Effects of larger heterospecifics and structural refuge on the survival of a coral reef fish, *Thalassoma hardwicke*

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ABSTRACT: Structural refuge and competition can influence the survival of coral reef fishes; however, the effect of structural refuge on the outcome of competition remains unclear. In Moorea, French Polynesia, surveys were used to quantify habitat association for juvenile *Thalassoma hardwicke* and 7 sympatric labroid species. Having identified the 3 species most similar to focal *T. hardwicke* in habitat association, a field assay was used to determine if the presence of larger individuals of these species adversely affected the survival of focal individuals. Finally, a field experiment was used to test how competition with larger residents and structural refuge interact to influence survival of transplanted *T. hardwicke.* Surveys demonstrated that *Gomphosus varius, Pseudocheilinus hexataenia*, and *T. quinquevittatum* were most similar to *T. hardwicke* in habitat association. In the field assay, the presence of *T. quinquevittatum* had the greatest negative effect on survival of *T. hardwicke*. The field experiment revealed that competition with *T. quinquevittatum* and structural refuge both altered *T. hardwicke* survival, although their effects were not interactive. Survival of *T. hardwicke* was 2.3 times greater in treatments without *T. quinquevittatum* relative to those with *T. quinquevittatum*, and 2.8 times greater in treatments with structural refuge relative to those without structural refuge. The additive effect may have occurred via the establishment of social dominance hierarchies between transplanted *T. hardwicke* and resident *T. quinquevittatum* independently of structural refuge, suggesting that it is important to account for interactions occurring independently of resources when examining resource competition.

KEY WORDS: Habitat complexity · Competition · Structural refuge · Reef fish · Labroid

INTRODUCTION

Habitat specific survival may result from intrinsic differences in habitat quality, or because the effects of competitors and predators differ among habitat types (Ebersole 1985, Holt 1987, Rosenzweig 1991, Almany 2004a,b, Bonin et al. 2009). For example, asymmetric competition can lead to the exclusion of subordinates from mutually preferred habitats (Connell 1983, Schoener 1983). Competitive subordinates are expected to survive better when competitive dominants are removed (Colwell & Fuentes 1975), or when competition is alleviated by a change in habitat composition (Ebersole 1985, Rosenzweig 1991).

Increased habitat complexity is expected to mitigate the negative effects of competition and predation by providing a greater spectrum of resources, increasing structural refuge, or decreasing encounter rates due to reduced manoeuvrability and/or the ability to visually detect competitors/prey (Anderson 1984, Main 1987, Persson & Eklov 1995, Lindholm et al. 1999). Conversely, rates of predation may increase if habitat complexity increases predator encounter rates. For example, the efficiency of ambush predators may improve in structurally complex habitats that provide more sites from which predators can attack, or which decrease the visibility of predators to prey (Coen et al. 1981, Rilov et al. 2007). Consequently, natural

heterogeneity in the provisioning of structural complexity and refuges (or other habitat features) may drive variability in the strength of competition and predation.

Competitive interactions have previously been shown to play a fundamental role in coral reef community dynamics, e.g. between algae and coral (McCook et al. 2001, Jompa & McCook 2003), sponges and coral (Hill 1998, Lopez-Victoria et al. 2006), vermetid gastropods (Gagern et al. 2008) and fishes (Holbrook & Schmitt 2002, Forrester & Steele 2004, Bonin et al. 2009). Coral reefs consist of structurally diverse microhabitats, with the availability of structural refuges within these microhabitats capable of determining the magnitude of competitive interactions. Bonin et al. (2009) demonstrated that the complexity of structural refuges and interspecific competition both influenced early post-settlement survival of a damselfish, with survival in the presence of competitors greatest on intricately-structured habitats. Alternatively, Almany (2004a) found that increasing the complexity of structural refuges increased the abundance of adults in the presence of predators and competitors, but did not affect the abundance of recruits. Thus, the phenomenon of post-settlement competitive effects being weakened by increasing the complexity or availability of structural refuge may be situation- or species-specific. For example, many reef fishes are social, with competitive interactions (e.g. posturing, chases) occurring independently of resources during the establishment of social dominance hierarchies; therefore, the general expectation that increasing the complexity or availability of structural refuge will mitigate the negative effects of competition may not hold when social hierarchies dictate resource access.

This study examines the influence of structural refuge, competition and their interaction on the early post-settlement survival of transplanted *Thalassoma hardwicke* (the sixbar wrasse). *T. hardwicke* is a common resident of Indo-Pacific coral reefs that maintains tight associations with preferred habitats immediately following settlement (Shima 2001a, Shima & Osenberg 2003, Lecchini et al. 2007, Shima et al. 2008). To determine how competition for structural refuge influences post-settlement survival, quantitative surveys of habitat use and availability were first conducted to describe similarity in habitat use between focal *T. hardwicke* and 7 sympatric labroid species. Then a field assay was used to determine whether the presence of larger individuals of the 3 species with the greatest degree of similarity in habitat association with *T. hardwicke* adversely affected the post-settlement survival of focal individuals. Finally, a patch reef experiment was used to tease apart the effects of 2 factors potentially affecting the

post-settlement survival of transplanted *T. hardwicke*: (1) the presence and absence of a larger interspecific competitor (*T. quinquevittatum*), and (2) the presence and absence of structural refuge (*Turbinaria ornata*). It was predicted that the provisioning of structural refuge would increase post-settlement survival and reduce the influence of larger competitors, and the presence of larger competitors would reduce post-settlement survival.

MATERIALS AND METHODS

Study system. This study was conducted in the northern lagoon of Moorea, French Polynesia (17° 30′ S, 149° 50′ W). The northern lagoon is interspersed with patch reefs within a matrix of sand, fine coral rubble and coral pavement (Galzin & Pointer 1985). Patch reefs are predominantly *Porites* spp., often surmounted by smaller colonies of branching corals, dead coral skeletons, patches of macroalgae, or lush stands of filamentous algae. The structure of patch reefs varies over small spatial scales (Galzin & Pointer 1985).

There are 104 recognized labroid species in Moorea (Moorea Biocode Databases 2009. BSCIT University of California, Berkeley. Accessed 19 February 2009. http://biocode.berkeley.edu/). Here, the 8 most common species were examined, which together comprise ~84% of juvenile labroids within the lagoon (Table 1) and often co-occur: *Gomphosus varius*, *Halichoeres hortulanus*, *H. trimaculatus*, *Pseudocheilinus hexataenia*, *Scarus sordidus*, *Stethojulis bandanensis*, *Thalassoma hardwicke* and *T. quinquevittatum*. These species undergo pelagic larval development before settling in pulses to benthic reef habitat (Victor 1986). Settlement occurs preferentially to microhabitats that provide structural refuge, such as branching corals and macroalgae (Shima & Osenberg 2003, Lecchini et al. 2007, Shima et al. 2008). Sequential settlement pulses create communities of discrete, mixed-species cohorts. Interspecific aggressive interactions are common between and within these cohorts (Geange & Stier 2009). Following settlement, recruits generally remain site-attached for up to 6 mo (Geange unpubl. data).

Surveys of habitat availability and habitat association. Within Moorea's northern lagoon, 3 transects were established. Each transect was ~800 m in length, and ran from shore to the barrier reef crest. Along each transect, 5 approximately equally spaced sites were identified (90 ± 3, 180 ± 7, 289 ± 7, 409 ± 7, and 508 ± 11 m from the reef crest). Within each site, 16 patch reefs (hereafter reefs) of similar size (n = 240, average surface area = 7.98 ± 0.24 m², average

Table 1. Labrid recruit counts (<25 mm standard length) on 240 patch reefs within the northern lagoon of Moorea. Each patch reef was counted once between 27 May and 6 June 2005. Separate totals for the focal species examined in this study (84% of total ind.) and other species

Focal species	Number
Gomphosus varius	123
Halichoeres hortulanus	13
Halichoeres trimaculatus	42
Pseudocheilinus hexataenia	61
Scarus sordidus	57
Stethojulis bandanensis	35
Thalassoma hardwicke	333
Thalassoma quinquevittatum	339
Total	**1003**
Other species	Number
Cheilinus chlorourus	16
Cheilinus trilobatus	7
Cheilio inermis	1
Coris aygula	7
Coris gaimond	3
Epibulus insidiator	4
Halichoeres marginatus	3
Iniistius pavo	1
Labrid spp.	65
Labroides bicolor	32
Novaculichthys taeniourus	3
Scarus altipinnis	5
Scarus spp.	22
Thalassoma amblycephalum	23
Total	**192**

height = 0.83 ± 0.01 m) were haphazardly selected. For each reef, and a 1 m halo surrounding the reef, percent cover of 16 substrate categories was visually estimated: *Porites massive*, *Porites rus*, *Montipora* spp., *Pocillopora* spp., *Acropora* spp., other live coral, *Turbinaria* spp., *Dictyota* spp., *Halimeda* spp., turf (a mixed filamentous red algal assemblage consisting predominately of *Polysiphonia* spp.), sponge, bare, pavement, sand, coral rubble, and other. For a subset of 45 reefs, the accuracy of visual estimates of percent cover against fixed point contact (FPC) estimates of percent cover (a commonly accepted standard; Floyd & Anderson 1987) was evaluated. Visual estimates of percent cover were 84.8% accurate relative to FPC estimates and include better estimates of rare habitat than FPC (Meese & Tomich 1992). Habitat surveys were conducted between 7 March and 29 April 2005.

On each reef and the surrounding 1 m halo, the identity of all juvenile labroids was recorded and their standard length (SL; to the nearest mm) visually estimated. The substrate directly below each individual at the time it was first observed was also recorded. Juveniles

were defined as individuals <25 mm SL. The accuracy of visual estimates of SL made in the field was evaluated by capturing a subset of fish (n = 298 from 8 different species) and comparing visual estimates of SL for these individuals to SL measured in the lab with callipers. Based on mean absolute error (MAE), visual estimation of SL was 94.7% accurate. Fish surveys were conducted between 08:00 and 16:00 h (peak activity time for diurnal benthic fishes: Galzin 1987) from 27 May to 6 June 2005.

Habitat association for each species was quantified by calculating Manly's alpha (Manly et al. 1972, Chesson 1978). Manly's alpha measures the proportion of a species on a given habitat, relative to the availability of that habitat:

$$\alpha_i = \frac{\dfrac{F_i}{H_i}}{\displaystyle\sum_{i=1}^{n} \dfrac{F_i}{H_i}} \qquad i = 1, \ldots, n \qquad (1)$$

where H is the proportion of surveyed habitat of a given type (i) and F is the proportion of individuals censused on that habitat type. Habitat use (α) was evaluated separately for each species, in each habitat type (1 through n), within a given replicate sampling unit (reef). α ranges between 0 and 1: 0 indicates habitat is never used, 1 indicates habitat is exclusively used, and 1/n indicates random use. Not all habitat types were present on all reefs; therefore, 1/n was reef specific. The frequency of over-association was determined as the proportion of reefs for which $\alpha > 1/n$ (for each species on each habitat type). All reefs for which a focal fish was present were used to calculate the frequency of over-association.

Habitat association was quantified between *Thalassoma hardwicke* and the 7 candidate species by using Bray-Curtis dissimilarity indices to compare mean α values. From the resulting similarity matrix, a dendrogram and non-metric multidimensional scaling (nMDS) were constructed using the vegan package in R 2.7.0 (R Development Core Team 2008).

Identifying *Thalassoma hardwicke* competitors. A field assay was used to identify whether the presence of larger individuals of each of 3 candidate species (*Gomphosus varius*, *Pseudocheilinus hexataenia* and *Thalassoma quinquevittatum*; the 3 species most similar to *T. hardwicke* in terms of habitat use; see 'Results: Surveys of habitat availability and habitat association') negatively effected the survival of transplanted *T. hardwicke*. Within 80 m of the reef crest, 32 reefs were selected. Reefs consisted of a live *Porites* spp. base, surmounted by 1 to 2 *Pocillopora verrucosa* colonies and small patches (<10% surface area) of macroalgae. Reefs had an average area of 5.43 ± 0.34 m², a mean height of 0.77 ± 0.04 m, and

were isolated from their nearest neighbour by 4.71 ± 0.25 m. Of these 32 reefs, 8 were inhabited by 2 to 5 (mean ± SE: 2.8 ± 0.4) *T. quinquevittatum*, 8 reefs by 2 to 5 (3.4 ± 0.4) *G. varius*, and another 8 reefs by 2 to 4 (3 ± 0.3) *P. hexataenia*. The SL of individuals of all candidate species ranged between 12 and 30 mm. All reefs lacked fish of the other species (e.g. reefs with *G. varius* did not have *P. hexataenia* or *T. quinquevittatum*). In addition, 8 reefs lacked *G. varius, P. hexataenia* and *T. quinquevittatum*. All reefs were interspersed with each other within the lagoon. Before the field assay, all resident *T. hardwicke* were removed from all reefs.

Thalassoma hardwicke settlers were collected from reefs ~600 m from the study site using the fish anaesthetic eugenol (clove oil) and hand nets. All fish were held in tanks with running seawater for 12 h, then individually tagged with different colors of visible implant elastomer (VIE) (Northwest Marine Technology) forward of the caudal peduncle. VIE tags are clearly visible 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), have been used to tag fish as small as 8 mm (Frederick 1997), and a preliminary study confirmed no tag-induced mortality of 20 tagged *T. hardwicke* held in aquaria for 72 h. Tagging and handling effects were therefore assumed negligible. After tagging, fish were returned to aerated aquaria for 12 h before being measuring to the nearest 0.1 mm SL. Three tagged *T. hardwicke* individuals (14.8 ± 0.2 mm SL; ~2 wk post-settlement age) were then transplanted onto each reef (which is representative of natural densities). To estimate the survival rates of transplanted individuals, reefs were surveyed daily (~9 a.m.) for 5 d (beginning 1 June 2005). At the same time, the abundance of competitors was recorded and any untagged *T. hardwicke* (2 untagged *T. hardwicke* were removed, both <10 mm) was removed. Neighbouring non-experimental reefs were also searched for tagged immigrant *T. hardwicke*; none were found. Previous research has suggested that recent *T. hardwicke* settlers rarely move between reefs separated by as little as 3 m (Shima 2001b). The disappearance of a tagged fish was therefore assumed to be due to mortality rather than migration. The mean proportion of *T. hardwicke* remaining in each treatment on the last day of the assay was used as the response variable because by the end of the assay, survival trajectories had stabilized (see Fig. 3).

Statistical analysis was conducted using a generalized linear model (GLM) because the response variable was count data modelled as proportions (with unequal variance and non-normally distributed errors:

Crawley 2007). Using a GLM (specifying a binomial error distribution and a logit link function), an analysis of covariance was conducted to estimate *Thalassoma hardwicke* survival. Proportional survival was modelled as a function of treatment, a categorical variable with 4 levels: (1) no competitors present, (2) *Gomphosus varius* present, (3) *Pseudocheilinus hexataenia* present, and (4) *T. quinquevittatum* present. Because reefs varied in size, likelihood ratio tests were used to determine the significance of adding the additional terms of competitor density, the density of transplanted *T. hardwicke*, and the interactions between treatment, competitor density, and the density of transplanted *T. hardwicke* to the model. None of the additional terms significantly contributed to the model (p > 0.1 in all cases); therefore, the results focus on the main effects of treatment only. Data were not overdispersed (residual deviance = 28.414, residual df = 28). Effect sizes were calculated using backtransformed mean proportions from the GLM model.

Influence of larger heterospecifics and structural refuge on the post-settlement survival of *Thalassoma hardwicke*. Results from the field assay identified larger *Thalassoma quinquevittatum* as strongly competing with focal *T. hardwicke*. A factorial experiment was used to evaluate the effect of competition with larger *T. quinquevittatum* and the provisioning of structural refuge on the survival of transplanted *T. hardwicke*. Structural refuge was increased by adding *Turbinaria ornata* (a structurally complex, locally common macroalga) to reefs. The thallus of *T. ornata* consists of a holdfast, a central stipe up to 33 cm in length, with rigid pyramid-shaped blades at its distal end encircled by rows of coarse teeth (Prathep et al. 2007). The spaces between closely packed blades provide cryptic habitat and structural refuge. *T. ornata* is easy to manipulate, and juveniles of both *T. hardwicke* and *T. quinquevittatum* (1) over-associate with *T. ornata* (see Fig. 1); and (2) shelter within the interstitial spaces of blades when threatened (pers. obs.).

A total of 20 reefs were haphazardly selected with an average surface area of 5.46 ± 0.36 m^2, a mean height of 0.79 ± 0.03 m, and isolated from their nearest neighbour by 3.02 ± 0.19 m. All reefs initially had 3 to 5 (mean ± SE: 3.38 ± 0.16) resident *Thalassoma quinquevittatum* (22.1 ± 0.56 mm SL) and lacked *Turbinaria ornata*. The presence/absence of *T. ornata* was crossfactored with the presence/absence of *T. quinquevittatum*, and treatments were randomly assigned to reefs. On reefs assigned to the presence of *T. quinquevittatum*, selective removals were conducted so that each reef had 3 similarly sized *T. quinquevittatum* individuals that were larger than focal *Thalassoma hardwicke* individuals. For *T. ornata* present treatments, whole *T. ornata* plants were attached to recipient reefs with

cable ties so that ~15% of habitat cover was *T. ornata*. Before the experiment, all resident *T. hardwicke* were removed from the reefs.

A total of 3 *Thalassoma hardwicke* individuals (13.69 ± 0.51 mm SL; collected and tagged as per the field assay) were transplanted onto each reef and their survival surveyed daily (~9 a.m.) for 5 d. Each morning, immigrant *T. quinquevittatum* (3 immigrants were observed) and new *T. hardwicke* that had settled the previous night (8 settlers) were removed. Neighbouring non-experimental reefs were also searched for tagged *T. hardwicke* immigrants. No tagged immigrants were found; therefore, the disappearance of a tagged fish was assumed to be due to mortality rather than migration (as for the field assay). Using the same reefs, the experiment was run in 2 temporal blocks (beginning 12 June 2005 and 12 May 2007), yielding 10 replicates (5 in each temporal block) for each of the 4 treatments. The mean proportion of *T. hardwicke* remaining in each treatment on the last day of the experiment was used as the response variable because by the end of each experimental run, survival trajectories had stabilized (see Fig. 4).

Using a GLM, a factorial analysis of covariance (specifying a binomial error distribution and a logit link function) was used to model survival of *Thalassoma hardwicke* after 5 d against the presence and absence of both *T. quinquevittatum* and *Turbinaria ornata.* The full model included 4 explanatory variables: (1) *T. quinquevittatum* (present/absent), (2) *T. ornata* (present/absent), (3) run (2005/2007: a term for temporal block), and (4) reef area (continuous). Likelihood ratio tests were used to determine the significance of adding the additional terms of reef area, run (2005/2007: a term for temporal block), and the interactions between *T. quinquevittatum, T. ornata,* reef area and run. None of the additional terms significantly contributed to the model (p > 0.1 in all cases); therefore, results focus on the main effects of *T. quinquevittatum* and *T. ornata* only. Data were not overdispersed (residual deviance = 29.445, df = 37). Effect sizes were calculated using backtransformed mean proportions from the reduced GLM.

All statistical analyses were conducted in R 2.7.0 (R Development Core Team 2008).

RESULTS

Surveys of habitat availability and habitat association

Focal species were observed on 11 of 16 habitat categories (no fish were enumerated in the categories other, other coral, *Dictyota* spp., *Halimeda* spp., or sponge). While most species (7 of 8) over-associated with the highly rugose coral *Porites rus* (Fig. 1), strong associations with other habitat types differed among species. *Thalassoma hardwicke, T. quinquevittatum, Gomphosus varius* and *Pseudocheilinus hexataenia* were more similar in habitat association with one another (associating more with branching & massive corals and macroalgae) than they were with *Stethojulis bandanensis, Scarus sordidus, Halichoeres hortulanus* and *H. trimaculatus* (Fig. 2), which as a group showed stronger associations with macroalgae, rubble and sand (Fig. 1). *T. quinquevittatum* was the species most similar to *T. hardwicke* in habitat association, with both species over-associating with *P. rus, Pocillopora* spp. and *Turbinaria ornata* on more than 30% of reefs (Table 2).

Identifying *Thalassoma hardwicke* competitors

Mortality of transplanted *Thalassoma hardwicke* was greatest in the first 3 d, after which survival stabilized (Fig. 3A). Relative to controls, mean survival of *T. hardwicke* was lower in the presence of each of the potential competitor species; however, larger *T. quinquevittatum* produced the only statistically significant negative effect (Table 3). Survival of *T. hardwicke* ranged from 8% (SE = 5) in the presence of *T. quinquevittatum* to 50% (SE = 9) in the control treatment (Fig. 3B); thus, survival of *T. hardwicke* was on average 6 times greater in controls than treatments with larger *T. quinquevittatum* competitors (p = 0.004; Table 3; Fig. 3B).

Influence of larger heterospecifics and structural refuge on the post-settlement survival of *Thalassoma hardwicke*

Competitive effects occurred rapidly and then stabilized after 3 d (Fig. 4A). Survival of *Thalassoma hardwicke* ranged between 3% (SE = 3) when larger *T. quinquevittatum* were present and *Turbinaria ornata* absent, and 37% (SE = 8) when larger *T. quinquevittatum* were absent and *T. ornata* present (Fig. 4B). The minimum adequate GLM included the main effects of *T. quinquevittatum* and *T. ornata* only (Table 4). Survival of *T. hardwicke* was 2.3 times greater in treatments without larger *T. quinquevittatum* competitors relative to those with larger *T. quinquevittatum* competitors (p = 0.036; Table 4) and 2.8 times greater in treatments with *T. ornata* relative to treatments without *T. ornata* (p = 0.012; Table 4). The effects of structural refuge were therefore greater than the effects of larger competitors (the ratio of the effects of structural refuge to competitive effects was 1.24).
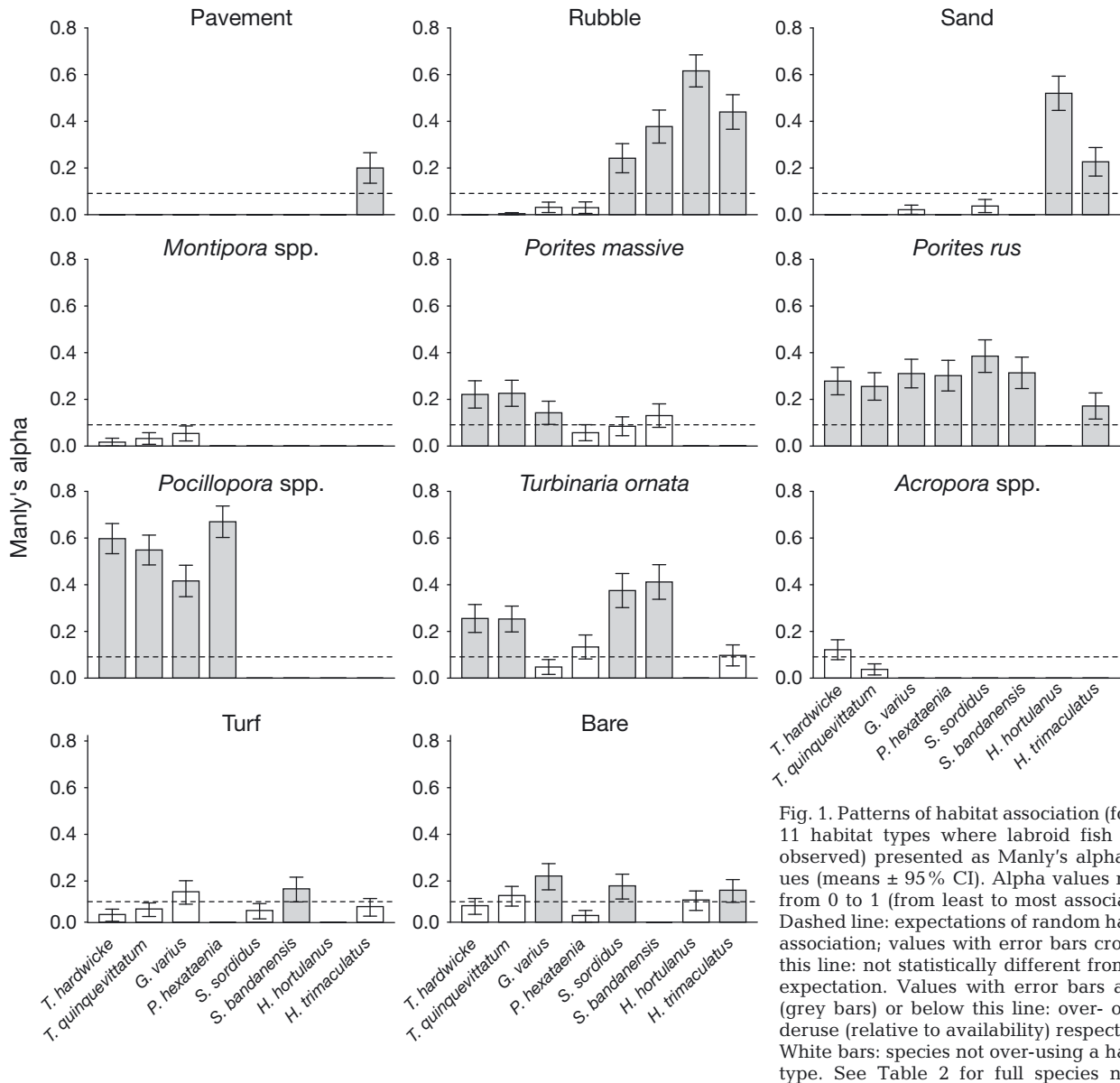
Fig. 1. Patterns of habitat association (for the 11 habitat types where labroid fish were observed) presented as Manly's alpha values (means ± 95% CI). Alpha values range from 0 to 1 (from least to most associated). Dashed line: expectations of random habitat association; values with error bars crossing this line: not statistically different from this expectation. Values with error bars above (grey bars) or below this line: over- or underuse (relative to availability) respectively. White bars: species not over-using a habitat type. See Table 2 for full species names

Table 2. Proportion of reefs where each species occurred with Manly's alpha values greater than expected under conditions of random association (calculated: 1/number of available habitats). Reefs total number given within (). Note: the 2 measures are not directly comparable

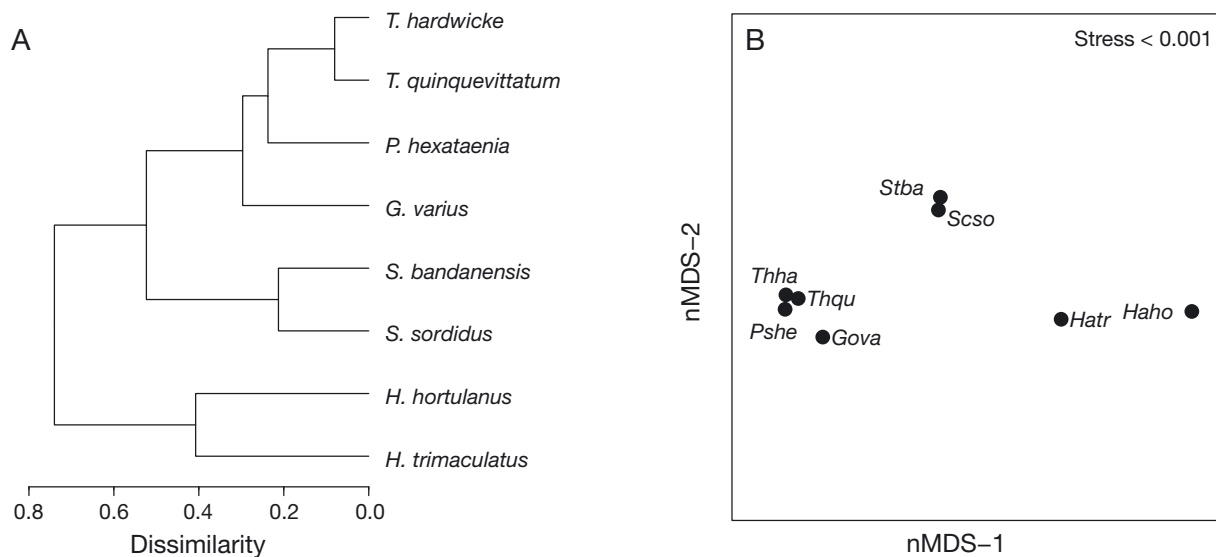| Substrate	Thalassoma hardwicke	Thalassoma quinquevittatum	Gomphosus varius	Pseudocheilinus hexataenia	Scarus sordidus	Stethojulis bandanensis	Halichoeres hortulanus	Halichoeres trimaculatus
Porites massive	0.229 (118)	0.273 (88)	0.143 (49)	0.057 (35)	0.080 (25)	0.130 (23)	0.000 (9)	0.000 (25)
Porites rus	0.364 (66)	0.308 (39)	0.414 (29)	0.346 (26)	0.400 (20)	0.364 (11)	0.000 (5)	0.176 (17)
Montipora spp.	0.025 (81)	0.036 (56)	0.059 (34)	0.000 (23)	0.000 (9)	0.000 (11)	0.000 (6)	0.000 (16)
Pocillopora spp.	0.688 (80)	0.635 (63)	0.500 (40)	0.697 (33)	0.000 (12)	0.000 (14)	0.000 (8)	0.000 (14)
Acropora spp.	0.192 (26)	0.053 (19)	0.000 (14)	0.000 (13)	0.000 (5)	0.000 (5)	0.000 (4)	0.000 (4)
Turf	0.032 (62)	0.103 (29)	0.130 (23)	0.000 (21)	0.050 (20)	0.143 (14)	0.000 (3)	0.067 (15)
Turbinaria ornata	0.302 (63)	0.351 (37)	0.048 (21)	0.133 (15)	0.375 (16)	0.412 (17)	0.000 (2)	0.100 (10)
Bare	0.105 (114)	0.141 (85)	0.213 (47)	0.029 (35)	0.160 (25)	0.000 (22)	0.111 (9)	0.143 (21)
Sand	0.000 (108)	0.000 (55)	0.025 (40)	0.000 (30)	0.037 (27)	0.000 (22)	0.600 (5)	0.261 (23)
Rubble	0.000 (100)	0.013 (76)	0.068 (44)	0.029 (35)	0.269 (26)	0.400 (20)	0.778 (9)	0.440 (25)
Pavement	0.000 (34)	0.000 (34)	0.000 (15)	0.000 (7)	0.000 (5)	0.000 (11)	0.000 (5)	0.200 (5)

Fig. 2. Interspecific similarities in resource use presented as: (A) a dendrogram, and (B) non-metric multidimensional scaling (nMDS). Both representations are based upon Bray-Curtis dissimilarity matrices, calculated from mean Manly's alpha values. Gova: *Gomphosus varius*, Haho: *Halichoeres hortulanus*, Hatr: *H. trimaculatus*, Pshe: *Pseudocheilinus hexataenia*, Scso: *Scarus sordidus*, Stba: *Stethojulis bandanensis*, Thha: *Thalassoma hardwicke*, and Thqu: *T. quinquevittatum*
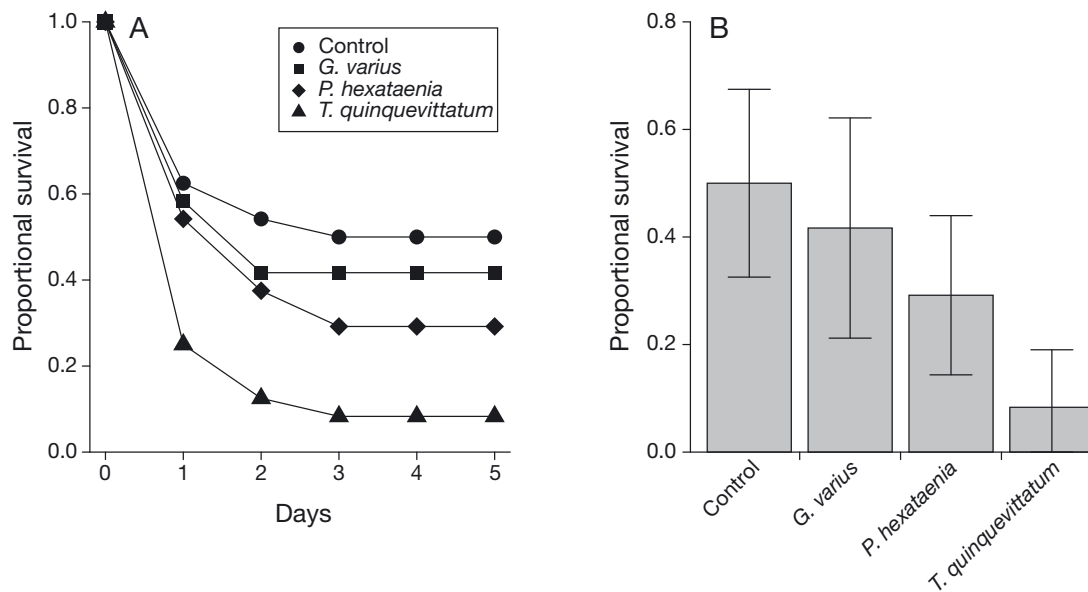

Fig. 3. *Thalassoma hardwicke*. Observed proportional survival in a field assay. *T. hardwicke* settlers were introduced to reefs with 1 of 4 competitor treatments: larger *Gomphosus varius* present; larger *Pseudocheilinus hexataenia* present; larger *T. quinquevittatum* present; or Control (all 3 competitors absent). (A) Survival trajectories of *T. hardwicke* over the 5 d the assay ran (error bars omitted for clarity). (B) Proportional survival (means ± 95% CI) of *T. hardwicke* on Day 5 of the assay. n = 8 sites per treatment

DISCUSSION

The importance of interspecific competition in structuring marine communities is well recognized (e.g. Byers 2000, McCook et al. 2001, Munday et al. 2001, Connell et al. 2004, Turra & Denadai 2004, Lopez-Victoria et al. 2006, Gagern et al. 2008); however, attributes of the current environment may influence the intensity of interspecific competition. For instance, structural refuge is generally expected to mitigate the negative effects of competition (Holt 1987, Beukers & Jones 1998, Almany 2004a,b). In the current study, *Thalassoma hardwicke* showed selectivity for complex habitats, which provided structural refuge. Cross-factoring the presence and absence of *Turbinaria ornata* (structural refuge: a beneficial effect) with the pres-

Table 3. *Thalassoma hardwicke*. Generalized linear model results (specifying a binomial distribution and logit link function) modelling survival of *T. hardwicke* against the presence of larger competitors: 4 levels; Control (no competitors), *Gomphosus varius*, *Pseudocheilinus hexataenia* and *T. quinquevittatum* (n = 8 per treatment). Values in **bold** are significant at p < 0.05

	Estimate	SE	z-value	p
Intercept	0.000	0.408	0.000	1.000
G. varius	−0.337	0.582	−0.579	0.563
P. hexataenia	−0.887	0.607	−1.462	0.144
T. quinquevittatum	−2.398	0.844	−2.842	**0.004**

Table 4. *Thalassoma hardwicke*. Best fitting generalized linear model results (specifying a binomial distribution and logit link function) modelling proportional survival of *T. hardwicke* vs. the presence and absence of larger *T. quinquevittatum* (competitor: deleterious effect) and *Turbinaria ornata* (structural refuge: beneficial effect). Proportional survival is documented for 2 temporal blocks (June 2005, May 2007). n = 5 sites per treatment and block. Blocking term and interaction were non-significant; therefore, focus is on the main effects of *T. quinquevittatum* and *T. ornata*. Values in **bold** are significant at p < 0.05

	Estimate	SE	z-value	p
Intercept	−1.774	0.461	−3.850	**<0.001**
T. quinquevittatum (present)	−1.072	0.512	−2.095	**0.036**
Turbinaria ornata (present)	1.319	0.528	2.500	**0.012**

ence and absence of larger *T. quinquevittatum* (competitor: a deleterious effect) produced additive effects. *Thalassoma hardwicke* survival significantly increased in the presence of *T. ornata* and significantly decreased in the presence of larger *T. quinquevittatum*. These results suggest that post-settlement survival of *T. hardwicke* will be greatest when structural refuge is present and larger competitors are absent, lowest when structural refuge is absent and larger competitors are present, and, in the presence of larger competitors, survival would be greatest when structural refuge is also present.

Classic competition theory suggests that competitive exclusion and niche diversification will lead to resource partitioning between species (Colwell & Fuentes 1975, Diamond 1978). Similar habitat associations between *Thalassoma hardwicke*, *Gomphosus varius*, *Pseudocheilinus hexataenia* and *T. quinquevittatum* suggest that juveniles of these species do not

partition habitat. If niche models apply to this system, resource partitioning must therefore involve other resources (e.g. the differentiation of food resources, enemies or habitat use). Alternatively, similar habitat associations may be evidence that functional equivalence is more important than functional differences, with random variation in births, deaths and dispersal driving the population dynamics of these species (e.g. Bell 2000, Hubbell 2001, Chave 2004, Leibold & McPeek 2006, Adler et al. 2007).

Previous studies have demonstrated that aggressive interactions between reef fishes can increase a subordinate's exposure to predators via displacement from refuge habitat (Carr et al. 2002, Holbrook & Schmitt 2002, Almany 2003). Additionally, agonistic behav-
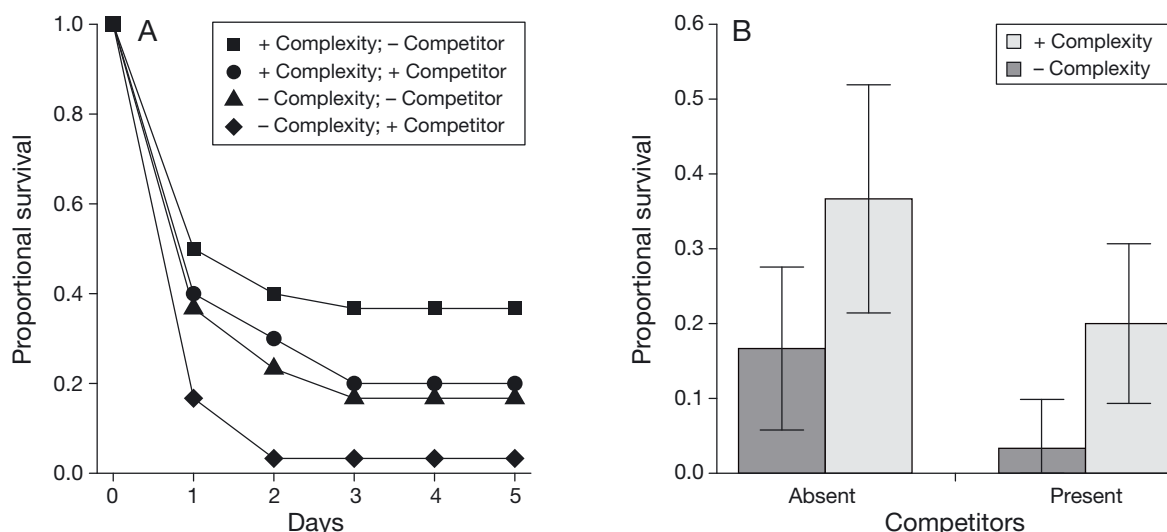

Fig. 4. *Thalassoma hardwicke*. Proportional survival in the presence or absence of larger *T. quinquevittatum* (competitor: deleterious effect) and *Turbinaria ornata* (structural refuge: beneficial effect). (A) Survival trajectories of *T. hardwicke* over the 5 d the experiment ran (error bars omitted for clarity). (B) Proportional survival (means ± 95% CI) of *T. hardwicke* on Day 5 of the experiment. n = 10 replicates per treatment. Proportional survival is pooled over 2 temporal blocks (June 2005, May 2007)

iours (e.g. posturing and chases) may attract the attention of predators (e.g. Elkin & Baker 2000) and/or be inversely proportional to vigilance, both of which may reduce survival. For example, Geange & Stier (2009) demonstrated that chases and fin bites by prior resident *Thalassoma quinquevittatum* forced subordinate *T. hardwicke* out of structural refuge (*Pocillopora verrucosa*), with the overall effect being a reduction in *T. hardwicke* survival. In the present study, which examined a broader suite of species, the effects of prior residents were species-specific. The presence of *Gomphosus varius* and *Pseudocheilinus hexataenia* did not significantly affect the survival of *T. hardwicke*, while survival was 2.3 times less when *T. quinquevittatum* was present. However, because competitors were not randomly assigned to replicate reefs (rather, replicates on which potential competitors naturally occurred were used), reef-specific effects (e.g. lack of suitable habitat for the focal species or spatial variation in predation pressure) could also drive these patterns. Additionally, competitors used in this study were older and larger than focal individuals. Because small age and/or size differences can have large impacts on competitive dominance hierarchies (Webster 2004, Wilson 2005, Samhouri et al. 2009), changes in the size of competitors relative to focal individuals (e.g. due to priority effects) may alter the magnitude and direction of competitive effects.

Increased survival of *Thalassoma hardwicke* in the presence of *Turbinaria ornata* suggests structural refuge was a limiting resource. Increasing the availability of limiting resources is expected to alleviate the deleterious effects of resource competition. Here, the effects of interspecific competition and habitat availability were additive, not interactive, suggesting the competitive effects of larger *T. quinquevittatum* occurred independently of the availability of appropriate *T. ornata* habitat. Competition may have either occurred for other limited resources (e.g. food), or independently of resources altogether (e.g. during the establishment of social dominance hierarchies). Many reef fishes are social and form mixed-species groups (Lukoschek & McCormick 2000). The establishment of social dominance hierarchies within groups may begin in early juvenile stages, with the relative position within social hierarchies, not resource availability, dictating resource access. This suggests the effect of increasing resource availability will vary according to group social structure. For groups where social dominance hierarchies do not occur, increasing the availability of limiting resources is likely to mitigate the negative effects of competition because all individuals have equal resource access. For groups of individuals where social dominance hierarchies are prevalent, increasing resource availability is unlikely to mitigate

the negative effects of competition because competitive interactions occur independently of resources. In this study, both *T. hardwicke* and *T. quinquevittatum* formed mixed species groups on patch reefs, with intense social interactions determining resource access (Geange & Stier 2009). Therefore, if competitive interactions were driven primarily by assimilation into existing social hierarchies rather than the provisioning of structural refuge, increasing the availability of structural refuge would unlikely mitigate the negative effects of competition.

The establishment of dominance hierarchies between larger resident *Thalassoma quinquevittatum* and transplanted *T. hardwicke* may also explain the rapid occurrence of competitive effects after transplantation. When individuals enter a community, they come into contact with prior residents and must integrate into established dominance hierarchies. The steep drop in survival immediately following transplantation may reflect intense aggressive interactions during the assimilation of transplanted individuals, with survival trajectories stabilizing once social dominance hierarchies have been re-established. Although this study does not provide behavioural data to validate this interpretation, some support exists in the use of transplanted individuals that were ~2 wk post-settlement and therefore likely had previous experience with competitors (including *Gomphosus varius, Pseudocheilinus hexataenia* and *T. quinquevittatum* given their ubiquity). The steep drop in survival suggests that experiences with specific reefs or dominance hierarchies rather than experience with competitors per-se is an important determinant of post-settlement survival.

Like Bonin et al. (2009), this study found (1) both competitive interactions and structural refuge can influence survival in reef fishes, and (2) the effects of structural refuge and competition were additive not interactive. In both of these studies, reef fishes form social groups, with competitive hierarchies potentially forming when relative position within the group determines resource access. This suggests that the lack of expected interactions between the availability of structural refuge and the presence of competitors may result from social interactions occurring independently of resource availability. If this is the case, it has important implications for ecologists attempting to evaluate the influence of resource limitation on the strength of competition, suggesting it is not only important to quantify resource limitation, but to also identify how individuals interact with one another independently of resources. Further work is needed to quantify the interplay between competition, resource availability and social hierarchies in reef fishes.

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