POPULATION ECOLOGY - ORIGINAL PAPER

High-quality habitat and facilitation ameliorate competitive effects of prior residents on new settlers

Thomas C. Adam

Abstract Many species disperse during their lifetime. Two factors that can affect the performance of individuals following dispersal are the presence of conspecifics and intrinsic habitat quality at the settlement site. Detecting the influence of these factors can be difficult for at least two reasons: (1) the outcomes of interactions with conspecifics are often variable including both competition and facilitation, and (2) selection of high quality habitats often leads to positive covariance between habitat quality and density. In this study, I investigate positive and negative effects of resident blue streak cleaner wrasse (*Labroides dimidiatus*) on the growth and survival of recently settled conspecifics while accounting for habitat quality. Juvenile *L. dimidiatus* settle near adult conspecifics, but likely have to compete with resident adults for access to food. However, field experiments indicate that settlers have access to more resources at occupied sites, and as a result, grow faster despite evidence for competition with residents. This result is a direct consequence of two factors: (1) resident conspecifics facilitate settlers by attracting client fish, and (2) resident conspecifics are strongly associated with high quality habitat. These results highlight the need to simultaneously consider habitat quality and competitive and facilitative interactions between conspecifics when making inferences about ecological processes from spatial patterns of individual performance.

Keywords Density-dependent growth · Habitat selection · *Labroides dimidiatus* · Coral reef · Fish

Communicated by Craig Osenberg.

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Introduction

Until recently, ecological research has focused disproportionately on negative interactions such as competition and predation compared to positive interactions (Stachowicz 2001; Bruno et al. 2003). This is especially true in population ecology where a strong focus on population regulation has generated enormous interest in understanding the processes that result in density dependence (Harrison and Cappuccino 1995; Hixon et al. 2002; Osenberg et al. 2002; White et al. 2010). Much less work has focused on processes that result in intraspecific facilitation (positive effects of density) despite appreciation that it is common and can have important implications for population dynamics (Courchamp et al. 1999; Stephens and Sutherland 1999). The relative importance of positive and negative effects can vary in space and time, making the net outcome of interactions difficult to predict without a mechanistic understanding of the multiple processes involved. Mechanistic studies have frequently partitioned the positive and negative components of interspecific interactions, particularly in plant communities (see Walker and Chapin 1986; Callaway et al. 1991; Holzapfel and Mahall 1999; Schmitt and Holbrook 2003), and this has led to an increased appreciation of the role of facilitation in determining the spatial and temporal patterns observed in communities (Callaway and Walker 1997; Bruno et al. 2003). Nonetheless, this has rarely been attempted with

intraspecific interactions (but see Bertness and Grosholz 1985; Bertness 1989; Booth 1995; Leslie 2005; Donahue 2006).

A strong suggestion that intraspecific facilitation is an important phenomenon for many species comes from behavioral ecology where studies have revealed new dispersers of many taxa (e.g., insects, birds, and marine invertebrates) frequently prefer to settle to sites occupied by resident conspecifics (independent of habitat quality) (e.g., Muller 1998; Ward and Schlossberg 2004; Donahue 2006). While these observations suggest that intraspecific facilitation may be common, new dispersers may also benefit indirectly from the presence of conspecifics if they are a reliable indicator of high quality habitat (i.e., conspecific cueing) (Stamps and Krishnan 2005). Indeed, the extent to which conspecific cueing versus intraspecific facilitation is likely to motivate different habitat selection strategies is seldom evaluated (but see Donahue 2006). Of course, competitive effects of prior residents on new settlers could offset any positive effects associated with residents or habitat (Wilson and Osenberg 2002; Shima and Osenberg 2003). Therefore, both the positive and negative effects of conspecifics as well as the influence of habitat quality on new settlers must be considered to fully understand habitat selection strategies as well as the influence of these strategies on population dynamics.

Here, I explore some potential positive and negative effects of residents on new settlers while simultaneously considering the role of habitat quality for the coral reef fish, *Labroides dimidiatus* (blue streak cleaner wrasse). Like many marine organisms, *L. dimidiatus* has a bipartite life-cycle with a planktonic larval phase followed by site-attached juvenile and adult stages. As juveniles and adults, *L. dimidiatus* remove large numbers of parasitic gnathiid isopods from client fish (Grutter 1996, 1999, 2000), and consequently, attract many species of clients to their territories (cleaner stations) (Bshary 2003; Grutter et al. 2003). Because juvenile and adult *L. dimidiatus* rely on cleaning for the majority of their nutrition, juveniles that settle at an established cleaner station are likely to have to compete with older conspecifics for access to parasitized clients. However, these juveniles could still benefit if adult cleaners preferentially occupy high quality habitat and/or attract client fish seeking to be cleaned. In this study, I investigated whether newly settled juvenile cleaners were associated with residents more often than would be expected if settlement was random. I then tested whether adult *L. dimidiatus* were associated with high quality habitat, and whether they have the potential to facilitate new settlers by attracting client fish to reefs. Finally, I used a field experiment to quantify the positive and negative effects of associating with residents on the growth and survival of new settlers. I hypothesized that most or all

competitive effects of resident cleaners on new settlers would be offset because: (1) residents occupied high quality habitat, and (2) residents directly facilitated new settlers by attracting client fish to their territories.

Materials and methods

Study site

Field work was conducted in the shallow lagoons surrounding Cook's Bay on the north shore of Moorea, French Polynesia (17°30′S, 149°50′W). The east entrance to Cook's Bay was characterized by nearly continuous coverage of the mounding coral *Porites rus* in its branching and plating forms. The surrounding lagoons were characterized by small (ranging in size from <1 to ∼40 m^2), semi-isolated patch reefs composed of a combination of live and dead coral and algae; live coral was dominated by massive species of *Porites* (e.g., *P. lobata*) as well as *P. rus*. Individual patch reefs were occupied by zero, one or two *L. dimidiatus* adults with some reefs also occupied by a juvenile. While adults move between patch reefs, most spend the majority of their time at a single patch reef used as a cleaning territory; in contrast, juveniles under ∼45 mm total length (TL) generally do not move between reefs (personal observation). For this study, I operationally defined a reef a cleaner station if at least one *L. dimidiatus* adult or juvenile was present on more than 50% of my visits (I visited reefs with *L. dimidiatus* multiple times (most >10 times) throughout each 3-month field season).

Association between recent settlers and resident cleaners

To assess if recently settled *L. dimidiatus* were found near older conspecifics more often than expected by chance, I conducted nearest-neighbor surveys on continuous and patch reefs. In July 2007, divers located, captured and measured all recently settled *L. dimidiatus* (individuals <21 mm TL, median size = 17.6 mm TL, max. time since settlement <5 weeks) in a 200 m × 50 m area of continuous reef and measured the distance from each settler (*n* = 13) to the nearest conspecific. To generate an expected distribution of distances based on random settlement, I placed three 100-m transects in the same area (following the contour of the reef) and measured the distance of the closest *L. dimidiatus* (excluding recent settlers) at 5-m intervals along each transect. Only points landing on living *Porites rus* colonies were used to generate the expected distribution (*n* = 58 points total).

In July–August 2008, I recorded the locations of all patch reefs with *L. dimidiatus* residents, and used GPS to

map all patch reefs that were at least 1.5 m in diameter and 0.75 m in height in a $\sim$40,000 m^2 area of the mid-lagoon (*L. dimidiatus* were never found associated with smaller reefs; Adam, unpublished data). I searched each reef for recently settled *L. dimidiatus*, estimated the total length of each settler to the nearest mm ($n = 10$, median estimated size = 24 mm all individuals <30 mm TL), and measured the length, width, and height of each reef. To calculate an expected distribution of nearest-neighbor distances based on random settlement, I measured distances from each square meter of available habitat (i.e., mapped patch reefs) to the nearest resident *L. dimidiatus* (excluding recent settlers) ($n = 2,367$ m^2 of suitable habitat) using the 'Nearest feature extension' (v. 3.8; J. Jenness, Flagstaff, A, USAZ) in ArcView GIS 3.2 (ESRI, Redlands, CA, USA). For both analyses, I compared expected distributions to the actual distributions using Kolmogorov–Smirnov (KS) tests.

Patterns of resource availability at reefs with resident cleaners

To evaluate whether patch reefs with resident *L. dimidiatus* had more potential clients than reefs without resident *L. dimidiatus*, I surveyed 16 paired reefs with and without *L. dimidiatus* at several different sites on the north shore of Moorea during the 2004 and 2005 austral winters. Paired reefs were located within 60 m of each other, were chosen to be similar with respect to size, shape, and coral composition, and were surveyed within 10 min of one another. Surveys focused on transient fish (fish that were not restricted to a single patch reef) because they were the primary clients of *L. dimidiatus* at these sites (Adam, unpublished data). I surveyed a permanent 2 m × 2 m quadrat at focal areas of each reef (focal areas were selected to be centered on *L. dimidiatus* feeding territories and often included a prominent feature of the patch reef such as a ledge; similar features were selected as focal areas at reefs lacking cleaners). During each survey, one snorkeler slowly approached a reef and recorded all fish entering the quadrat during a 3-min period while maintaining a distance of 5–10 m before searching closely for fish that may have initially been missed. I surveyed all reefs several times (median = 4) and conducted analyses on the mean number of potential client fish recorded within each quadrat. Furthermore, I categorized clients as "preferred" or "less preferred" (Manly's alpha; Chesson 1983: see Appendix 1 for details). Therefore, I analyzed the total number of clients, as well as the number of "preferred" and "less preferred" clients. To test if cleaner stations had more potential client fish than similar reefs nearby, I used a mixed-effect ANOVA with cleaner presence/absence as a fixed effect and pair as a random effect. Data were log-transformed (ln) before analyses to homogenize variances and meet the assumption of normality.

Habitat associations of resident cleaners and relationship to resource availability

To characterize the physical structure of the patch reefs mapped for the nearest-neighbor surveys and determine their influence on use by adult cleaners and their clients, I quantified size, internal cavity space, number of holes (with diameter >10 cm), and the percent cover of the dominant substrates at each patch reef. I measured reef diameter and height with transect tapes and calculated the total volume and area of each reef using ellipsoid formulae. To estimate the internal cavity volume, I estimated the proportion of the reef consisting of internal cavity space and multiplied it by the total volume. I also estimated visually proportional cover of the three dominant substrates [*Porites lobata*-like massive corals, branching and plating forms of *Porites rus*, and dead coral (frequently having a thin diatom film, small amount of filamentous algae or crustose coralline algae on it)] and multiplied these by the reef area to estimate the surface area of each substrate at each reef (visual estimates of cover were concordant with fixed point contacts conducted on a subsample of reefs; Adam, unpublished data; see also Dethier et al. 1993).

To reduce the number of variables needed to include in subsequent analyses of reef characteristics, I conducted a principal components analysis (PCA) on the correlation matrix of the physical attributes of reefs (total volume, total number of holes, hole density (number of holes/m^2), internal cavity volume, and surface area of the three most common substrates—massive *Porites*, *Porites rus*, and dead coral were included in the PCA). The first two axes of the PCA both had eigenvalues greater than one (3.50 and 1.50, respectively) and together explained approximately 72% of the total variance in physical attributes among the 433 patch reefs encountered (Table 1). Total volume, number of holes and internal cavity space had the highest loadings on PC 1. Hole density and total number of holes had the highest loadings on PC 2 and were negatively correlated with total area of massive *Porites* (Table 1).

To elucidate whether *L. dimidiatus* preferentially occupied reefs with certain physical characteristics, I used logistic regression to test if PC 1, PC 2, or an interaction between them were related to the probability a reef would be occupied by *L. dimidiatus* during the 2008 austral winter. To test for a relationship between physical characteristics of reefs and the number of potential clients available to cleaners, 88 patch reefs were surveyed a total of 771 times during the 2005–2008 austral winters (see Appendix 2 for additional sampling details). Surveys followed the same protocol described earlier except they were conducted within 3 h of sunrise which corresponds to peak cleaning time (Grutter 1996). Because some factors were at the survey level (i.e., time surveyed), others were at the reef level (i.e., physical characteristics), and others applied

Table 1 Loadings from principal components analysis on 433 patch reefs

Attribute	PC 1 (50%)	PC 2 (22%)
Maximum total volume	**0.50**	0.00
Massive *Porites* area	0.20	**−0.49**
Porites rus area	0.36	0.00
Bare space area	0.39	−0.01
Total number of holes	**0.43**	**0.40**
Hole density	0.11	**0.74**
Interior empty volume	**0.47**	−0.07

Variables with the highest loadings are indicated in bold. *PC 1* was associated most strongly with attributes of reef size that could indicate shelter availability for large transient fish; *PC 2* was associated most strongly with variables that distinguish large massive *Porites* colonies with little structural complexity from smaller, more complex reefs. Together, the first two principal components accounted for 72% of the variation in the measured habitat attributes

to reefs in some years but not others (i.e., occupancy by a cleaner), I used a linear mixed model to assess correlations between physical characteristics and the number of client fish at a reef. To meet the assumptions of normality and homoscedacity, number of client fish was log (ln) transformed. The model was solved with JMP 8.0 statistical software (SAS Institute, Cary, NC) using the restricted maximum likelihood method (REML), with degrees of freedom calculated according to Kenward and Roger (1997). I included reef, year, and reef nested in year as random effects, cleaner occupancy as a fixed effect, and PC 1, PC 2, and time (min) after sunrise as covariates. I also tested for all possible interactions between the fixed effect and the three covariates, sequentially removing non-significant interactions to arrive at the final model ($P > 0.3$ for all interactions removed). Separate analyses were also conducted on "preferred" and "less preferred" clients.

Experimental test of client attraction by resident cleaners

To test whether *L. dimidiatus* attract client fish to cleaner stations, I haphazardly selected ten pairs (reefs were paired in space) of small ($\sim$3–13 m^2), semi-isolated patch reefs (>4 m from nearest patch reef) previously unoccupied by cleaners. I surveyed all reef pairs three to five times over a period of 28 days using the same survey methods described earlier. I then randomly assigned one member of each pair to a cleaner addition or control treatment and transplanted one juvenile cleaner (<45 mm TL) to each experimental reef. I then surveyed the experimental and control reefs two to four times in the following 40 days. Transplanted cleaners disappeared repeatedly from three of the ten experimental reefs and these were eliminated from further consideration, reducing the sample size to seven paired

reefs. To test for an effect of the cleaner addition on the change (ln transformed) in the abundance of potential client fish, I conducted paired *t* tests. Separate analyses were also conducted on "preferred" and "less preferred" clients.

Experimental assessment of costs and/or benefits of settling near resident cleaners

To determine the costs and benefits to *L. dimidiatus* of settling at an established cleaner station, I transplanted recently settled individuals (15–24 mm TL) to: (1) reefs occupied by one adult conspecific, (2) reefs occupied by two adult conspecifics, (3) reefs lacking resident conspecifics, or (4) reefs where all resident conspecifics had been removed. Because there is a time lag of more than a month before client fish significantly reduce their visits to a cleaner station following the removal of a cleaner (Bshary 2003; Grutter et al. 2003), settlers at the removal reefs should benefit from the positive effect that resident cleaners had on the abundance of clients as well as the possibility that residents were associated with high quality habitat. Settlers at the occupied reefs should also benefit from these factors, but these benefits may be offset if there is competition with adults for access to parasitized clients. Finally, settlers at unoccupied reefs will not have to compete with adults, but also will not receive any direct or habitat related benefits associated with established cleaner stations. Prior to the initiation of the experiment, I randomly assigned ten of 21 established cleaner stations in a $\sim$25,000 m^2 area of the lagoon to the removal treatment and removed all adult *L. dimidiatus* from these reefs. Of the 11 reefs where resident adults were not removed, 4 had two resident adults and 7 had a single resident adult. I also removed individuals of three relatively uncommon and patchily distributed species (juvenile bicolor cleaners *Labroides bicolor*, cleaner mimics *Aspidontus taeniatus*, and piano fang blennies *Plagiotremus tapeinosoma*) that could have a negative impact on *L. dimidiatus* settlers from all reefs where they occurred. I selected unoccupied reefs to be similar to occupied cleaner stations; however, most of the larger reefs in the area were occupied by *L. dimidiatus*. Consequently, unoccupied reefs were consistently smaller than many of the cleaner stations. I collected *L. dimidiatus* settlers away from the study site with hand nets and quinaldine, and housed fish in flow through aquaria for 48 h prior to outplant. Handling effects were minimal (<3% mortality). To initiate the experiment, I added one settler to each of the 31 reefs and monitored growth and survival for 19–21 days. Missing individuals were not found in searches of nearby patch reefs and were presumed to have died.

At the termination of the experiment, I collected focal fish during the late morning or early afternoon and sacrificed them within 1 h of collection so that their gut contents could be analyzed. I immediately placed focal fish on ice, and soon

after measured, weighed, and photographed them. I placed the entire gut in a 5% formaldehyde solution, and later counted the number of gnathiid isopods under a dissecting microscope (>90% of the identifiable items in the gut were gnathiids). I assessed change in length by analyzing photos from the beginning and end of the experiment with the image analysis program Scion Image (Scion, Frederick, MD, USA), and obtained estimates of daily growth rates by dividing change in length by the number of days fish were on the reef.

I evaluated differences in mortality rates with a four-sample extension of Fisher's exact test comparing the total proportion of settlers that disappeared from each treatment over the course of the experiment. I used analysis of covariance (ANCOVA) to evaluate difference in growth rates, including habitat characteristics (PC 1 and PC 2) and initial size of each settler as covariates. Post hoc Tukey tests were then performed for all pairwise comparisons between treatments. To test for a relationship between feeding and growth, I regressed the growth rates of settlers (adjusted for initial size using the residuals from a linear regression) on the log (ln) of the number of gnathiid isopods present in their gut at the termination of the experiment.

Results

### Association between recent settlers and resident cleaners

Nine of 13 (69%) and 6 of 10 (60%) settlers were found within 3 m of an older conspecific on the continuous reef and patch reef habitats, respectively, compared to 16 of 58 points (28%) and 466 of 2,367 points (20%) from the expected distributions indicating that settlers in both habitats were found close to conspecifics more often than expected by chance (KS test, $D = 0.50$, $P < 0.01$; Fig 1a; $D = 0.44$, $P < 0.05$; Fig. 1b).

Patterns of resource availability at reefs with resident cleaners

The number of client fish was significantly greater at reefs with resident *L. dimidiatus* (ANOVA, $F_{1,15} = 24.67$, $P < 0.001$) with "preferred" and "less preferred" clients approximately 2.3 and 1.6 times greater at cleaner stations relative to reefs without cleaners (ANOVA, $F_{1,15} = 15.14$, $P = 0.001$; $F_{1,15} = 15.07$, $P = 0.002$; Fig. 2), respectively.

### Habitat associations of resident cleaners and relationship to resource availability

The probability that a reef would be occupied by a resident *L. dimidiatus* was positively correlated with PC 1 (logistic
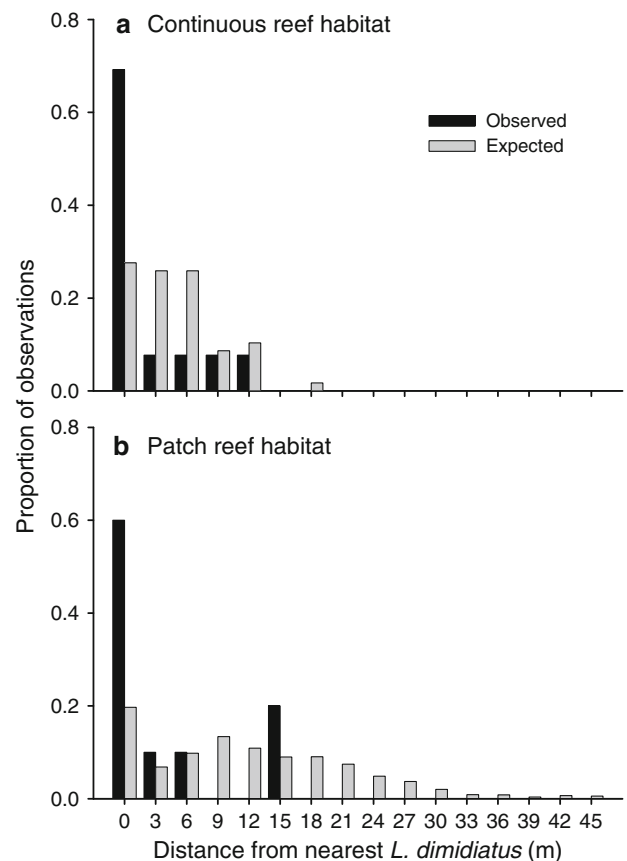

Fig. 1 Distribution of observed distances between recent *Labroides dimidiatus* settlers and their nearest conspecific neighbors on **a** continuous reef ($n = 13$) and **b** patch reef habitat ($n = 10$) compared to expected distributions based on random settlement to suitable habitat (based on **a** $n = 58$, and **b** $n = 2,367$). The two distributions were significantly different on both continuous reef [Kolmogorov–Smirnov (KS) test, $P < 0.01$] and patch reef habitat (KS test, $P < 0.05$)

regression, $P < 0.001$; Fig. 3a) but not PC 2 ($P = 0.116$). However, there was a significant interaction between PC 1 and PC 2 on the probability of occupancy ($P = 0.006$). The interaction appeared to be driven by two unoccupied reefs that had very high values of PC 1 (>98% of other reefs) and very low values of PC 2 (<97% of other reefs). After removal of these reefs, only PC 1 remained significantly correlated with occupancy (PC 1, $P < 0.001$; PC 2, $P = 0.178$; PC 1 × PC 2, $P = 0.172$; Fig. 3).

There was a significant interaction between PC 1 and min after sunrise on the number of potential client fish ($P < 0.001$) indicating a positive correlation between PC 1 and potential client fish that was strongest early in the morning (Fig. 4, Appendix 2 Table A2-2). Early morning corresponds with peak cleaning activity of *L. dimidiatus* (personal observation; Grutter 1996), and is also a time when many diurnal fish have yet to start foraging and remain close to shelter areas (personal observation; Hobson
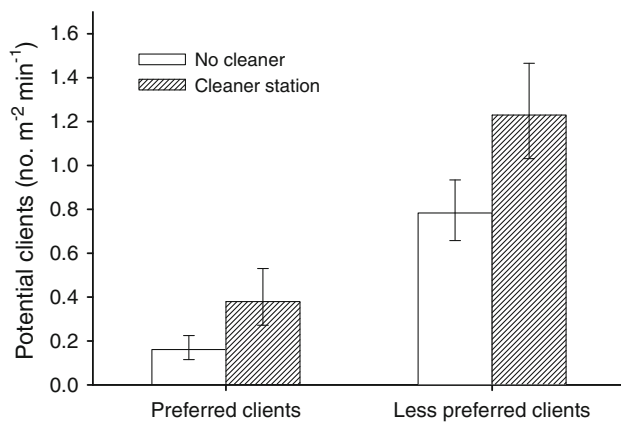
Fig. 2 Number of preferred and less preferred client visitors (determined by Manly's α; see on-line resources Appendix 1 for details) at paired reefs without and with cleaners ($n = 16$ pairs). All clients entering a 2 m × 2 m quadrat at each reef during a 3-min period were counted. Analyses were conducted on natural log-transformed data, results were back-transformed; *error bars* back-transformed 95% confidence intervals. Both client types were significantly more abundant at reefs with cleaners (preferred clients: ANOVA $F_{1,15} = 15.14$, $P = 0.001$; less preferred clients: ANOVA, $F_{1,15} = 15.07$, $P = 0.002$)
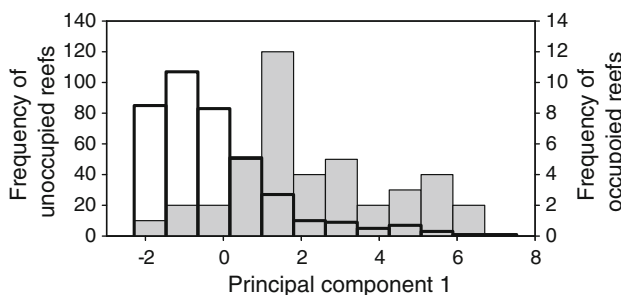
Fig. 3 Distributions of principal component 1 (PC 1) for unoccupied (*transparent bars*) and occupied (*gray bars*) reefs. PC 1 was strongly positively correlated with the probability that a reef would be occupied by a resident *L. dimidiatus* (logistic regression, $P < 0.001$)

1972). In addition, reefs with *L. dimidiatus* had significantly more potential client fish than reefs without *L. dimidiatus* after controlling for habitat characteristics ($P < 0.001$; Fig. 4; Appendix 2, Table A2-2). While both "preferred" and "less preferred" clients were positively associated with habitat characteristics (PC 1) and resident cleaners, overall patterns of abundance were largely driven by abundant "less preferred" clients (see Appendix 2).

Experimental test of client attraction by resident cleaners

Neither the total number of client fish nor the "less preferred" clients increased at the cleaner addition reefs relative to the controls (paired *t* test, $t = -0.09$, $P = 0.934$; $t = -0.87$, $P = 0.417$). However, there was a marginally

significant effect of the cleaner addition on "preferred" clients with these clients increasing by approximately 74% relative to controls (paired *t* test, $t = 2.11$, $P = 0.079$).

Experimental assessment of costs and/or benefits of settling near resident cleaners

Disappearance rates of *L. dimidiatus* did not differ significantly between treatments (individuals were lost from five unoccupied reefs, one occupied reef with two adults, three occupied reefs with one adult, and three removal reefs; Fisher's exact test, $P = 0.779$). By contrast, there were significant differences in growth rates among the four treatments ($F_{3,12} = 8.7$, $P = 0.002$). After accounting for habitat (PC 1 and PC 2), settlers grew fastest at removal reefs and slowest at reefs with zero and two resident cleaners (post hoc Tukey test $P < 0.05$; Fig. 5a), while growth was intermediate at reefs with one resident cleaner. In addition, growth rates of settlers were significantly positively correlated with PC 1 ($F_{1,12} = 8.12$, $P = 0.015$) (Fig. 5b) and PC 2 ($F_{1,12} = 6.40$, $P = 0.026$) indicating that intrinsic habitat characteristics of reefs influenced growth; reefs with cleaners tended to have higher values of PC 1 (Fig. 5c). There was also a significant negative relationship between initial size and change in length ($F_{1,12} = 10.90$, $P = 0.006$). After correcting for initial size, the number of gnathiid isopods found in the gut of a recent settler at the termination of the experiment was a significant positive predictor of the growth rate of that fish over the entire experimental period ($F_{1,17} = 12.51$, $P = 0.003$, $r^2 = 0.42$; Fig. 5d).

Discussion

Organisms often settle near resident conspecifics (Sweatman 1985; Schmitt and Holbrook 1996; Russo and Augspurger 2004; Ward and Schlossberg 2004), and these new settlers may have to compete with residents for access to resources. However, competitive effects of residents can be partially or totally offset if they occupy high quality habitat, and/or if they benefit new settlers in some way. Understanding the balance between these factors is clearly important for understanding how settlement patterns affect individual fitness and population dynamics, yet disentangling the influences of each can be difficult. For example, failure to recognize positive interactions between potential competitors (whether conspecifics or heterospecifics) can lead to overestimates of habitat quality (Forsman et al. 2002). Alternatively, if organisms preferentially settle to high quality habitat (as is predicted by simple habitat selection models; i.e., Fretwell and Lucas 1969), this can mask the strength of competitive interactions (or other
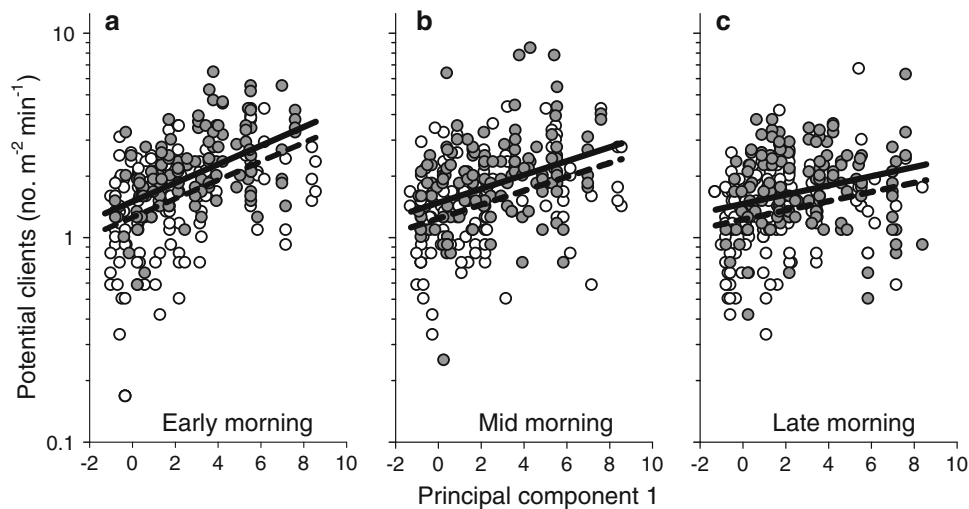
Fig. 4 The number of potential client visitors in relation to habitat characteristics (PC 1) in **a** early, **b** mid- and **c** late morning surveys for reefs unoccupied by *L. dimidiatus* (*white circles*) or occupied by at least one *L. dimitiatus* (*gray circles*). All clients entering a 2 m × 2 m quadrat at each reef during a 3-min period were counted. Surveys were not binned for the analysis (time was treated as a continuous variable) but are binned in the figure; each point represents a single survey. The predicted relationship between PC1 and potential client density at unoccupied reefs (*broken lines*) and at reefs occupied by resident cleaners (*solid lines*) is shown using the mean survey time for reefs in each panel; lines generated from parameters in Table A2-2. Note log scale on *y*-axis

Fig. 5 a Growth rates (mean +1SE) of recent settlers on reefs unoccupied by resident cleaners (*n* = 5), reefs where resident cleaners were removed (*n* = 7) and reefs occupied by one (*n* = 4) or two (*n* = 3) resident adults. *Bars* not sharing the same *letter* are significantly different at *P* < 0.05 based on Tukey HSD. **b** Leverage plot of PC 1 versus growth rate, after making both orthogonal to the other predictors in the model: initial size, PC 2 and treatment. **c** PC 1 values for each reef. **d** Number of gnathiid isopods found in the gut of each recent settler plotted against the size-corrected growth rate of that individual (natural log fit). *Symbol colors* in all panels correspond to treatments in panel (**a**)
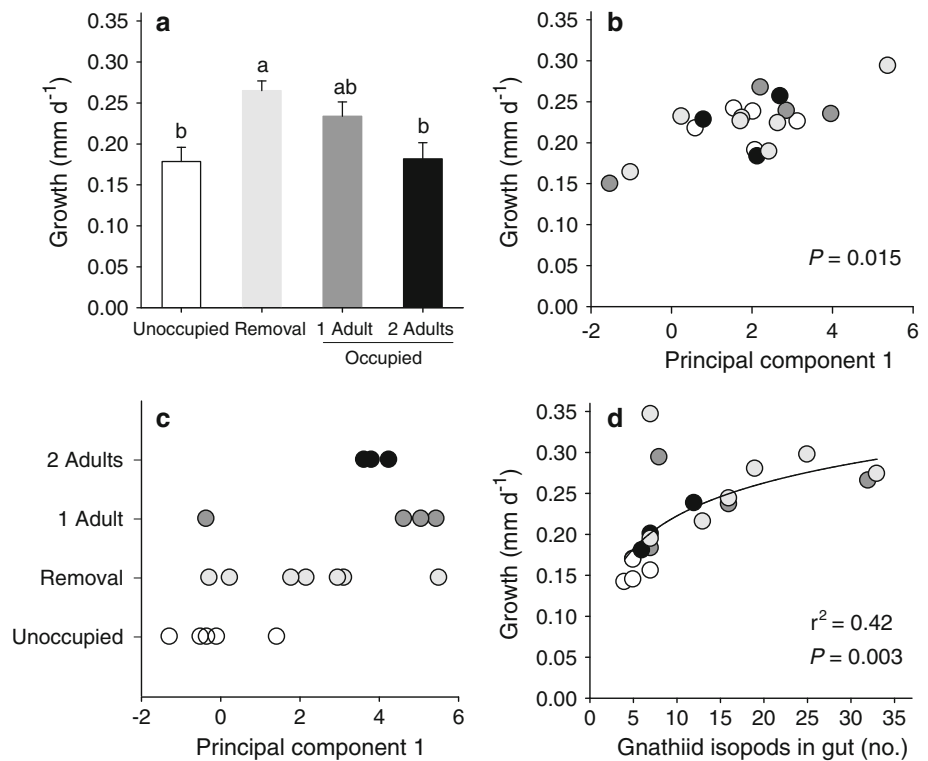
negative density-dependent phenomena; Wilson and Osenberg 2002; Shima and Osenberg 2003; Helms and Hunter 2005; Shima et al. 2008).

In this study, *L. dimidiatus* settlers were more likely to be found near resident conspecifics than expected by chance, and there were consistently more potential client fish (likely a limiting resource for cleaners) at these locations; as a result, settlers ate more gnathiid isopods and grew faster at cleaner stations despite having to compete with residents for access to clients. This indicates that the benefit of settling to a cleaner station likely outweighs the costs. However, whether the benefit is driven primarily by facilitation by resident

adults (through the attraction of clients to cleaner stations), or the association of adult cleaners with high quality habitat (places where client fish tend to aggregate) is not immediately clear. My results, as well as other recent experimental work, have demonstrated that cleaners attract some types of client fish to reefs (Bshary 2003; Grutter et al. 2003). However, this study also demonstrates that adult cleaners preferentially occupy large, hollow reefs that consistently harbor a higher density of client fish. Interestingly, the most abundant clients of *L. dimidiatus* (herbivorous surgeon fishes—mainly *Ctenochaetus striatus*) are not preferred clients, do not increase their visitation rates to reefs following cleaner additions, and occur primarily on large hollow reefs (i.e., those of high quality; Adam, unpublished data). Their local density may be determined primarily by physical habitat traits rather than the presence of cleaners. In contrast, less abundant preferred clients are apparently attracted to cleaners (in addition to being influenced by habitat). Taken together, these results suggest that settling near an adult cleaner can benefit young *L. dimidiatus* because adults occupy high quality habitat, and because they attract preferred clients to that habitat.

The positive correlation between shelter space for visiting clients (i.e., PC 1) and the growth rates of settlers suggests that new settlers grow faster at cleaner stations at least in part due to habitat characteristics. Furthermore, the fact that habitat characteristics do not account for all of the differences in growth rates of settlers at reefs with and without cleaners suggests a benefit of being at a cleaner station in addition to habitat. Finally, settlers grew less in the presence of residents compared to the removal treatment indicating that some of the benefit of being at an established cleaner station is offset by the presence of residents, likely because settlers have to compete with residents for access to clients. Indeed, on several occasions residents were observed preventing a settler access to clients, suggesting interference competition between residents and settlers as a mechanism influencing growth rates. The strong relationship between the number of gnathiid isopods found in the gut and the growth rates of all but two experimental fish support this interpretation, although client fish behavior could have also contributed to this pattern if clients prefer adult cleaners to juveniles (see Potts 1973; Mahon 1994). While the impact of settlers on resident adults was not measured, it seems likely that competition was highly asymmetric. Size-structured dominance hierarchies are common in many taxa (e.g., fish, birds and arthropods) and frequently result in asymmetric competitive effects of larger dominant individuals on smaller subordinates (e.g., Whiteman and Côté 2004; Garnet 1981; Issa et al. 1999).

Growth rates are often related to an individual's fitness through the strong relationship between size and fecundity (Wooton 1998) and the effects of size-selective predators (Sogard 1997). While few natural predation events on

obligate cleaners have been reported (reviewed in Côté 2000), hawkfish (Cirrhitidae) have been observed preying on small *Labroides phthirophagus* in Hawaii (Lobel 1976), and I observed arc-eye hawkfish (*Paracirrhites arcatus*) successfully attack *L. dimidiatus* twice while out-planting fish for the growth experiment. These small predators are probably important sources of mortality for *L. dimidiatus* settlers in Moorea, and consequently, cleaners experiencing faster growth rates will more quickly move through a window when they are most susceptible to predation. While shelter space is often believed to be a limiting resource for many reef fish, and interactions between shelter limitation and predation appear to be important drivers of density-dependent mortality for many of these fish (e.g., Holbrook and Schmitt 2002), the results of this study suggest that an interaction between competition for food resources, growth, and predation could be important drivers of density-dependent mortality of *L. dimidiatus*. Competition for food and consequent feedbacks between growth and mortality or condition and mortality are common in fish (Sogard 1997), and deserve more attention as potential density-dependent mechanisms operating on reef fishes (e.g., Forrester 1990; Booth 1995).

An important limitation of this study is that settlement of *L. dimidiatus* was not directly measured, and therefore the positive association observed between recent settlers and older conspecifics may to some degree also reflect post-settlement processes. For example, the same pattern of association could arise if *L. dimidiatus* settled at random but were more likely to survive near established cleaner stations. While this possibility cannot be ruled out, there is no evidence from my experiment that settlers experienced lower mortality rates at cleaner stations compared to other locations. However, it is also possible that individuals move after their initial settlement to the reef and that this contributes to the patterns observed (post-settlement movement may be particularly likely on continuous reef since individuals would not have to cross unfavorable habitat).

While it is widely appreciated that the structure and dynamics of most ecological communities is controlled in part by facilitative interactions between species, the role of intraspecific facilitation is less often considered in studies of population dynamics. Results from this study indicate that adult cleaners likely facilitate new settlers by attracting preferred clients to cleaner stations, and consequently, facilitation between adults and settlers has the potential to affect population dynamics. In particular, facilitation (along with the potential for habitat selection by settlers) could affect spatial and temporal patterns of cleaner station occupancy across multiple generations of cleaners (although habitat selection by adult cleaners is also likely to be an important factor; i.e., Robertson 1972). This could potentially lead to more stable patterns of occupancy than would be predicted based on

habitat characteristics alone. Interestingly, the fact that adult cleaners modify the suitability of habitat by attracting preferred clients to their territories is conceptually similar to ecosystem engineering (sensu Jones et al. 1994, 1997) except that cleaners modify the behavior of organisms rather than the physical structure of the environment.

Understanding the consequences of settlement patterns on the fitness of new settlers requires simultaneously considering habitat quality and the potential facilitative and competitive effects of prior residents on settlers. For example, in this study, if only the competitive effects of resident cleaners had been considered (i.e., comparing the removal treatment with the occupied treatments), then it would appear counterintuitive for *L. dimidiatus* to preferentially settle near adult cleaners (or near other habitat characteristics that co-vary with the presence of adults). However, when both habitat quality and the potential for direct facilitation between residents and new settlers are considered, it becomes apparent that settling near an adult conspecific confers a net positive fitness advantage to the settler. In addition to providing context for understanding potential habitat selection strategies, the results also have important implications for studies which attempt to use spatial patterns of individual performance to understand population dynamics. This is because the results suggest not only that covariance between habitat quality and density (or occupancy) can mask competitive effects (e.g., Shima and Osenberg 2003) but also that failing to explicitly consider the possibility of intraspecific facilitation can lead to overestimates of habitat quality.

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