



FEATURE ARTICLE

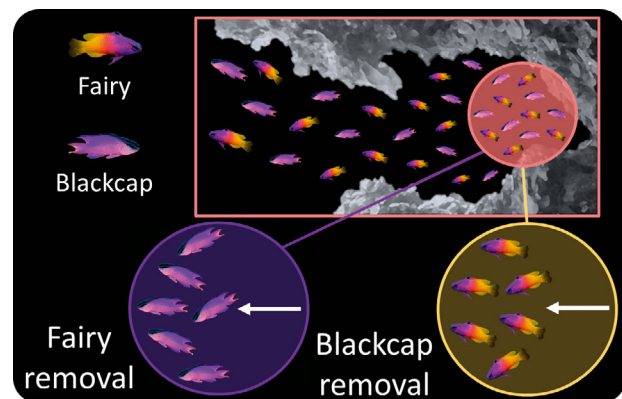
Symmetrical effects of interspecific competition on congeneric coral-reef fishes

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ABSTRACT: Zonation in marine fishes occurs along depth gradients in both temperate and tropical habitats, yet the importance of competition in causing these patterns has only been unequivocally demonstrated in temperate systems. Throughout Caribbean reefs, fairy basslets *Gramma loreto* and blackcap basslets *G. melacara* are segregated by depth with a narrow zone of overlap. Local populations of these planktivores are found under isolated reef ledges, where fairy basslets compete with conspecifics for access to prime feeding positions at the outer edges. I investigated the existence, mechanisms, and effects of interspecific competition on the local distribution and demography of basslets. I documented aggression and feeding rates of both species and conducted a reciprocal removal experiment comparing the response of each basslet in competitor-removal versus unmanipulated populations of both species. Positioning of both basslets under ledges was consistent with an overall size hierarchy, with larger fish progressively closer to the outer edges of ledges. Fairy basslets were more aggressive, yet competition had symmetrical effects on the juveniles of both species. Interference between species drove juveniles further back under ledges, where feeding and growth rates of individuals were reduced. Competition had no effect on the density of basslets during this 8 wk experiment. Aggression occurred between larger basslets, but with no consequential effects on any parameters measured. This study demonstrates symmetrical effects of interspecific competition on juvenile coral-reef fishes, a phenomenon that has rarely been documented previously.

KEY WORDS: Species interaction · Interference interaction · Distribution · Size hierarchy · Zonation · Basslets · *Gramma loreto* · *Gramma melacara*



Response of fairy and blackcap basslets (*Gramma loreto* and *G. melacara*, respectively) in competitor-removal (lower) versus control populations (upper right). Following removals, juveniles of each species shift toward the front of reef ledges where individual feeding and growth rates are enhanced.

Diagram: Tye L. Kindinger

INTRODUCTION

Distinct patterns of community structure occur universally in species along environmental gradients, and this zonation is determined by both abiotic and biotic mechanisms. For example, striking zonation on rocky intertidal shores (Stephenson & Stephenson 1972) is driven simultaneously by a combination of competition and predation, and physical factors (Connell 1975). Competition is a fundamental process that often drives patterns of abundance and distribution (Connell 1983, Schoener 1983, Gurevitch et al. 1992), thereby influencing zonation in terrestrial and aquatic systems (e.g. Connell 1961, Hairston 1980, Lubchenco 1980, Neet & Hausser 1990, Bertness 1991, Wilson & Tilman 1991).

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Vertical zonation in marine fishes often occurs along a depth gradient throughout subtidal regions and beyond, and has been described in temperate habitats such as rocky reefs and kelp beds (Stephens et al. 2006), as well as throughout tropical coral reefs (Williams 1991). Large-scale manipulations consisting of reciprocal removals of entire populations of potential competitors in temperate systems have unequivocally demonstrated the importance of interspecific competition in causing such bathymetric zonation of fishes (Hixon 1980, Larson 1980, Holbrook & Schmitt 1986). In contrast to temperate systems, and although a growing number of studies have explored competition in coral-reef fishes (Bonin et al. 2015, Forrester 2015), the importance of interspecific competition in causing patterns in the local distribution of these fishes has seldom been demonstrated experimentally (but see Robertson & Gaines 1986, Robertson 1996).

Fairy basslets *Gramma loreto* and blackcap basslets *G. melacara* are small coral-reef fishes (8–10 cm maximum size) which are commonly found under reef ledges (rock overhangs) where individuals shelter in cracks and holes, and which feed primarily on the same suite of passing copepods and other zooplankton (Böhlke & Randall 1963). Throughout reefs of the greater Caribbean region, these congeners are segregated by depth, with a narrow zone of overlap: greater abundances of fairy basslets are observed in shallower water (1–30 m), and blackcap basslets increase in abundance in deeper water (30–180 m), where the abundance of fairy basslets diminishes (Starck et al. 1978). Böhlke & Randall (1963) described these species as being syntopic (occupying the same ledges) at intermediate depths ranging from 30 to 50 m, which encompasses depths that are not logistically conducive for performing manipulative experiments with SCUBA. Recently, however, syntopic populations were observed in The Bahamas at depths as shallow as 9 m (T. Kindinger pers. obs.), providing a unique opportunity to test for competition between these species by means of controlled field experiments. While populations of blackcap basslets in isolation from fairy basslets remain too deep (>40 m) to definitively test for the causes of zonation (sensu Hixon 1980, Larson 1980, Holbrook & Schmitt 1986), investigating the existence and mechanisms of competition within the zone of overlap can determine the drivers of abundance and distribution in basslets at the scale of local populations under reef ledges.

Tagging of individuals in previous studies (Webster & Hixon 2000, Webster 2003, 2004) and during the present study (described in 'Materials and methods:

Reciprocal removal experiment') indicate that both species have extremely high site fidelity with negligible immigration and emigration among ledges. Therefore, each reef ledge that is spatially isolated contains an independent local population of basslets. Within these local populations, intraspecific competition of fairy basslets has been well-documented as being based on a size hierarchy, in which larger individuals maintain positions closer to the front of ledges by aggressively chasing smaller individuals that encroach on their positions (Webster & Hixon 2000, Webster 2004). Positions closer to the front of ledges are simultaneously more conducive to higher feeding rates on passing plankton (Webster & Hixon 2000) and overlap less frequently with resident predators that are typically positioned at the back of ledges (Webster 2004). Given this understanding of within-species competition, I hypothesized that interspecific competition via aggression influences the local distribution, growth, and density of fairy and blackcap basslets where these fishes co-occur under reef ledges.

To test this hypothesis, I first observed local populations of basslets within the zone of overlap and characterized fish behavior under ledges where the species co-occur. I predicted that (1) if interference competition exists between basslets, then interspecific aggression should be evident. I then performed a reciprocal removal experiment to compare the response of each species in the presence versus the absence of the potential competitor. I predicted that (2) if interspecific competition affects both basslets, then each species should exhibit in the manipulated absence (versus presence) of the competitor (a) a shift in local distribution closer to the front of ledges, where they will have (b) higher feeding rates, (c) higher individual growth rates, and (d) increases in density.

MATERIALS AND METHODS

Basslet behavior

During July and August of 2013, I observed the behavior of fairy and blackcap basslets in local populations under reef ledges within the depth zone inhabited by both species (hereafter, zone of overlap). Populations were located within 2 isolated, large reefs (322 and 533 m²) surrounded by sand off the southwest end of Eleuthera, The Bahamas (24°48'23" N, 76°20'41" W), where I maintained native fish communities by regularly removing invasive lionfish (weekly) with hand nets and pole spears. I selected 3 local populations in each reef (n = 6 populations total,

Table S1A in the Supplement at www.int-res.com/articles/suppl/m555p001_supp.pdf) that were located under ledges varying in surface area from 0.90 to 9.99 m² (sum of area of overhang and area of back wall). Initial densities of fairy and blackcap basslets based on direct counts ranged from 2.30 to 13.3 and 0.21 to 11.1 fish m⁻², respectively.

Aggression

To quantify any interference competition between basslets, I observed aggressive chases by filming each local population ($n = 6$) with a digital video camera in an underwater housing for 4 min at a time, ensuring all individuals within each population were simultaneously filmed. Because the activity levels of planktivorous fishes can vary throughout the day with shifts in food availability and predation risk (Hobson 1991), I filmed every population twice during each of 3 times of day: dawn (06:08–06:50 h, or 37–83 min post-sunrise); midday (11:59–16:24 h); and dusk (18:15–20:00 h, or 8 min before through 60 min after sunset). From the video footage, I counted and characterized each chase that occurred between basslets by the respective species and sizes (total length, TL) of the aggressor and recipient. To test whether the role of basslets in observed chases differs between species, I calculated the relative frequency in which each fish was an aggressor versus recipient. Within each role, I also tested whether each fish chased (aggressor) and/or was chased (recipient) more often by heterospecifics than by conspecifics.

Prior to statistical analyses of these response variables, I accounted for variance in density of basslets among local populations, which could potentially influence the likelihood of individual fish encountering each other. Therefore, I divided the response of each focal basslet by the proportional density of the interacting species (density of interacting basslet/total density of basslets in population). I performed statistical analyses (see 'Statistical analyses') of the response of each basslet species (separately), testing for a relationship between the relative frequency of chases and the size class of fish (2 cm: 1.5–2.0 cm; 3 cm: 2.5–3.0 cm; 4 cm: 3.5–4.0 cm; 5 cm: 4.5–5.0 cm), time of day (dawn, midday, dusk), and/or role of basslets (aggressor or recipient). Similarly, I tested whether the number of chases involving each species (separately) as aggressors was correlated with the size of the aggressor ('agg size'), species of the recipient ('rec species'), and/or time of day. I repeated this process to test for a relationship between the number

of chases in which fish were recipients and the size of the recipient ('rec size'), species of the aggressor ('agg species'), and/or time of day.

Feeding rate

To determine the importance of positioning under ledges for acquiring planktonic food, I observed the feeding rate of basslets in the 6 local populations during the same dives conducted to measure aggression (twice per local population during each of 3 times of day). Following the methods of Webster & Hixon (2000), I visually divided each ledge into 4 equal positions from back to front (ledge widths ranged from 0.45 to 1.7 m). In each position (back, midback, midfront, and front), I selected one 2.0–2.5 cm fish and counted *in situ* the number of feeding bites observed in 1 min, repeating this process with individuals of both species. If a fish within the size range was not present within a ledge position, I counted the bites of the nearest fish of the focal size. I converted counts to rates (number of feeding bites in 60 s) and tested for a relationship between feeding rates and categorical variables, ledge position, time of day (dawn, midday, or dusk), and/or species (fairy or blackcap basslet).

Reciprocal removal experiment

Throughout the summer months of 2014 (June to August), I tested for effects of interspecific competition on fairy and blackcap basslets in local populations within the zone of overlap via a reciprocal removal experiment. In each of 3 isolated, large reefs (344–1023 m²) off the southwest end of Eleuthera, The Bahamas, I selected 3 populations of co-occurring basslets (Table S1B). Ledges were located within a limited depth range of 13.4 to 15.8 m, and initial densities of fairy and blackcap basslet ranged from 2.37 to 12.6 and 0.84 to 11.1 fish m⁻², respectively.

Following baseline censuses of these populations (detailed methods in the following subsections), I performed controlled reciprocal removals of each species, resulting in 3 treatments per reef: (1) unmanipulated populations of both species (control); (2) removal of fairy basslets, leaving blackcap basslets (fairy removal); and (3) removal of blackcap basslets, leaving fairy basslets (blackcap removal). Every week, I maintained these basslet treatments by removing fish with small aquarium hand nets and the fish anesthetic quinaldine. I also performed weekly

removals of invasive lionfish with hand nets and pole spears to maintain native fish communities on reefs containing experimental populations.

Ledge position

To test for an effect of interspecific competition on the distribution of basslets under ledges, I performed baseline and weekly censuses during pre- and post-manipulation (respectively) of potential competitors for a total of 9 wk. Censuses of each population ($n = 9$ populations in total) consisted of mapping the ledge position and visually estimating the TL of every fish. Following the methods of Webster & Hixon (2000), I used these maps to measure the absolute ledge position of each fish (distance between fish and the front of ledge) and then standardized these values by the size of each respective ledge, resulting in relative ledge positions: $1 - (\text{absolute position}/\text{ledge depth})$. Relative ledge positions ranged from 0 to 1, indicating positions from back to front, respectively.

For each local population, I calculated a single mean value of the relative ledge position per size class (2, 3, 4, and 5 cm) of fairy and blackcap basslets (separately) during each week of observation. These measures were then converted to the weekly change in ledge position from baseline values ($\text{position}_{\text{week}(t)} - \text{position}_{\text{week}(0)}$), where t is the week number (0–8). For each species, I analyzed the change in ledge position by size class (2, 3, 4, and 5 cm), testing whether the response differed through time and/or between basslet treatments ('comp,' basslet-removal versus unmanipulated control).

Growth rate

I used a mark–recapture method to test for an effect of interspecific competition on the growth of basslets. In all 9 local populations, I captured the smallest fish possible (mean initial TL \pm SEM: fairy basslet, 2.24 ± 0.05 cm; blackcap basslet, 2.34 ± 0.05 cm) using small aquarium hand nets and the fish anesthetic quinaldine. Prior to the release of each fish, I measured the TL to the nearest mm and injected a unique visible tag of fluorescent elastomer (Frederick 1997). Fish were recaptured and measured after about 1 mo (31–36 d, July to August). Growth rates of individuals were calculated by dividing the change in TL by the number of days between initial and final measurements. I also accounted for variance in density among populations that could potentially influence the

ability of individuals to access resources by dividing each growth rate by the mean density of basslets in each respective population during the interval of time each fish was observed. Growth rates of fairy basslet were compared between blackcap-removal and control populations ($n = 15$ and 19 fish, respectively), and growth rates of blackcap basslets were compared between fairy-removal and control populations ($n = 18$ and 11 fish, respectively).

Population density

In The Bahamas, population densities of fairy basslets peak in late summer as individuals recruit to reefs (Webster 2003). To test for an effect of interspecific competition on the local density of basslets, I calculated the weekly density of 2, 3, 4, and 5 cm size classes of each species from censuses of local populations ($n = 9$ populations). These measures were converted to the weekly changes from baseline values ($\text{density}_{\text{week}(t)} - \text{density}_{\text{week}(0)}$). Within each species, the response was analyzed by size class, testing whether the change in density differed through time and/or between basslet-removal versus unmanipulated control populations ('comp').

Statistical analyses

All statistical analyses were performed by fitting linear mixed effects models to account for the spatial nesting of ledges (local basslet populations) within reefs. Full models were fitted for each response variable with the respective fixed effects as described above, and ledge nested within reef as random effects (Pinheiro & Bates 2000, Bolker et al. 2009, Zuur et al. 2009). All fixed effects were categorical variables (including time), because I had no *a priori* reason to assume any linear relationships with response variables.

When visual examination of residuals indicated a violation of normality in any model, I log-transformed the response. Full models included weighted terms that allowed variances to differ among reefs and AR1 structures in models with the fixed effect, time, to further account for temporal autocorrelation. Full and reduced models (with versus without weighted terms and/or AR1 structures) were then fitted using restricted maximum likelihood (REML) and compared using Akaike's information criterion (AIC) and likelihood ratio tests (LRTs). Best-fit models met all assumptions of normality, homogeneity, and independence based on visual examination of model residuals.

The significance of fixed effects was assessed using LRTs of these models refitted using maximum likelihood estimation (Zuur et al. 2009), and any variables that were not significant were sequentially dropped from the model. Final models were refitted using REML in order to calculate effect sizes and parameter estimates. If LRTs indicated a significant interaction between 2 fixed effects, I performed multiple comparisons and adjusted all p-values of linear contrasts to maintain an approximate 5% family-wise error rate (Hothorn et al. 2008). All statistical analyses were conducted using the statistical software R version 3.1.2 (R Core Team 2014) with the associated packages *nlme* (Pinheiro et al. 2014, version 3.1-118) and *multcomp* (Hothorn et al. 2008, version 1.3-7).

RESULTS

Basslet behavior

Aggression

Basslets of all sizes aggressively chased each other, but overall, fairy basslets were more aggressive than blackcap basslets. From a total of 144 min of video footage, I observed fairy basslets chasing other individuals a total of 356 times: 303 times chasing fairy basslets and 53 times chasing blackcap basslets. In contrast, blackcap basslets chased a total of 80 individuals during the same video footage: 60 blackcap and 20 fairy basslets. In almost every instance of aggression, basslets chased individuals that were equal or smaller in size, with the exception of 5 chases in which 2 cm fairy aggressors chased 3 cm ($n = 3$) and 4 cm ($n = 2$) blackcap recipients.

In chases between basslets, the relative frequency of roles was different in each species (Table S2 in the Supplement, Fig. 1, fairy basslet: role LRT, $p = 0.002$; blackcap basslet: role LRT $p = 0.034$), in which fairy basslets were aggressors $95.8 \pm 4.22\%$ (SEM) of the time (aggressor vs. recipient: 0.96 ± 0.31 chases, $p = 0.002$) and blackcap basslets were recipients $95.4 \pm 4.15\%$ of the time (recipient vs. aggressor: 0.95 ± 0.02 chases, $p = 0.034$). Fairy aggressors chased both species with similar frequency, with no significant difference in the number of chases directed at fairy versus blackcap recipients (Table S3 in the Supplement, Fig. 2A). However, the recipient species of blackcap aggression did significantly differ (Table S3, Fig. 2B): blackcap aggressors chased conspecifics $42.7 \pm 4.95\%$ (0.56 ± 0.18 interactions) more frequently than heterospecifics.

Whether fairy basslets were chased was related to the size of the fairy recipient and the species of the aggressor (rec size \times agg species LRT, $p < 0.001$). All but 5 cm fairy recipients were chased significantly more by fairy than blackcap aggressors, and both species rarely chased 5 cm individuals (Table S3, Fig. 2C). In contrast, blackcap basslets of all sizes were chased by both species, with no significant difference in the number of chases between aggressor species (Table S3, Fig. 2D).

Feeding rate

Feeding rates of 2.0–2.5 cm individuals did not significantly differ between fairy and blackcap basslets (Table S4A & Fig. S1 in the Supplement), but were related to the positioning of basslets under ledges. The interaction between ledge position and time of day (LRT, $p = 0.026$) was correlated with feeding

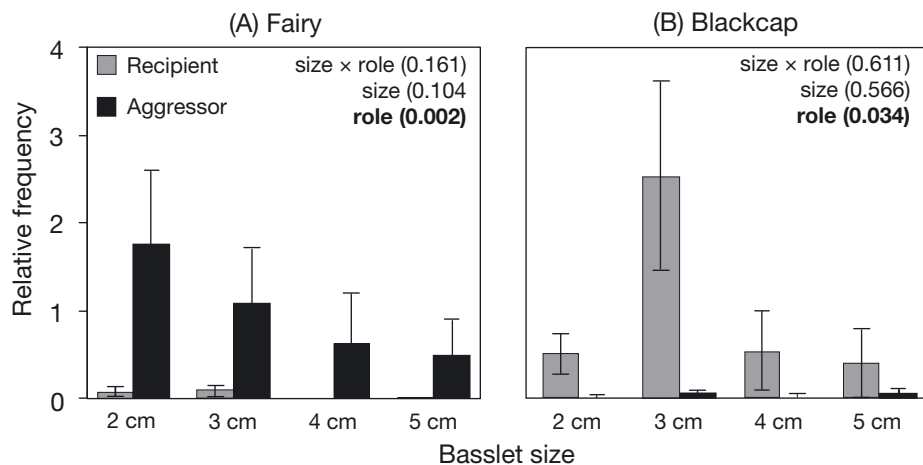


Fig. 1. Relative frequency in which 2, 3, 4, and 5 cm size classes of (A) fairy basslets *Gramma loreto* and (B) blackcap basslets *G. melacara* were aggressors versus recipients ('role') in chases between species observed in local populations of both basslets ($n = 6$ populations). Shading of bars represents the role of fish; error bars are SEM. Results of likelihood ratio tests are shown in the upper right of each plot, and variables with significant correlations and p-values are in **bold**

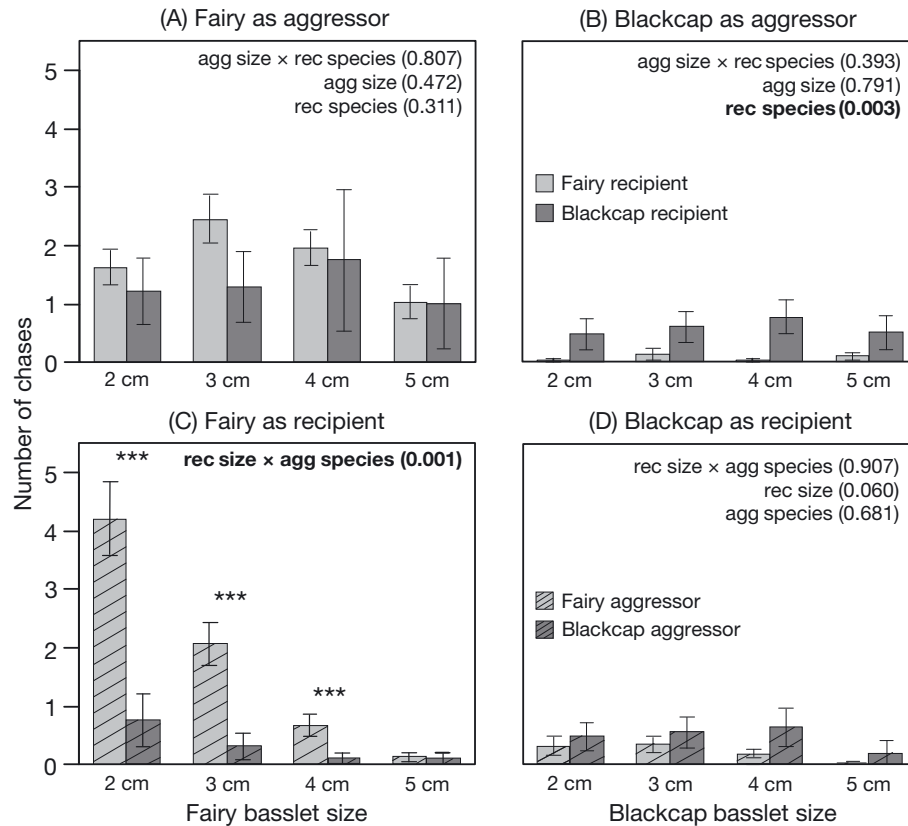


Fig. 2. Number of instances in which (A,C) fairy basslets *Gramma loreto* and (B,D) blackcap basslets *G. melacara* chased ('agg'; A,B, solid bars) and were chased ('rec'; C,D, striped bars) by 2, 3, 4, and 5 cm size classes ('agg size' or 'rec size') of each species (shading of bars) in local populations of both fishes ($n = 6$ populations). Error bars are SEM. Results of likelihood ratio tests are shown in the upper right of each plot, and variables with significant correlations and p-values are in **bold**. In the instance where the interaction between recipient size and aggressor species ('rec size × agg species') was significant, the marginal differences between aggressor species were examined in each size class; adjusted p-values to obtain an approximate family-wise error rate of 5% are indicated for each size class (***) $p < 0.001$

rates. Throughout all times of day, feeding rates significantly increased from ledge positions at the back to the front of ledges (Table S4B, Fig. 3), and these rates were significantly lower at dusk when compared to rates at both dawn and midday (Table S4C, Fig. 3).

Reciprocal removal experiment

Ledge position

The distribution of basslets under ledges through time varied by size, consistent with an overall size hierarchy. The smallest individuals were observed furthest back under ledges, and individuals of increasing size maintained positions that were progressively closer to the front of ledges (Fig. S2A,C in the Supplement). Following the removal of blackcap basslets, 2 and 3 cm fairy basslets shifted closer to the

front of ledges (Table 1, comp × time LRT, $p = 0.001$; comp LRT, $p = 0.015$, respectively). By the end of the experiment (8 wk), 2 cm fairy basslets were on average (\pm SEM) $46.3 \pm 13.9\%$ closer to the front of ledges (Fig. 4C), and 3 cm fairy basslet were consistently closer to the front of ledges through time by $14.4 \pm 4.19\%$ in blackcap-removal versus control populations.

Similarly, after removing fairy basslets from populations, 2 cm blackcap basslets shifted closer to the front of ledges through time (Table 1, comp × time, LRT $p = 0.043$), reaching positions that were $61.3 \pm 13.8\%$ closer to the front of ledges than in control populations by the end of 8 wk (Fig. 4D). Blackcap basslets (3 cm) were $14.8 \pm 8.40\%$ closer to the front of ledges through time in fairy-removal versus control populations, but this difference was not significant (Table 1, comp LRT, $p = 0.083$). The removal of the potential competitor did not have a significant effect on the ledge positions of 4 and 5 cm size classes of either species (Table S5 in the Supplement).

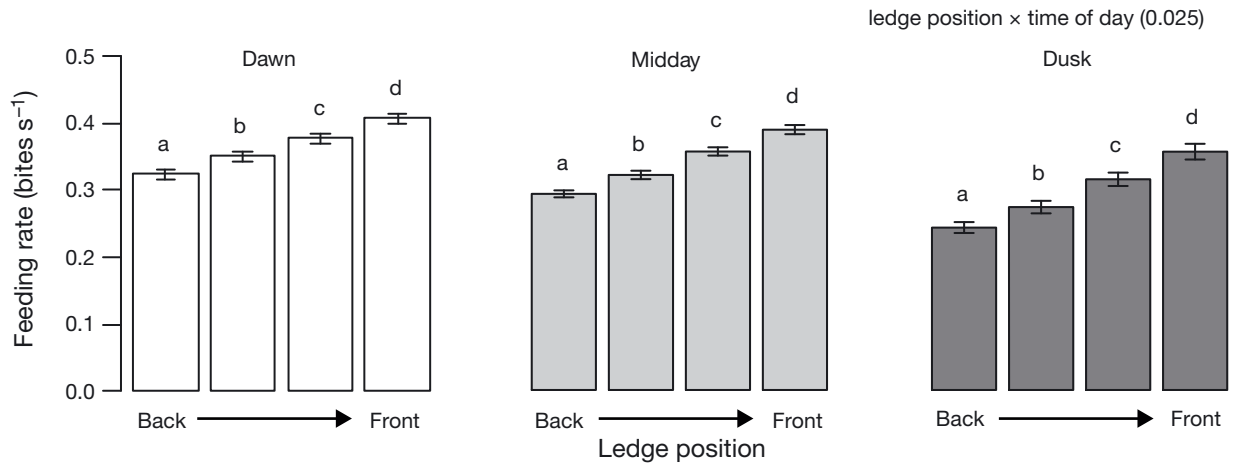


Fig. 3. Feeding rate of 2.0–2.5 cm basslets (fairy basslets *Gramma loreto* and blackcap basslets *G. melacara* combined) in positions from the back to front of ledges ('ledge position') in local populations of both species ($n = 6$) at dawn, midday, and dusk ('time of day'). Error bars are SEM. Results of likelihood ratio tests (upper right) indicated a significant interaction between ledge position and time of day ($p = 0.025$). Letters within each plot indicate significant differences in feeding rate ($p_{\text{cor}} < 0.020$) among ledge positions within each time of day (see Table S4B for exact corrected p -values)

Growth rate

Interspecific competition had an effect on the growth rates of ~2 cm individuals of both species (Table 1, comp LRT, $p < 0.001$ and $p = 0.032$, respectively). Both species exhibited increased growth rates in competitor-removal versus unmanipulated control populations (Fig. 4E,F; comp) that were $75.2 \pm 4.47\%$ (fairy) and $70.1 \pm 2.58\%$ (blackcap) higher in the absence of the competitor (0.002 ± 0.00 and $0.001 \pm 0.01 \text{ cm d}^{-1}$, respectively).

Population density

Consistent with expected seasonal patterns of recruitment, densities of smaller basslets (2 and 3 cm) tended to increase through time, whereas larger fish (4 and 5 cm) maintained densities that were relatively unchanged (Fig. S2B,D). The mean density of 2 cm blackcap basslets was higher in competitor-removal versus unmanipulated control populations, but this difference in density between competitor treatments was largely driven by 1 population of blackcap basslets (fairy-removal treatment) that exhibited an extraordinarily high influx of 2 cm individuals. Counts of this size class increased from 0 to 34 fish between baseline and Week 1 censuses, and over 35 fish were maintained in this population over the following weeks. The next largest count of any size class of either basslet species during the entire experiment was 19 fish within a single popula-

tion. Interspecific competition did not significantly affect the density of 2 cm basslets (Table 1, Fig. 4A,B), nor the densities of any larger size classes of fish (Table S5).

DISCUSSION

Interspecific competition via aggression negatively affects the distribution and growth of juvenile basslets (mostly 2 cm) in local populations under reef ledges. Observations of fish behavior and the results of the reciprocal removal experiment were consistent with expectations of substantial competition between these species. Clear interference competition was observed between basslets, and the juveniles of both species exhibited shifts in distribution towards the front of ledges (where feeding rates were higher) and increased growth rates in the absence (versus presence) of the competitor. Contrary to expectations, there was no evidence of interspecific competition influencing the local population density of either basslet. However, an observational period of 8 wk may have been too short an experiment to see such effects (cf. Hixon & Jones 2005). Once basslets reached larger sizes, interspecific aggression still occurred, but with no consequential effects on any of the demographic parameters measured in this study.

Despite an overall imbalance in aggression, with fairy basslets engaged in many more chases than blackcap basslets, the effects of interspecific competition on the ledge position and growth of juveniles

Table 1. Results of likelihood ratio tests (LRTs) of the hypothesized effect of the potential competitor (comp) and time on the change in ledge position and density of 2 and 3 cm fairy basslets *Gramma loreto* and blackcap basslets *G. melacara*, and the effect of the potential competitor on the individual growth rates of ~2 cm basslets in a reciprocal removal experiment. Responses were compared between local populations with the potential competitor removed versus unmanipulated populations of both species (n = 3 populations per treatment). If there was evidence of a significant interaction (comp × time), p-values associated with these specific linear combinations were adjusted (p_{cor}) to achieve an approximate family-wise error rate of 5%. Variables with significant ($p < 0.05$) effects and corresponding p-values are in **bold**

Response variable	Size (cm)	Fixed effect	LRT p	Week	p_{cor}			
Fairy basslet								
Change in ledge position	2	comp × time	0.001	1	0.467			
				2	0.998			
				3	0.453			
				4	0.611			
				5	0.250			
	3	comp × time	0.143	6	0.050			
				7	0.034			
				8	0.004			
	Growth rate	~2	comp	<0.001	comp	0.371		
					time	0.724		
comp					0.516			
time					0.460			
comp × time					0.662			
Change in density	2	comp × time	0.460	comp	0.662			
				time	0.024			
				3	comp × time	0.460	comp	0.662
							time	0.024
							comp × time	0.024
Blackcap basslet								
Change in ledge position	2	comp × time	0.043	1	0.254			
				2	0.997			
				3	0.642			
				4	0.088			
				5	<0.001			
	3	comp × time	0.578	6	0.003			
				7	<0.001			
				8	<0.001			
	Growth rate	~2	comp	0.032	comp	0.083		
					time	0.050		
3					comp × time	0.578	comp	0.083
							time	0.050
							comp × time	0.050
Change in density	2	comp × time	0.358	comp	0.201			
				time	0.479			
				3	comp × time	0.298	comp	0.910
							time	<0.001
							comp × time	<0.001

were symmetrical between species. This inconsistency suggests the need to consider the potential energetic costs associated with aggression per se, both in terms of the energetic demands required for physical movement when chasing and/or being chased, as well as a reduction in time allocated for

feeding (and other vital behaviors such as vigilance, reproductive behaviors, etc.). Further research is also needed to directly compare the effects of intra-versus interspecific competition (e.g. Forrester et al. 2006), because observations in the present study revealed that fairy basslets were engaged in over 5 times the number of within-species chases and over twice the amount of between-species chases compared to blackcap basslets.

Intraspecific competition among fairy basslets maintains a size hierarchy within local populations, whereby larger individuals are found in ledge positions closer to the front and thus have higher feeding rates (Webster & Hixon 2000). Observations from the present study demonstrate that a size hierarchy is retained in local populations consisting of both fairy and blackcap basslets, and a positive correlation between feeding rates of fish and positioning from the backs to fronts of ledges is consistent in both species. Native predators of basslets (including the Families Aulostomidae, Carangidae, Lutjanidae, and Serranidae) have also been previously documented spending significantly more time at the back of reef ledges (Webster 2004). Therefore, as interspecific competition causes shifts in the distribution of juvenile basslets towards the backs of ledges, individuals may simultaneously experience lower feeding rates and an increase in spatial overlap with predators. Both of these mechanisms may contribute to the measured decreases in growth rates of juvenile basslets from the presence of the competitor, with lower feeding rates indicating less food being obtained (and therefore less energy for growth), and an increase in risk of predation potentially increasing the amount of time and energy basslets allocate for predator avoidance and/or antipredator response (i.e. non-consumptive effects, see, for example, reviews by Lima & Dill 1990, Werner & Peacor 2003, Peckarsky et al. 2008).

Very few studies have tested for effects of interspecific competition on the growth of coral-reef fishes, and findings have been highly inconsistent (Bonin et al. 2015, Forrester 2015). To my knowledge, only one other study has demonstrated reciprocal negative effects on growth between species (Forrester et al. 2006). My findings differ slightly in that Forrester et al. (2006) found effects of competition on the growth of adult fishes, and I measured the growth of only juveniles. Further testing of such sub-lethal effects of interspecific competition (e.g. growth and reproduction) across all life stages of coral-reef fishes is needed to better understand the generality and symmetry of these effects.

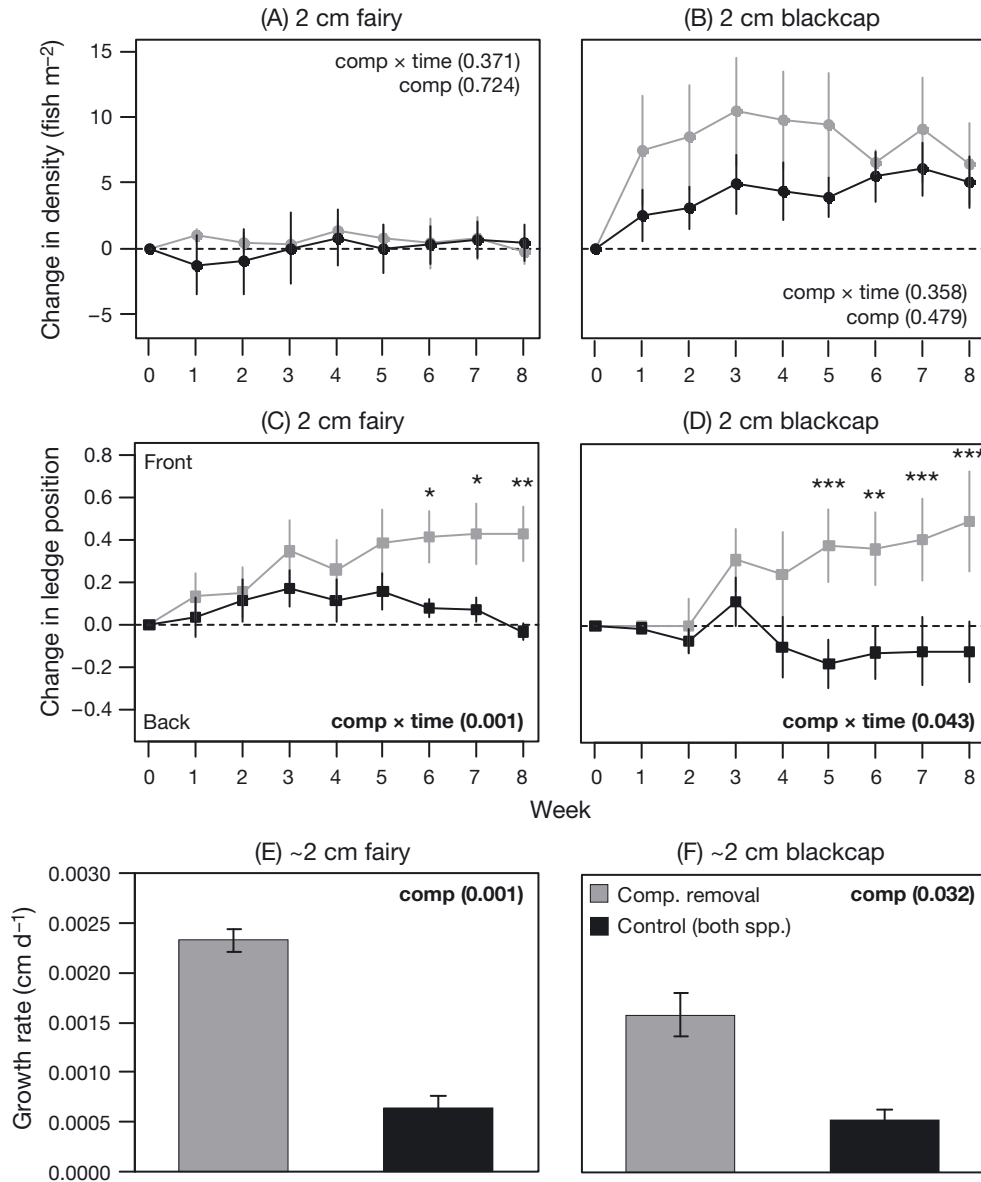


Fig. 4. Change in (A,B) density and (C,D) ledge position through time (week), and (E,F) growth rates of ~2 cm individuals of fairy basslets *Gramma loreto* and blackcap basslets *G. melacara* following the removal of the potential competitor versus unmanipulated control populations ($n = 3$ populations per treatment; lighter and darker shading, respectively). Error bars are SEM. Results of likelihood ratio tests are shown in each plot, and variables with significant effects and p-values are in **bold**. Where the interaction between competitor presence and time was significant ('comp × time'), the marginal differences between treatments were examined during each week; adjusted p-values to obtain an approximate family-wise error rate of 5% are indicated (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$)

Interspecific competition that is highly asymmetrical has been shown to influence the distribution of coral-reef fishes among microhabitats (e.g. Ebersole 1985, Robertson & Gaines 1986, Clarke 1989, Munday et al. 2001, McCormick & Weaver 2012). At a similar scale (within local populations), I have demonstrated that competition that is symmetrical between species can also determine the distribution

of juvenile coral-reef fishes. However, this mechanism is not common (Bonin et al. 2015, Forrester 2015). Earlier research by Munday (2004) and recent work by Pereira et al. (2015) demonstrated that the juveniles of 2 Pacific coral-dwelling gobies also compete for habitat with similar competitive abilities, but this is currently the only other documented instance of symmetrical competition between coral-reef fishes.

The zonation of each basslet species across larger spatial scales is likely driven by a variety of abiotic and biotic mechanisms that may not be mutually exclusive. Abiotic conditions such as water temperature, visible light, fluid pressure, water circulation, etc. likely vary with depth and potentially form a gradient that influences the depth limits of basslets. These factors may directly affect the depth distribution of basslets based on the environmental tolerance and corresponding fitness and survival, and/or influence the dispersal of larval fishes. Also, these factors may indirectly affect populations of basslets by driving the distribution of their planktonic food and/or predators.

Asymmetrical competition among coral-reef fishes, such as surgeon- and damselfishes, can determine the distribution of these species across reef zones (Robertson & Gaines 1986, Robertson 1995). If the depth range of basslets also contains habitats that are highly preferred by both species, then asymmetry in aggression characterized in this study may influence the overall zonation of these fishes. Additional biotic factors that could potentially be important in driving this broad-scale distribution include habitat selection by larvae as they recruit to reefs (Shima & Osenberg 2003), including possible priority effects in which resident fishes (e.g. predators, conspecifics etc.) influence incoming recruits (Shulman et al. 1983, Almany 2003, 2004, Shulman 2015). Relative predation risk could also differ between species with depth, given that blackcap basslets may be more cryptic (i.e. much darker in coloration) than their competitor. However, this difference may vary in deeper depths where recognition of basslets by visual predators may be further influenced by changes in the level of ambient light, shading, penetration of wavelengths of light, as well as the composition of retinal pigments of predators with depth. Mortality rates of basslets could further vary if the overall community structure differs across a broad depth range, potentially modifying the strength or even presence of direct and indirect interactions that involve basslets.

Coral-reef fishes form the most diverse and complex assemblages of vertebrates in the world (Sale 2002), and understanding the processes that enable these ecosystems to support such species-rich communities remains a fundamental challenge in marine ecology. Here, I demonstrated the symmetrical effects of interspecific competition on the distribution and growth of 2 congeneric coral-reef fishes in local populations. Additional experimental work investigating competition between marine fishes is needed (Hixon 2006, Link & Auster 2013, Bonin et al. 2015,

Forrester 2015) to increase the number of species and families on which we base our understanding of competition, and to assess the importance of interspecific competition in determining the zonation and range limits of these organisms. Identifying the processes that influence the distribution of organisms is essential for understanding broad-scale patterns in biodiversity, and for predicting the response of species (and species interactions) to global environmental change (Parmesan et al. 2005).

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LITERATURE CITED

- Almany GR (2003) Priority effects in coral reef fish communities. *Ecology* 84:1920–1935
- Almany GR (2004) Priority effects in coral reef fish communities of the Great Barrier Reef. *Ecology* 85:2872–2880
- Bertness MD (1991) Zonation of *Spartina patens* and *Spartina alterniflora* in New England salt marsh. *Ecology* 72:138–148
- Böhlke JE, Randall JE (1963) The fishes of the western Atlantic serranoid genus *Gramma*. *Proc Acad Nat Sci Phila* 115:33–52
- Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MHH, White JSS (2009) Generalized linear mixed models: a practical guide for ecology and evolution. *Trends Ecol Evol* 24:127–135
- Bonin MC, Boström-Einarsson L, Munday PL, Jones GP (2015) The prevalence and importance of competition among coral reef fishes. *Annu Rev Ecol Syst* 46:169–190
- Clarke RD (1989) Population fluctuation, competition and microhabitat distribution of two species of tube blennies, *Acanthemblemaria* (Teleostei: Chaenopsidae). *Bull Mar Sci* 44:1174–1185
- Connell JH (1961) The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. *Ecology* 42:710–723
- Connell JH (1975) Some mechanisms producing structure in natural communities: a model and evidence from field experiments. In: Cody ML, Diamond JM (eds) *Ecology and evolution of communities*. Belknap Press of Harvard University, Cambridge, MA, p 460–490
- Connell JH (1983) On the prevalence and relative importance of interspecific competition: evidence from field experiments. *Am Nat* 122:661–696
- Ebersole JP (1985) Niche separation of two damselfish species by aggression and differential microhabitat utilization. *Ecology* 66:14–20

- Forrester GE (2015) Competition in reef fishes. In: Mora C (ed) Ecology of fishes on coral reefs. Cambridge University Press, Cambridge, p 34–40
- Forrester GE, Evans B, Steele MA, Vance RR (2006) Assessing the magnitude of intra- and interspecific competition in two coral reef fishes. *Oecologia* 148:632–640
- Frederick JL (1997) Evaluation of fluorescent elastomer injection as a method for marking small fish. *Bull Mar Sci* 61:399–408
- Gurevitch J, Morrow LL, Wallace A, Walsh JS (1992) A meta-analysis of competition in field experiments. *Am Nat* 140:539–572
- Hairston NG (1980) The experimental test of an analysis of field distributions: competition in terrestrial salamanders. *Ecology* 61:817–826
- Hixon MA (1980) Competitive interactions between California reef fishes of the genus *Embiotoca*. *Ecology* 61:918–931
- Hixon MA (2006) Competition. In: Allen LG, Horn MH (eds) The ecology of marine fishes: California and adjacent waters. University of California Press, Berkeley, CA, p 449–465
- Hixon MA, Jones GP (2005) Competition, predation, and density-dependent mortality in demersal marine fishes. *Ecology* 86:2847–2859
- Hobson ES (1991) Trophic relationships of fishes specialized to feed on zooplankters above coral reefs. In: Sale PF (ed) The ecology of fishes on coral reefs. Academic Press, San Diego, CA, p 69–95
- Holbrook SJ, Schmitt RJ (1986) Food acquisition by competing surfperch on a patchy environmental gradient. *Environ Biol Fishes* 16:135–146
- Hothorn T, Bretz F, Westfall P (2008) Simultaneous inference in general parametric models. *Biom J* 50:346–363
- Larson RJ (1980) Competition, habitat selection, and the bathymetric segregation of two rockfish (*Sebastes*) species. *Ecol Monogr* 50:221–239
- Lima SL, Dill LM (1990) Behavioral decisions made under the risk of predation: a review and prospectus. *Can J Zool* 68:619–640
- Link JS, Auster PJ (2013) The challenges of evaluating competition among marine fishes: Who cares, when does it matter, and what can one do about it? *Bull Mar Sci* 89:213–247
- Lubchenco J (1980) Algal zonation in the New England rocky intertidal community: an experimental analysis. *Ecology* 61:333–344
- McCormick MI, Weaver CJ (2012) It pays to be pushy: intracohort interference competition between two reef fishes. *PLOS ONE* 7:e42590
- Munday PL (2004) Competitive coexistence of coral-dwelling fishes: the lottery hypothesis revisited. *Ecology* 85:623–628
- Munday PL, Jones GP, Caley MJ (2001) Interspecific competition and coexistence in a guild of coral-dwelling fishes. *Ecology* 82:2177–2189
- Neet CR, Hausser J (1990) Habitat selection in zones of parapatric contact between the common shrew *Sorex araneus* and Millet's shrew *S. coronatus*. *J Anim Ecol* 59:235–250
- Parmesan C, Gaines S, Gonzalez L, Kaufman DM, Kingsolver J, Townsend Peterson A, Sagarin R (2005) Empirical perspectives on species borders: from traditional biogeography to global change. *Oikos* 108:58–75
- Peckarsky BL, Abrams PA, Bolnick DI, Dill LM and others (2008) Revisiting the classics: considering nonconsumptive effects in textbook examples of predator–prey interactions. *Ecology* 89:2416–2425
- Pereira PHC, Munday PL, Jones GP (2015) Competitive mechanisms change with ontogeny in coral dwelling gobies. *Ecology* 96:3090–3101
- Pinheiro JC, Bates DM (2000) Mixed-effects models in S and S-PLUS. Springer Science & Business Media, New York, NY
- Pinheiro JC, Bates DM, DebRoy S, Sarkar D, R Core Team (2014) *nlme*: linear and nonlinear mixed effects models. R package version 3.1-118. <http://CRAN.R-project.org/package=nlme>
- R Core Team (2014) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. www.r-project.org
- Robertson DR (1995) Competitive ability and the potential for lotteries among territorial reef fishes. *Oecologia* 103:180–190
- Robertson DR (1996) Interspecific competition controls abundance and habitat use of territorial Caribbean damselfishes. *Ecology* 77:885–899
- Robertson DR, Gaines SD (1986) Interference competition structures habitat use in a local assemblage of coral reef surgeonfishes. *Ecology* 67:1372–1383
- Sale PF (2002) Coral reef fishes: dynamics and diversity in a complex ecosystem. Academic Press, San Diego, CA
- Schoener TW (1983) Field experiments on interspecific competition. *Am Nat* 122:240–285
- Shima JS, Osenberg CW (2003) Cryptic density dependence: effects of covariation between density and site quality in reef fish. *Ecology* 84:46–52
- Shulman MJ (2015) Priority effects. In: Mora C (ed) Ecology of fishes on coral reefs. Cambridge University Press, Cambridge, p 242–246
- Shulman MJ, Ogden JC, Ebersole JP, McFarland WN, Miller SL, Wolf NG (1983) Priority effects in the recruitment of juvenile coral reef fishes. *Ecology* 64:1508–1513
- Starck II, Walter A, Colin PL (1978) *Gramma linki*: a new species of grammid fish from the tropical western Atlantic. *Bull Mar Sci* 28:146–152
- Stephens JS Jr, Larson RJ, Podella D (2006) Rocky reefs and kelp beds. In: Allen LG, Horn MH (eds) The ecology of marine fishes: California and adjacent waters. University of California Press, Berkeley, CA, p 227–252
- Stephenson TA, Stephenson A (1972) Life between tide-marks on rocky shores. Freeman and Company, San Francisco, CA
- Webster MS (2003) Temporal density dependence and population regulation in a marine fish. *Ecology* 84:623–628
- Webster MS (2004) Density dependence via intercohort competition in a coral-reef fish. *Ecology* 85:986–994
- Webster MS, Hixon MA (2000) Mechanisms and individual consequences of intraspecific competition in a coral-reef fish. *Mar Ecol Prog Ser* 196:187–194
- Werner EE, Peacor SD (2003) A review of trait-mediated indirect interactions in ecological communities. *Ecology* 84:1083–1100
- Williams DD (1991) Patterns and processes in the distribution of coral reef fishes. In: Sale PF (ed) Ecology of coral reef fishes. Academic Press, San Diego, CA, p 437–474
- Wilson SD, Tilman D (1991) Component of plant competition along an experimental gradient of nitrogen availability. *Ecology* 72:1050–1065
- Zuur A, Ieno EN, Walker N, Saveliev AA, Smith GM (2009) Mixed effects models and extensions in ecology with R. Springer Science & Business Media, New York, NY