 d vs. 12 d	0.173	1.19	19	(0.65–2.17)	0.570
<i>T. quinquevittatum</i> focal individuals					
Absent vs. (0 d, 5 d, 12 d)	0.419	1.52	52	(0.83–2.80)	0.180
0 d vs. (5 d, 12 d)	0.658	1.93	93	(1.02–3.64)	0.042
5 d vs. 12 d	–0.096	1.10	10	(0.48–1.72)	0.770
B) Intraspecific effects					
<i>T. hardwicke</i> focal individuals					
Absent vs. (0 d, 5 d, 12 d)	0.844	2.33	133	(1.17–4.60)	0.015
0 d vs. (5 d, 12 d)	0.330	1.39	39	(0.76–2.55)	0.290
5 d vs. 12 d	0.496	1.64	64	(0.84–2.22)	0.150

Notes: For each focal species, we ran three orthogonal survival analyses: (1) competition (absent vs. 0 d and 5 d and 12 d); (2) priority (0 d vs. 5 d and 12 d); and (3) degree of priority (5 d vs. 12 d). See Table 1 for a description of the treatments. Abbreviations are: HR, hazard ratio; CMR, change in mortality rate; CI, confidence interval.

loadings of total chases (64–68%) and fin bites (63–68%) and weak negative loadings of time-in-*Pocillopora* (31–44%). Thus, we interpret this first PCA axis as a gradient of overall aggression. We analyzed PCA 1 scores with a one-way ANOVA, using a relaxed variance assumption (Dalggaard 2002). For significant ANOVAs ($P < 0.05$), we used Bonferroni-adjusted pairwise *t* tests, with unequal variances, to compute all possible pairwise comparisons.

RESULTS

Interspecific priority effects

Over the seven days that we monitored the survival of *T. hardwicke* focal individuals, percentage of survival was $46\% \pm 8.76\%$ (mean \pm SE), $21\% \pm 8.76\%$, $13\% \pm 6.12\%$, and $8\% \pm 5.44\%$ for absent, 0-d, 5-d, and 12-d treatments, respectively (Fig. 2a, b). Percentage of survival of *T. quinquevittatum* after seven days was $46\% \pm 8.77\%$, $46\% \pm 10.78\%$, $21\% \pm 8.76\%$, and $21\% \pm 6.12\%$, for absent, 0-d, 5-d, and 12-d treatments, respectively (Fig. 2c, d).

Analysis of competitive effects (absent vs. 0 d, 5 d, 12 d) indicated that the likelihood of mortality for *T. hardwicke* individuals entering reefs where *T. quinquevittatum* residents were present increased by 196%, compared to reefs where *T. quinquevittatum* was absent ($P < 0.001$; Fig. 2a, b, Table 2). When arriving simultaneously, *T. hardwicke* had lower survival than *T. quinquevittatum* (proportional survival 0.208 ± 0.059 vs. 0.458 ± 0.074 for *T. hardwicke* and *T. quinquevittatum*, respectively). Mortality of *T. hardwicke* increased as *T. quinquevittatum* were given greater residence times, but these effects were not significant (0 d vs. 5 d, 12 d, P

$= 0.082$, CMR = 66%; 5 d vs. 12 d, $P = 0.570$, CMR = 19%; Fig. 2a, b; Table 2).

Survival of *T. hardwicke* decreased with increase in the PCA-derived composite aggression score (Fig. 2b). As *T. hardwicke* entered reefs progressively later than *T. quinquevittatum*, aggression from residents towards focal individuals increased ($P < 0.001$) and survival decreased ($P < 0.001$). Aggression was significantly higher on reefs on which *T. quinquevittatum* arrived either 5 d or 12 d prior to *T. hardwicke* relative to reefs on which *T. quinquevittatum* was absent (Fig. 2b). Likewise, aggression was significantly higher on reefs on which *T. quinquevittatum* arrived 12 d prior to *T. hardwicke* relative to reefs on which *T. quinquevittatum* arrived simultaneously (Fig. 2b).

When the sequence of arrival was reversed, there was not a significant competitive effect of *T. hardwicke* on *T. quinquevittatum* (absent vs. 0 d, 5 d, 12 d, $P = 0.180$, CMR = 52%; Fig. 2c, d, Table 2). However, when *T. quinquevittatum* arrived on reefs later than *T. hardwicke*, mortality risk of *T. quinquevittatum* increased by 93% (0 d vs. 12 d and 5 d, $P = 0.042$; Fig. 2c, d, Table 2). There was no demonstrable difference when *T. hardwicke* arrived 5 d vs. 12 d prior to arrival of *T. quinquevittatum* ($P = 0.770$, CMR = 10%; Fig. 2c, d, Table 2).

Survival decreased with increase in the PCA-derived composite aggression score (Fig. 2d). As *T. quinquevittatum* entered reefs later than *T. hardwicke*, aggression from residents towards focal individuals increased ($P < 0.001$) and survival decreased ($P = 0.001$). Aggression was significantly higher on reefs on which *T. hardwicke* arrived either 5 d or 12 d prior to *T. quinquevittatum* relative to reefs on which *T. hardwicke* were absent or arrived simultaneously with *T. quinquevittatum* (Fig. 2d).

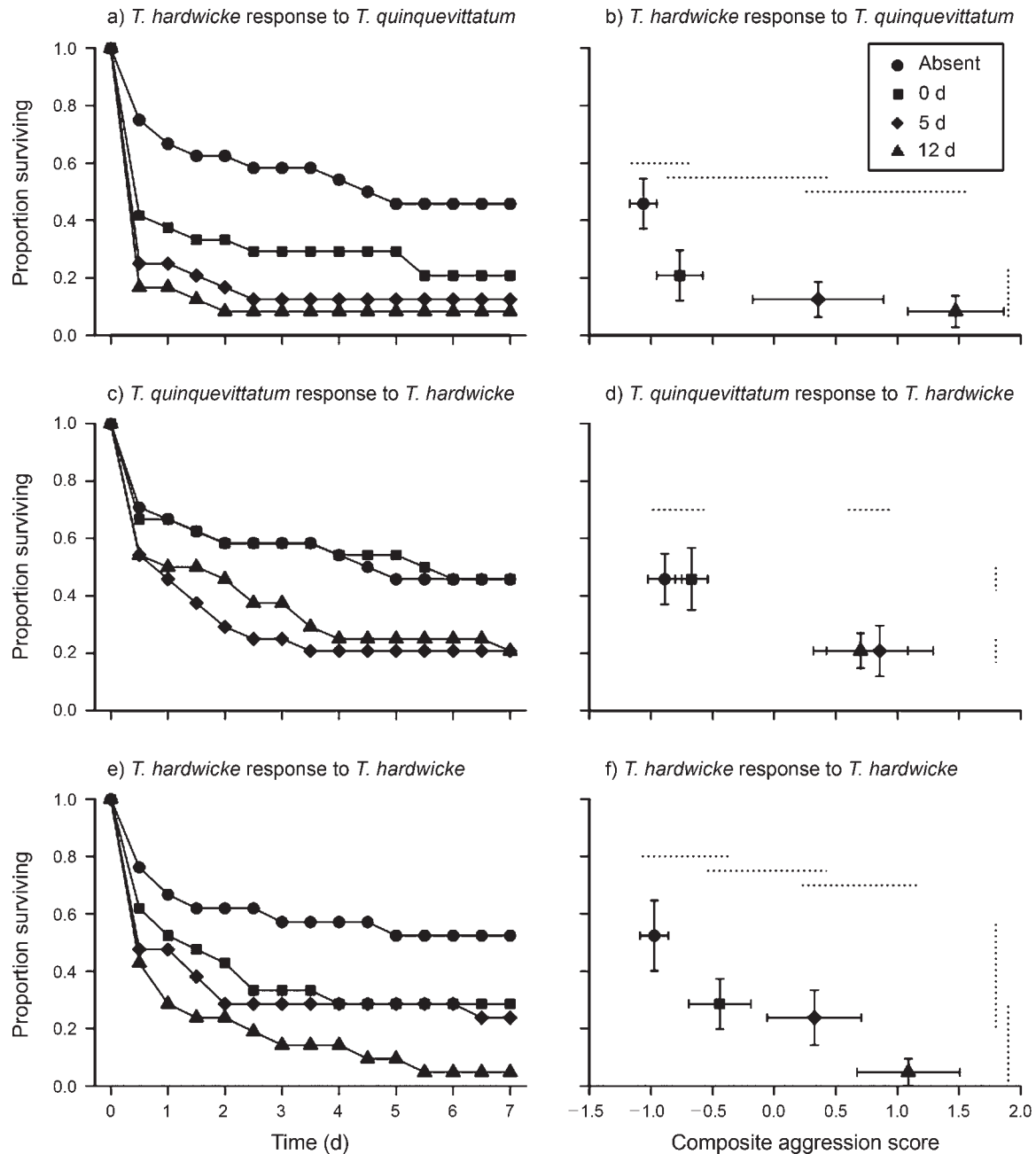


FIG. 2. Survival of focal individuals in response to presence, relative timing of arrival (0 d [the same time], 5 d prior, or 12 d prior), and relative aggression of a competitor. Temporal trends of survival are depicted for (a) *Thalassoma hardwicke* in response to *T. quinquevittatum*, (c) *T. quinquevittatum* in response to *T. hardwicke*, and (e) *T. hardwicke* intraspecific responses. Error bars of temporal trends are omitted for clarity. (b, d, f) Corresponding survival (proportion alive at the end of the experiment) in relation to composite aggression scores (modeling chases, fin bites, and time spent inside *Pocillopora*; see *Methods: Behavioral observations*; means \pm SE). Broken lines overlap treatments that are not significantly different.

Intraspecific priority effects

Over the seven days that we monitored the survival of *T. hardwicke*, percentage of survival was $52\% \pm 8.35\%$ (mean \pm SD), $29\% \pm 5.91\%$, $24\% \pm 6.47\%$, and $5\% \pm 3.23\%$, for absent, 0-d, 5-d, and 12-d treatments, respectively (Fig. 2e, f). Risk of *T. hardwicke* mortality

increased by 133% when conspecific residents were already present on reefs relative to conspecific-absent treatments (absent vs. 0 d, 5 d, 12 d, $P = 0.015$; Fig. 2e, f, Table 2). Mortality of focal *T. hardwicke* increased as competing conspecifics were given greater residence times, but these effects were not significant: (0 d vs. 5



PLATE 1. Adult sixbar wrasse (*Thalassoma hardwicke*) on the reef at Moorea, French Polynesia. Adult wrasse represent the product of intracohort competitive interactions between wrasse settlers. Photo credit: S. W. Geange.

d, 12 d, $P = 0.290$, CMR = 39%; 5 d vs. 12 d, $P = 0.150$, CMR = 64%; Fig. 2e, f; Table 2).

Survival decreased with increase in the PCA-derived composite aggression score (Fig. 2f). As *T. hardwicke* entered reefs progressively later than conspecifics, aggression from residents towards focal individuals increased ($P < 0.001$) and survival decreased ($P < 0.001$). Aggression was significantly higher on reefs on which conspecifics arrived 12 d prior to *T. hardwicke* relative to reefs on which conspecifics were absent (Fig. 2f).

DISCUSSION

Formal analysis indicated strong inter- and intraspecific competitive effects, although strong support for priority effects only occurred in the response of *T. quinquevittatum* to the relative timing of arrival of *T. hardwicke* (Table 1, Fig. 2c). However, weaker priority effects are also evident for *T. hardwicke* (Fig. 2a, e). When both species arrived simultaneously, survival of *T. quinquevittatum* was similar to that when it arrived in communities devoid of *T. hardwicke*, whereas survival of *T. hardwicke* was lower than when it arrived in communities devoid of *T. quinquevittatum*. This suggests that when both species arrive simultaneously, *T. quinquevittatum* is competitively dominant over *T. hardwicke*.

Our findings suggest that variability in the timing of settlement pulses of *T. hardwicke* relative to *T. quinquevittatum* can have dramatic effects on recruit-

ment strength and success of both species. When both species arrived simultaneously, *T. quinquevittatum* survived better than *T. hardwicke*, which is indicative of an asymmetric competitive interaction between these species. However, when each species arrived at different times, reversals in sequence of arrival reversed the competitive advantage, indicating that competitive interactions were at least partially driven by priority effects, producing more symmetric competitive effects. The majority of short-term studies of interspecific competition between reef fishes have typically found competitive ability to be highly asymmetric, often resulting in local exclusion and habitat displacement (Hixon 1980, Larson 1980, Robertson and Gaines 1986, Schmitt and Holbrook 1986, Holbrook and Schmitt 1989). However, these studies may not be representative of most competitive interactions as species pairs were selected in part because closely related species showed very different patterns of habitat use. While other studies have identified symmetric competitive interactions between reef fishes (Schmitt and Holbrook 1990, Munday 2004), our results expand these findings by suggesting that the direction and magnitude of competition may, in part, be determined by the sequence and timing of species interactions.

Classic competition theory predicts that over evolutionary time, intraspecific competition should be stronger than interspecific competition because competitive exclusion and niche diversification will lead to resource partitioning among species (Colwell and Fuentes 1975,

Diamond 1978). Interspecific differences in distribution, resource use, environmental tolerances, or natural enemies act as stabilizing processes, buffering per capita population growth rates of a species in a community (Chesson 2000), resulting in intraspecific effects being more negative than interspecific effects.

Alternatively, neutral theory (Bell 2000, Hubbell 2001) and the "lottery model" (Sale 1976, 1978) both predict that intra- and interspecific competition should be of equal magnitude. Neutral models suggest that the only drivers of population dynamics are random variation in births, deaths, and dispersal (Adler et al. 2007), with species identity playing no role because species do not differ from one another in ways that distinguish their population dynamics (Chave 2004, Leibold and McPeck 2006). Likewise, the lottery model assumes that space is a limiting resource, vacant space is recolonized by the first available settler, and that once recolonized the individual holds the space until it dies (i.e., there is a strong "priority effect"). Coexistence is favored if arrival is higher for one species at some times or places and higher for the other species at other times or places (Chesson and Warner 1981). We found that the strength of competitive effects was primarily related to relative arrival time and poorly explained by the identity of prior residents. This is consistent with both neutral theory and the lottery model: reversals in sequence of arrival reversed the direction of competition, and late-arriving fish did poorer than fishes arriving simultaneously with their competitors or before their competitors (as evidenced by the "no competition" treatment). Because we found order of arrival and not species identity to be important here, our results are more consistent with neutral processes structuring communities than niche-based theories.

Although we never explicitly tested mechanisms underlying priority effects in this study, we propose three: (1) a residency advantage, in which, if residents are able to deplete renewable resources to low levels, longer time in residency means that more depletion occurs, increasing the intensity of exploitative competition; (2) a size advantage in which larger (or older) fish (i.e., prior residents) induce stronger competitive effects than smaller (or younger) fish through either exploitative or interference competition (Jones 1987, Wilson 2005); (3) an experience advantage, in which more experienced individuals (i.e., prior residents) gain knowledge of the local environment (e.g., greater awareness of established boundaries with neighbors and knowledge of hiding spaces), facilitating their ability (relative to later-arriving fish) to acquire resources (i.e., exploitative competition), defend home ranges (i.e., interference competition) or evade predators. Of these three mechanisms, we have most evidence for the second and third. We found that aggression increased with increasing mortality risk and increasing temporal separation of species arrival, suggesting that aggressive behavior by residents toward focal individuals increased

the mortality risk of focal individuals. This aggression gradient is suggestive of both size and experience advantages, which, because larger individuals are often also more experienced, are not mutually exclusive. Previous research has shown that: (1) individuals less experienced with a site are less likely to engage in competitive interactions because they exhibit fear-like behaviors incompatible with aggression (Figler et al. 1976); and (2) larger individuals are often more successful in the acquisition and defense of food or cover, resulting in increased growth or reduced mortality (Robertson 1984, Szabo 2002). As individuals gain experience with a site they may also increase in confidence and more readily engage in aggressive interactions. Therefore, over timescales of minutes to hours in which new arrivals exhibit fear-like behaviors, experience advantages (or conversely an unwillingness by new arrivals to engage in aggressive interactions) may be determining factors in the outcome of interference competition. Over timescales of hours to days, when new arrivals have overcome any initial fear-like behaviors, size advantages may be critical, as larger individuals are able to physically dominate smaller individuals during interference competition.

Based on previous work in coral reef fish communities, predation is likely the ultimate cause of mortality in recently settled reef fishes, with competition increasing a subordinate's exposure to predators due to displacement of subordinates from refuge habitat (Carr et al. 2002, Holbrook and Schmitt 2002, Almany 2003). The ability to find (and defend) shelter sites may therefore increase competitive advantage. Shima (2002) found that the frequency of agonistic interactions between resident *T. hardwicke* scaled with density- and number-dependent losses to predation, suggesting that behavioral interactions rather than proximate resource limitation may underlie observed mortality. We have evidence that these patterns also hold true here, for both intraspecific interactions between *T. hardwicke* and interspecific interactions between *T. hardwicke* and *T. quinquevittatum*, with the likely agents of mortality both resident (cardinalfish, eels, lizardfish, sandperch, triggerfish) and transient (jacks) predators (see Appendices A and B). We add a caveat to these interpretations. Our experimental design effectively doubled the density of the experimental species when residents and focal individuals were present on the same reef relative to reefs on which prior residents were absent. We acknowledge that this design does not distinguish competitive effects from apparent competition (i.e., the response of predators to overall increases in prey density) because neither competitor density nor predator effects were controlled for.

Communities are rarely devoid of established residents. Colonists and newborns immediately encounter a community's current residents. Previous research has demonstrated that the degree to which resident-settler interactions affect the persistence of settlers can depend

on the identity of both the resident and the settler (Shulman et al. 1983, Sweatman 1985, Munday et al. 2001, Almany 2003, 2004, Hixon and Jones 2005, Forrester et al. 2006). Here we have expanded on this by showing that not only does the identity of the players in resident–settler interactions affect the outcome of these interactions, but so does the sequence and timing of these interactions. This has important implications for ecologists attempting to evaluate interaction strengths among species, suggesting that it is not only important to identify the direction and magnitude of interaction strengths, but also variability in the direction and magnitude of interaction strengths through time.

ACKNOWLEDGMENTS

Craig Osenberg, Jeff Shima, Jada-Simone White, Ben Bolker, Todd Palmer, and two anonymous reviewers provided many helpful comments on versions of this manuscript. Staff of the Richard B. Gump South Pacific Research Station provided invaluable logistical support, and Natasha Dallin, Shelby Boyer, and Anne Duploux helped in the field and laboratory. This project was possible with financial support from NSF (OCE-0242312), a VUW Ph.D. Scholarship awarded to S. W. Geange, a Fulbright-Ministry of Research, Science and Technology Graduate Student Award to S. W. Geange, and a Three Seas Fellowship to A. C. Stier.

LITERATURE CITED

- Adler, P. B., J. HilleRisLambers, and J. M. Levine. 2007. A niche for neutrality. *Ecology Letters* 10:95–104.
- Almany, G. R. 2003. Priority effects in coral reef fish communities. *Ecology* 84:1920–1935.
- Almany, G. R. 2004. Priority effects in coral reef fish communities of the Great Barrier Reef. *Ecology* 85:2872–2880.
- Almany, G. R., and M. S. Webster. 2006. The predation gauntlet: early post-settlement mortality in reef fishes. *Coral Reefs* 25:19–22.
- Bell, G. 2000. The distribution of abundance in neutral communities. *American Naturalist* 155:606–617.
- Benke, A. C. 1978. Interactions among coexisting predators—a field experiment with dragonfly larvae. *Journal of Animal Ecology* 47:335–350.
- Beukers, J. S., G. P. Jones, and R. M. Buckley. 1995. Use of implant microtags for studies on populations of small reef fish. *Marine Ecology Progress Series* 125:61–66.
- Blaustein, L., and J. Margali. 1996. Priority effects in temporary pools: nature and outcome of mosquito larva–toad tadpole interactions depend on order of entrance. *Journal of Animal Ecology* 65:77–84.
- Carr, M. H., T. W. Anderson, and M. A. Hixon. 2002. Biodiversity, population regulation, and the stability of coral-reef fish communities. *Proceedings of the National Academy of Sciences (USA)* 99:11241–11245.
- Caselle, J. E. 1999. Early post-settlement mortality in a coral reef fish and its effect on local population size. *Ecological Monographs* 69:177–194.
- Chave, J. 2004. Neutral theory and community ecology. *Ecology Letters* 7:241–253.
- Chesson, J. 1978. Measuring preference in selective predation. *Ecology* 59:211–215.
- Chesson, P. 2000. Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics* 31: 343–366.
- Chesson, P., and R. Warner. 1981. Environmental variability promotes coexistence in lottery competitive systems. *American Naturalist* 117:923–943.
- Colwell, R. K., and E. R. Fuentes. 1975. Experimental studies of the niche. *Annual Review of Ecology and Systematics* 6: 281–310.
- Cox, D. R. 1972. Regression models and life-tables. *Journal of the Royal Statistical Society Series B* 34:187–220.
- Cox, D. R., and D. Oakes. 1984. *Analysis of survival data*. Chapman and Hall, London, UK.
- Craig, P. C. 1998. Temporal spawning patterns of several surgeonfishes and wrasses in American Samoa. *Pacific Science* 52:35–39.
- Dalgaard, P. 2002. *Introductory statistics with R*. Springer, New York, New York, USA.
- Dayton, G. H., and L. A. Fitzgerald. 2005. Priority effects and desert anuran communities. *Canadian Journal of Zoology* 83: 1112–1116.
- Diamond, J. M. 1978. Niche shifts and the rediscovery of interspecific competition. *American Scientist* 66:322–331.
- Doherty, P. J. 1988. Large-scale variability in the recruitment of a coral reef fish. Pages 667–672 in *Proceedings of the Sixth International Coral Reef Symposium, Australia*. Executive Committee, Townsville, Australia.
- Doherty, P. J. 1991. Spatial and temporal patterns in recruitment. Pages 261–293 in P. F. Sale, editor. *The ecology of fishes on coral reefs*. Academic Press, San Diego, California, USA.
- Dufour, V., and R. Galzin. 1993. Colonization patterns of reef fish larvae to the lagoon at Moorea Island, French Polynesia. *Marine Ecology Progress Series* 102:143–152.
- Figler, M. H., R. M. Klein, and H. V. S. Peeke. 1976. The establishment and reversibility of dominance relationships in jewel fish, *Hemichromis bimaculatus* Gill (Pisces, Cichlidae): effects of prior exposure and prior residence situations. *Behaviour* 58:254–270.
- Forrester, G. E., B. Evans, M. A. Steele, and R. R. Vance. 2006. Assessing the magnitude of intra- and interspecific competition in two coral reef fishes. *Oecologia* 148:632–640.
- Frederick, J. L. 1997. Evaluation of fluorescent elastomer injection as a method for marking small fish. *Bulletin of Marine Science* 61:399–408.
- Freund, R. J., and W. J. Wilson. 1998. *Regression analysis: statistical modeling of a response variable*. Academic Press, San Diego, California, USA.
- Gibbs, H. L., and P. R. Grant. 1987. Ecological consequences of an exceptionally strong El Niño event on Darwin's Finches. *Ecology* 68:1735–1746.
- Hixon, M. A. 1980. Competitive interactions between California reef fishes of the genus *Embiotoca*. *Ecology* 61:918–931.
- Hixon, M. A., and G. P. Jones. 2005. Competition, predation, and density-dependent mortality in demersal marine fishes. *Ecology* 86:2847–2859.
- Holbrook, S. J., and R. J. Schmitt. 1989. Resource overlap, prey dynamics, and the strength of competition. *Ecology* 70: 1943–1953.
- Holbrook, S. J., and R. J. Schmitt. 2002. Competition for shelter space causes density-dependent predation mortality in damselfishes. *Ecology* 83:2855–2868.
- Hubbell, S. P. 2001. *The unified neutral theory of biodiversity and biogeography*. Princeton University Press, Princeton, New Jersey, USA.
- Imbert, H., L. Beaulaton, C. Rigaud, and P. Elie. 2007. Evaluation of visible implant elastomer as a method for tagging small European eels. *Journal of Fish Biology* 71: 1546–1554.
- Jones, G. P. 1987. Competitive interactions among adults and juveniles in a coral reef fish. *Ecology* 68:1534–1547.
- Larson, R. J. 1980. Competition, habitat selection, and the bathymetric segregation of two rockfish (*Sebastes*) species. *Ecological Monographs* 50:221–239.

- Lawler, S. P., and P. J. Morin. 1993. Temporal overlap, competition, and priority effects in larval anurans. *Ecology* 74:174–182.
- Leibold, M. A., and M. A. McPeck. 2006. Coexistence of the niche and neutral perspectives in community ecology. *Ecology* 87:1399–1410.
- Louette, G., and L. D. Meester. 2007. Predation and priority effects in experimental zooplankton communities. *Oikos* 116: 419–426.
- Manly, B. F., P. Miller, and L. M. Cook. 1972. Analysis of a selective predation experiment. *American Naturalist* 106: 719–736.
- Munday, P. L. 2004. Competitive coexistence of coral-dwelling fishes: the lottery hypothesis revisited. *Ecology* 85:623–628.
- Munday, P., G. Jones, and M. Caley. 2001. Interspecific competition and coexistence in a guild of coral-dwelling fishes. *Ecology* 82:2177–2189.
- Myers, R. F. 1999. Micronesian reef fishes. Coral Graphics, Guam.
- Osenberg, C. W., J. S. Shima, and C. M. S. Mary. 2006. Habitat degradation and settlement behavior: effects on fish settlement, survival, and recruitment. Pages 257–263 in Y. Suzuki, T. Nakamori, M. Hidaka, H. Kayanne, B. E. Casareto, K. Nadaoka, H. Yamano, and M. Tsuchiya, editors. Proceedings of the 10th International Coral Reef Symposium, Okinawa, Japan. Japanese Coral Reef Society, Tokyo, Japan.
- Price, J. E., and P. J. Morin. 2004. Colonization history determines alternate community states in a food web of intraguild predators. *Ecology* 85:1017–1028.
- R Development Core Team. 2007. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Randall, J. E. 2005. Reef and shore fishes of the South Pacific: New Caledonia to Tahiti and the Pitcairn Islands. University of Hawaii Press, Honolulu, Hawaii, USA.
- Robertson, D. R. 1984. Cohabitation of competing territorial damselfishes on a Caribbean coral reef. *Ecology* 65:1121–1135.
- Robertson, D., and S. G. Gaines. 1986. Interference competition structures habitat use in a local assemblage of coral reef surgeonfishes. *Ecology* 67:1372–1383.
- Sale, P. F. 1976. Reef fish lottery. *Natural History* 85:60–65.
- Sale, P. F. 1978. Coexistence of coral reef fishes—a lottery for living space. *Environmental Biology of Fishes* 3:85–102.
- Schauber, E. M., D. Kelly, P. Turchin, C. Simon, W. G. Lee, R. B. Allen, I. J. Payton, P. R. Wilson, P. E. Cowan, and R. E. Brockie. 2002. Masting by eighteen New Zealand plant species: the role of temperature as a synchronizing cue. *Ecology* 83:1214–1225.
- Schmitt, R. J., and S. J. Holbrook. 1986. Seasonally fluctuating resources and temporal variability of interspecific competition. *Oecologia* 69:1–11.
- Schmitt, R., and S. Holbrook. 1990. Population responses of surfperch released from competition. *Ecology* 71:1653–1665.
- Shima, J. S. 2001. Regulation of local populations of a coral reef fish via joint effects of density- and number-dependent mortality. *Oecologia* 126:58–65.
- Shima, J. S. 2002. Mechanisms of density- and number-dependent population regulation of a coral-reef fish. *Marine and Freshwater Research* 53:175–179.
- Shima, J. S., C. W. Osenberg, and C. M. S. Mary. 2008. Quantifying site quality in a heterogeneous landscape: recruitment of a reef fish. *Ecology* 89:86–94.
- Shorrocks, B., and M. Bingley. 1994. Priority effects and species coexistence: experiments with fungal-breeding *Drosophila*. *Journal of Animal Ecology* 63:799–806.
- Shulman, M., J. Ogden, W. McFarland, S. Miller, N. Wolf, and J. Ebersole. 1983. Priority effects in the recruitment of juvenile coral reef fishes. *Ecology* 64:1508–1513.
- Simon, J. 2007. Evaluation of marking European silver eels with visible implant elastomer tags and alcian blue. *Journal of Fish Biology* 70:303–309.
- Srinivasan, M., and G. P. Jones. 2006. Extended breeding and recruitment periods of fishes on a low latitude coral reef. *Coral Reefs* 25:673–682.
- Sutherland, J. P., and R. H. Karlson. 1977. Development and stability of the fouling community at Beaufort, North Carolina. *Ecological Monographs* 47:425–446.
- Sweatman, H. P. A. 1985. The influence of adults of some coral reef fishes on larval recruitment. *Ecological Monographs* 55: 469–485.
- Szabo, A. R. 2002. Experimental tests of intercohort competition for food and cover in the tidepool sculpin (*Oligocottus maculosus* Girard). *Canadian Journal of Zoology* 80:137–144.
- Therneau, T. M., and P. M. Grambsch. 2000. Modeling survival data: extending the Cox model. Springer, New York, New York, USA.
- Victor, B. C. 1986. Duration of the planktonic larval stage of one hundred species of Pacific and Atlantic wrasses (family Labridae). *Marine Biology* 90:317–326.
- Wilson, J. A. 2005. Age class interactions in a marine goby, *Elacatinus prochilos* (Bohlke and Robins, 1968). *Journal of Experimental Marine Biology and Ecology* 327:144–156.
- Winemiller, K. O., and K. A. Rose. 1992. Patterns of life-history diversification in North American Fishes: implications for population regulation. *Canadian Journal of Fisheries and Aquatic Sciences* 49:2196–2218.

APPENDIX A

Non-manipulated reef community structure in the interspecific study examining intracohort priority effects (*Ecological Archives* E090-203-A1).

APPENDIX B

Non-manipulated community structure in the intraspecific study examining intracohort priority effects (*Ecological Archives* E090-203-A2).

APPENDIX C

Standard lengths of focal individuals and prior residents (*Ecological Archives* E-090-203-A3).