



Trade-offs in the ecological versatility of juvenile wrasses: An experimental evaluation



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ABSTRACT

A number of theories have been advanced to explain the evolution of specialists and generalists and how they coexist. According to trade-off theory, a species can improve performance by specialising on one habitat but does so at a cost of reduced performance in others. Specialists will outperform generalists in their preferred habitats but will be outperformed by generalists in other habitats. This study aimed to examine trade-offs in juvenile coral reef wrasses that vary in their degree to which they are specialised on microhabitats. We predicted that specialists would exhibit highest survival and growth on preferred habitats, and in contrast, generalists would tend to do equally well on all habitats. Furthermore, we predicted that specialists would outperform generalists on their preferred habitat, while generalists would outperform specialists on less preferred habitats. The predictions were tested by transplanting juveniles from four different species (two specialists, and two generalists) to patch reefs constructed from different kinds of microhabitats (live coral, dead coral, and rubble) and measuring growth and survival after 3 weeks in Kimbe Bay, Papua New Guinea. Prior to this, the degree of specialisation was assessed using resource selection ratio-based field observations of habitat use and availability. Results provided mixed evidence for the trade-off hypothesis. Specialists conformed to predictions, while generalists did not. Specialist species showed higher survival rate on their preferred habitat than generalist species and the mean growth was significantly higher on the preferred habitat than less preferred habitats for one specialist species. However, generalist species did not survive on all reefs, regardless of microhabitat. Growth rates between habitats could therefore not be compared for generalists and the presence of a trade-off in fitness expressed in growth may have been missed for these species. It is thus premature to reject the trade-off theory, and we encourage examining a greater range of specialist and generalist species, under conditions in which the fate of all individuals can be more accurately determined.

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1. Introduction

The causes and consequences of patterns in versatility among organisms have been the topics of considerable interest in ecology and evolutionary biology (MacNally, 1995). The degree of specialisation can often determine the patterns in distributions and abundances of organisms in nature (McPeck, 1996; Verberk et al., 2010). Specialists are commonly rare and display narrow distributions, while generalists often exhibit high local abundances and wide local and geographical distributions (Brown, 1984). A number of theories have been advanced to explain the evolution of specialists and generalists, and how they coexist. The traditional and most accepted view is the concept of trade-offs between traits that offer advantages to specialists and generalists (Kassen, 2002; Via and Hawthorne, 2002; Weiner and Xiao, 2012). This is based on the assumption that, all else being equal, a species cannot exhibit superior

performance in the acquisition of all resources (Futuyma and Moreno, 1988; Via and Hawthorne, 2002). That is, there must be a trade-off between performing a few activities well (specialist) and performing many activities poorly (generalist) (Wilson and Yoshimura, 1994). If the theory is correct, a specialist should outperform a generalist in exploiting preferred resources (Kassen, 2002), while a generalist should be more efficient at exploiting all other resources. This has given rise to the adage that a “jack-of-all-trades is a master of none”.

Despite the potential importance of trade-offs in ecological and evolutionary theory, empirical support has not always been forthcoming and trade-offs have been difficult to detect (Sanderson, 1991). Most studies have been tested for genetic trade-offs (e.g. Fry, 1996; García-Robledo and Horvitz, 2012; Kawecki, 1997; Mackenzie, 1996; Via and Hawthorne, 2002) as it is thought that a trade-off must be manifested as a genetic rather than a phenotypic effect if any evolutionary change to the population is to result (Kassen, 2002; Mackenzie, 1996). However, ecological trade-offs must first be demonstrated as a phenotypic response, before evaluating the underlying genetic mechanisms.

Descriptive comparisons of specialist and generalist species have largely supported the trade-off hypothesis (e.g. Drummond and

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Garcia, 1989; Mira and Bernays, 2002; Sanderson, 1990, 1991; Straub et al., 2011). However, the problem with measuring trade-offs from observational data alone is that the range of resources used and performance on different resources depends on their availability (Krebs, 1999). The best way to test for ecological trade-offs is by manipulating resources and looking at the responses in terms of fitness traits. So far, most of these experiments have been done in the laboratory under artificial conditions (e.g. Barkae et al., 2012; Rana et al., 2002; Torregrossa et al., 2012). There are few field experiments that have been specifically designed to compare the performance of specialist and generalist species given the controlled levels of resources in the field.

Most work on trade-offs has focused on insects (e.g. Barkae et al., 2012; Bernays and Minkenberg, 1997; Evans, 1982; Jackson and Hallas, 1986; Jaenike, 1990; Laverty and Plowright, 1988; Noriyuki and Osawa, 2012; Rana et al., 2002) and other terrestrial organisms (e.g. Drummond, 1983; Griffith and Sultan, 2012; Huey and Hertz, 1984; MacNally, 1995; Torregrossa et al., 2012), and little work has been conducted on marine organisms, especially coral reef fishes. A number of studies have documented relationships among specialisation, distribution, and abundance that are consistent with trade-off theory (Bean et al., 2002; Berkström et al., 2012; Jones et al., 2002). A few attempts to test for trade-offs in coral reef fishes have focused on morphological trade-offs and functional constraints (e.g. Ralston and Wainwright, 1997; Sanderson, 1990, 1991; Wainwright, 1988). However, only two recent studies in Australia tested for trade-offs in microhabitat usage and diet, one on gobies supporting the hypothesis (Caley and Munday, 2003) and one on butterflyfishes rejecting it (Berumen and Pratchett, 2008). The contradictory results highlight the need for more studies testing for trade-offs in coral reef fishes.

The aim of this study was to examine trade-offs between microhabitat usages in juvenile wrasses that vary in their degree to which they are specialised on microhabitats. If trade-offs exist between microhabitat generalists and specialists, we predicted that specialists would exhibit highest survival and growth on preferred habitats, and in contrast, generalists would tend to do equally well on all habitats. Furthermore, we predicted that specialists would outperform generalists on their preferred habitat, while generalists would outperform specialists on less preferred habitats. These predictions were tested under field conditions by transplanting juveniles (2 habitat specialists and 2 habitat generalists) to reefs constructed from different kinds of microhabitats (live coral, dead coral, and rubble) and measuring growth and survival over a 3-week period.

2. Methods

2.1. Study sites and species

This study was carried out at Kimbe Bay, West New Britain Province, Papua New Guinea (5°30'S; 150°05'E) in April 2002 (Fig. 1). Kimbe Bay has a dense network of platform reefs ranging in size from tens to hundred meters in diameter (Munday, 2002). Reefs close to shore extend down to depths of >200 m and break the surface at low tide (Berkström et al., 2012). Several small continental islands surrounded by well-developed fringing reefs are also present within the bay (Munday, 2002). An experimental manipulation was conducted in the lagoonal area adjacent to Schumann Island (Fig. 1). The Schumann lagoon consists of shallow sandy bottoms (2–6 m deep during high tide) surrounded by reefs, breaking the surface at low tide. The area is subjected to strong currents during the changeover of low and high tides.

Juvenile wrasses differing in their degree of specialisation in relation to microhabitat (2 specialist species and 2 generalist species) were chosen based on habitat use data from Berkström et al. (2012). The two apparent microhabitat specialists chosen for the present study were *Labrichthys unilineatus*, a coral specialist and *Paracheilinus filamentosus*, a rubble specialist. The two apparent microhabitat generalists were *Halichoeres melanurus* and *Thalassoma lunare*. Based on observational data from Berkström et al. (2012), *L. unilineatus* was only found associated with live coral and *P. filamentosus* was rarely found on anything but rubble. Both *H. melanurus* and *T. lunare* were found on most microhabitats examined, including the three habitats used in the present experiment. To avoid the complication of ontogenetic shifts in ecology, the present study focused on the juvenile life stage.

2.2. Habitat availability and resource selection ratios

To quantify apparent versatility in more detail for the four species, habitat use was compared with habitat availability, and resource selection ratios were calculated. Habitat use was estimated by randomly placing transects on the windward (two transects) and leeward (two transects) sides of three different reefs (Garbuna, Lady Di, and Limuka) in Kimbe Bay, a total of twelve transects (Fig. 1). Microhabitat (the habitat in which the fish was observed at that particular moment) was recorded for each juvenile within the 20-m wide transect. Transects were run from 20 m up the slope or wall, over the crest and across the

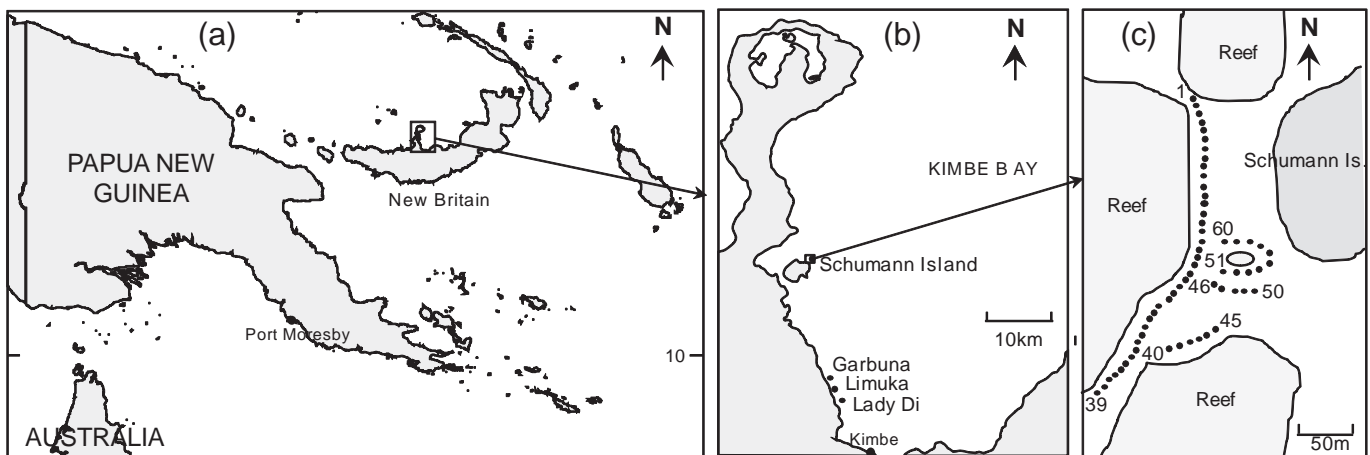


Fig. 1. Map of study site in (a) Papua New Guinea, showing (b) Kimbe Bay where habitat use and habitat availability for four species of juvenile wrasses (two habitat specialists and two habitat generalists) were collected on Garbuna, Limuka, and Lady Di coral reefs, and (c) site where experiments were conducted (Schumann Island). Dots in panel c represent constructed patch reefs consisting of 100% live coral, 100% dead coral, and 100% rubble. Numbers indicate patch at beginning and end of each row.

reef flat of each reef sampled. Transects ended where the reef broke the surface. The vast majority of the juveniles were found on the reef slope between 0 and 10 m. Microhabitat availability was estimated in this depth range using 50-m transects assigned with 100 random points. Four transects were placed at four different depths (0 m, 2 m, 6 m, and 10 m) on the front slopes of three different reefs (Garbuna, Lady Di, and Limuka), and the microhabitat under each point was recorded. The recorded microhabitat was assigned to one of the three microhabitat categories (live coral, dead coral, and rubble) used in the experiments, and the proportion of each microhabitat category per depth was calculated.

Selection ratios were used to calculate habitat use in relation to availability for the study species following Munday (2002). These ratios were calculated using the following formula: $w_i = o_i/a_i$, where w_i = Manly's selection ratio, o_i = proportion of habitat i available to a species, and a_i = proportion of individuals found on habitat i . To decide if a species used a habitat disproportionately to its availability (selected for or avoided), a Bonferroni corrected 95% confidence interval was estimated for each selection ratio, using the formula $Z_{\alpha/2k} \sqrt{\{o_i(1-o_i)/(u+ai^2)\}}$, where $Z_{\alpha/2k}$ = the critical value of the standard normal distribution, corresponding to an upper tail area of $\alpha/2k$, $\alpha = 0.05$, k = total number of habitats, o_i = proportion of habitat i available to a species, a_i = proportion of individuals found on habitat i , and u = total number of habitats (of all habitats) occupied by a species.

The use of a habitat is considered to be proportional to its availability where the 95% confidence interval of the selection ratio encompasses one and a habitat is considered to be used disproportionately to its availability where the 95% confidence interval does not encompass one (Manly et al., 1993). To further study whether or not the disproportional use of a habitat was due to selection or avoidance, selection ratios were graphed with 95% confidence intervals.

2.3. Transplant experiment

To test whether species with narrow niche breadths (specialists) outperformed species with broad niche breadths (generalists) within their preferred zone but suffered greater costs than generalists outside this range, manipulated experiments were carried out on juvenile wrasses. Experimental units (patch reefs) were constructed either of 100% live coral, 100% dead coral, or 100% rubble. The spatial design followed the margins of the reefs with the three different treatments in random order (Fig. 1). Sixty patch reefs were constructed and placed 10 m apart. The size of each patch reef was approximately 1 × 1 m. This patch size has successfully been used in studies on wrasse recruitment in Kimbe Bay, Papua New Guinea, and was therefore chosen for the present study (Srinivasan, 2003). Juvenile wrasses, differing in their degree of specialisation in relation to microhabitat, were transplanted to the patch reefs. The range of habitats used by the specialist species was included within the range of habitats used by generalist species.

2.4. Construction of experimental units (patch reefs)

The material for the construction of patch reefs was collected from reefs surrounding the study site. Live coral patches were constructed by *Pocillopora damicornis*. This coral species was chosen because the coral specialist *L. unilineatus* predominantly feeds on *P. damicornis* as juveniles (Cole, 2010). Dead coral patches were constructed by large bits of dead coral partly covered with turf or very fine sediment, and rubble patches were constructed by considerably smaller bits of dead coral and rock fragments partly covered with turf or very fine sediment. Five patch reefs per habitat were constructed for each study species, and eight juveniles per species were randomly placed on each patch resulting in a total of 60 patch reefs and 480 juvenile fishes. Species were not mixed together on patch reefs, i.e. each patch had 8 transplanted juveniles from the same species.

Before releasing juveniles onto the patch reefs, all other fish were removed to control for competition and predation. A fence net was placed around the patch to trap resident fish while clove oil was sprayed on the patch to anaesthetise fish. The patch reef was pulled apart, and every fish was removed and placed in a large plastic bag. The patch reef was put back together, and the resident fish were brought up to the boat and placed alive on reefs away from the study site.

2.5. Fish collection

Juvenile wrasses for the experiments were randomly collected from a number of reefs in Kimbe Bay. Fish were caught with a hand net after being anaesthetised with clove oil. A dilute clove oil solution has been found to be a highly effective anaesthetic for reef fishes, with a calm induction to anaesthesia and very high survival rates following anaesthesia (Munday and Wilson, 1997). After capture fish were placed in a small sealed plastic bag. Each bag was assigned a number to facilitate identification and keep track of individual juveniles.

2.6. Fish manipulation

Juveniles were measured and tagged on the boat with small, visible implant elastomer (VIE). VIE tags are specifically designed for use of small fish and are routinely used in studies of reef fishes. These tags have high retention rates and cause very little mortality (Beukers et al., 1995). The tags were made from a biocompatible, elastomer that was injected under the skin of the fish with a fine gauge needle. They did not protrude from the body and could therefore not be pulled out or cause the fish to be entangled. After being tagged and measured, juveniles were left in the plastic bag for 30–60 minutes to recover and were then released onto allocated patch reefs.

Juveniles caught in the afternoon were brought back to the laboratory overnight before being measured and tagged to reduce risk of predation. Fish released in the afternoon would not have time to get use to their new surroundings before dark and would hence be more prone to predation (Brown, 2001). Fish kept overnight were placed in an aquarium with sufficient air supply and little disturbance. There were no signs of increased stress in fish brought back to the laboratory overnight when compared to those caught and released the same day. Growth and survival were monitored over a period of 3 weeks, and remaining juveniles were recaptured with clove oil and re-measured at the end of the experiment. This time period was chosen as it is sufficient to measure growth differences in juvenile reef fishes (e.g. Jones, 1986), and a longer sampling period was not possible because of the high mortality at this life history stage (e.g. Almany and Webster, 2006).

Stationary predators found on patch reefs during the course of the experiment were removed using a small spear. However, these were few in numbers and predation on transplanted juveniles was assumed to be done by transient predators. The number of transplanted juveniles left after approximately 1 week, 2 weeks, and 3 weeks was noted as well as recruitment by other species.

2.7. Data analyses

Kruskal–Wallis tests were used to test for differences in survival among habitats because data did not meet the assumption of equal variances. Differences were tested on the percentage survival within species among the three different habitats (live coral, dead coral, and rubble) and between specialist and generalist species on the specialist's preferred habitat (live coral for comparisons between coral specialist *L. unilineatus* and generalists *T. lunare* and *H. melanurus* and rubble for comparisons between rubble specialist *P. filamentosus* and generalists *T. lunare* and *H. melanurus*). ANOVA was used to test for differences in growth among habitats for the rubble specialist *P. filamentosus*. A Tukey's HSD post hoc test was conducted to determine the nature of differences between means found by ANOVA.

3. Results

3.1. Habitat use in relation to availability (selection ratios)

H. melanurus was found to be the least specialised species in terms of its microhabitat use. It was found on all habitats and used dead coral and live coral in accordance to its availability. However, rubble was used more than expected (Table 1, Fig. 2). *T. lunare* was found on dead and live coral and used dead coral in proportion to its availability, but used live coral more than expected (Table 1, Fig. 2). *P. filamentosus* was only found on rubble and used this habitat more than expected (Table 1, Fig. 2). Similarly, *L. unilineatus* was only found on live coral and used live coral more frequently than expected (Fig. 2).

3.2. Fish remaining

Generalist species *H. melanurus* and *T. lunare* did not remain on all reefs, regardless of microhabitat, as predicted. Instead, only 3.5% of all *H. melanurus* juveniles remained on patch reefs (27% of all patches, two live coral and two rubble). Similarly, only 16.5% of all transplanted *T. lunare* remained on patch reefs (46.7% of all patches), including four live coral and three dead coral (Fig. 3).

Contrary to predictions, the rubble specialist *P. filamentosus* remained on most patches, with 28.5% of all transplanted juveniles remaining on 87% of all patches (five rubble, five live coral, and three dead coral; Fig. 3). However, only 17.5% of all coral specialists, *L. unilineatus*, remained on 33.5% of the patches, which all consisted of 100% live coral (Fig. 3).

Transplanted juveniles from all four species disappeared within the first week, in most cases within the first couple of days. The number of remaining fish then stayed fairly constant throughout the rest of the experiment (Table S1). Recruitment by other species was observed on the patch reefs during the 3-week experiment. Patches constructed of live and dead coral had more recruits than rubble patches. Other labrid (*H. scapularis* and *H. chloropterus*), pomacentrid, and apogonid recruits were found on all three habitats while chaetodontid, and *L. unilineatus* recruits were found on coral patches. Acanthurid, scarid, *H. melanurus*, and *T. lunare* recruits were found on both dead and live coral patches (Table S1).

As predicted, percentage fish remaining did not differ significantly among habitats for the generalist species *H. melanurus* ($p = 0.45$) but differed significantly among habitats for the specialist species *L. unilineatus* ($p = 0.001$) and *P. filamentosus* ($p = 0.005$; Fig. 4). However, contrary to predictions, percentage fish remaining differed among habitats for the generalist *T. lunare* ($p = 0.08$; Fig. 4).

Percentage fish remaining differed significantly among preferred habitats when comparing the coral specialist species *L. unilineatus* with generalist species *H. melanurus* and *T. lunare* on live coral ($p = 0.013$) and when comparing the rubble specialist species *P. filamentosus* with the generalist species on rubble ($p = 0.0005$), a pattern consistent with predictions. Specialist species showed lower losses on their preferred habitat (*P. filamentosus* 50% remaining on rubble, *L. unilineatus*

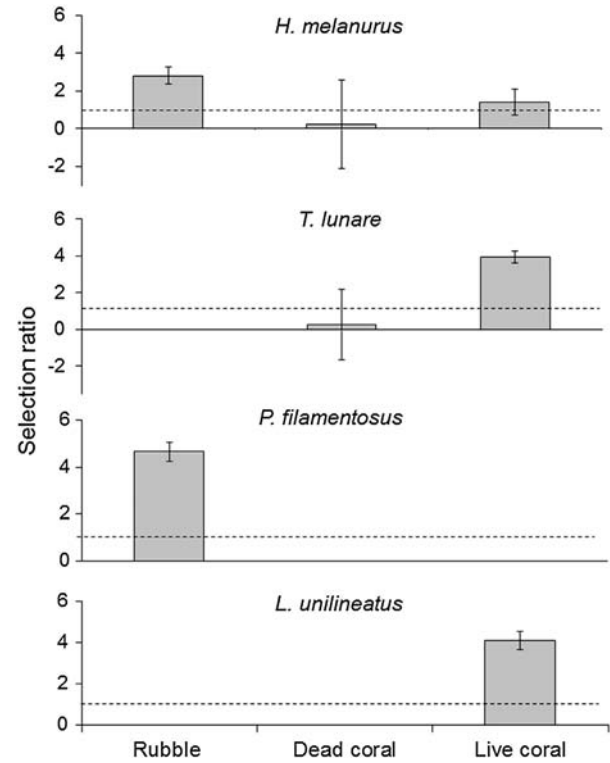


Fig. 2. Selection ratios for study species; two habitat generalists (*Halichoeres melanurus* and *Thalassoma lunare*) and two habitat specialists (*Paracheilinus filamentosus* and *Labrichthys unilineatus*). Error bars represent 95% confidence intervals. If bars are above one (dotted line), a species uses habitat more than expected. If bars are below one, a species uses habitat less than expected. If one is within bars, habitat is used in proportion to its availability.

62.5% remaining on live coral) than generalist species (*H. melanurus* 0.4% remaining on both live coral and rubble, *T. lunare* 30% remaining on live coral and 0% remaining on rubble, Fig. 5).

3.3. Growth

Growth among all three habitats could only be compared for one of the four species examined, *P. filamentosus* (rubble specialist), as this was the only species to remain on all three habitats, and hence making a comparison between habitats possible. Mean growth over the 3-week period of the experiment for *P. filamentosus* was 4.95 mm/3 weeks on dead coral, 5.30 mm/3 weeks on live coral, and 7.10 mm/3 weeks on

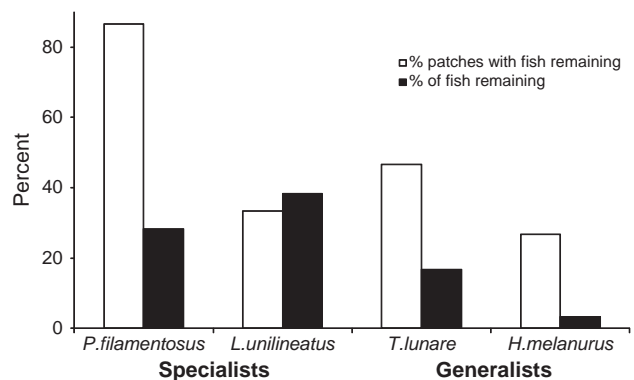


Fig. 3. Percent of patch reefs with fish remaining and percent fish remaining on all patches after ending transplant experiment with two habitat specialists (*Paracheilinus filamentosus* and *Labrichthys unilineatus*) and two habitat generalists (*Halichoeres melanurus* and *Thalassoma lunare*) in Kimbe Bay, Papua New Guinea.

Table 1

Significance of habitat use by two habitat specialists (*Paracheilinus filamentosus* and *Labrichthys unilineatus*) and two habitat generalists (*Halichoeres melanurus* and *Thalassoma lunare*) in Kimbe Bay using resource selection ratios and Bonferroni corrected 95% confidence intervals (+ = habitat used significantly more than expected, - = habitat used less than expected, and NS = habitat used in proportion to availability).

Species	Rubble	Dead coral	Live coral
<i>P. filamentosus</i>	+	-	-
<i>L. unilineatus</i>	-	-	+
<i>H. melanurus</i>	+	NS	NS
<i>T. lunare</i>	-	NS	+

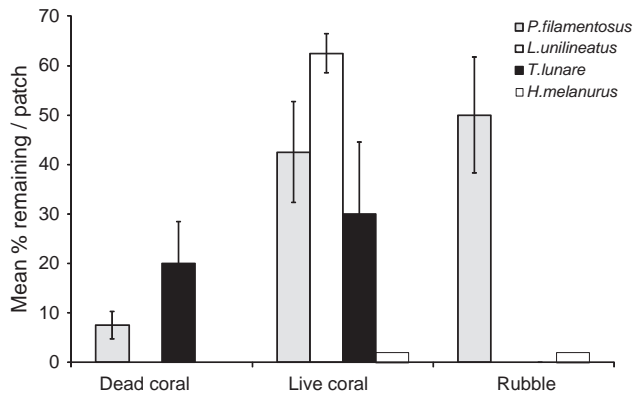


Fig. 4. Mean percent fish remaining per patch reef constructed of 100% dead coral, 100% live coral, and 100% rubble after ending transplant experiment for two habitat specialists (*Paracheilinus filamentosus* and *Labrichthys unilineatus*) and two habitat generalists (*Halichoeres melanurus* and *Thalassoma lunare*) in Kimbe Bay, Papua New Guinea.

rubble (Fig. 6). As predicted, mean growth differed significantly among habitats ($df = 2, f = 4.318, p = 0.022$). Tukey HSD post hoc analyses revealed that there was a significant difference in growth between preferred habitat (rubble) and live coral ($p = 0.034$). However, growth did not differ significantly between preferred habitat (rubble) and dead coral ($p = 0.163$).

The habitat generalists (*T. lunare* and *H. melanurus*) remained only on two habitats restricting the comparison in growth between specialists and generalists. *T. lunare* did not differ in growth among the two habitats live coral and dead coral, but growth differed between the two habitats live coral and rubble for *H. melanurus* (Fig. 6).

4. Discussion

The predictions concerning the trade-offs associated with different positions along the versatility gradient were only partially supported by this study. As predicted, specialist species exhibited higher survival and growth on their preferred habitats and also outperformed generalist species on preferred habitats. However, contrary to predictions, the two generalists (*H. melanurus* and *T. lunare*) did not do equally well on all habitats and none of the generalists outperformed specialists on less preferred habitats. In fact, the generalists performed much worse on all microhabitats.

According to the trade-off theory, specialisation increases the efficiency of exploiting any one resource, but at the cost of lower performance with respect to others (Futuyma and Moreno, 1988; Kassen, 2002; van Tienderen, 1991). This promotes coexistence between

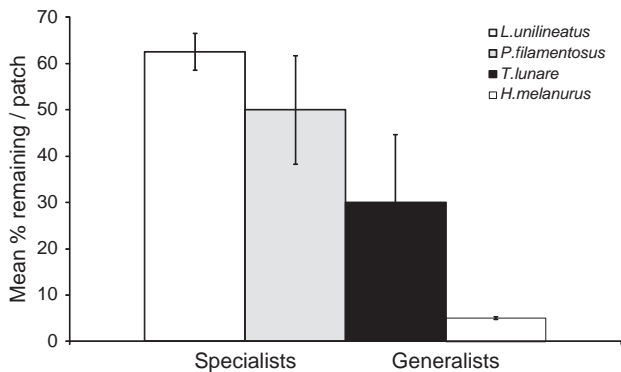


Fig. 5. Mean percent fish remaining per patch reef of preferred habitat for two habitat specialists (*Paracheilinus filamentosus* and *Labrichthys unilineatus*) and two habitat generalists (*Halichoeres melanurus* and *Thalassoma lunare*) in Kimbe Bay, Papua New Guinea.

species as a “superspecies” that did not have to trade-off efficiency when consuming a range of resources would displace all competitors (Vincent et al., 1996). The results for specialists in this study conform to this hypothesis, while generalists exhibited an unexpectedly high mortality. Specialists displayed significantly higher survival than generalists in preferred habitats, suggesting there is an increase in efficiency of exploiting resources with specialisation.

Studies on other reef fish specialists also confirm that specialists are commonly larger, show higher growth and feeding rates, and exhibit higher fecundities than more generalised species in their preferred habitats (e.g. Clarke, 1992; Ebersole, 1985; Robertson, 1995; Srinivasan, 2003). The significantly lower survival and growth rate displayed by specialists in less preferred habitats, suggests that specialisation on one habitat comes with a cost in performing well on others. Although mortality was high in all treatments, even subtle differences in mortality on different microhabitats could have a substantial impact on the likelihood of surviving to maturity (Jones, 1991).

Our results are consistent with studies on a variety of organisms, including fishes, which have detected a cost associated with specialisation (e.g. Griffith and Sultan, 2012; Jackson and Hallas, 1986; Meyer, 1989; Rana et al., 2002; Sanderson, 1990, 1991; Svanbäck and Eklöv, 2003). For example, Sanderson (1990, 1991) showed that a specialist wrasse species had a significantly lower capture success rate when capturing a prey type other than its preferred prey, compared to that of a generalist wrasse species. Most studies on the specialist–generalist continuum focused on morphological or behavioural trade-offs, rather than ecological trade-offs. To our knowledge, there are only three studies similar to the present one on fishes, where habitats or diets were manipulated, and ecological trade-offs tested. One was conducted on a group of coral-dwelling gobies at Lizard Island, Australia, where fishes of differing degree of apparent specialisation were transplanted to different microhabitats (coral species in this case) and growth rates were monitored and compared over time (Caley and Munday, 2003). Similar to the present study, specialist species outperformed generalists in their preferred habitats. However, contrary to the present study, generalists outperformed specialists on non-preferred habitats. Similar results were also obtained in a transplant experiment with sticklebacks in British Columbia, where trade-offs were found between morphs specialised on different habitats (littoral zone vs. open-water habitat) (Schluter, 1995). Berumen and Pratchett (2008), on the other hand, did not find evidence for trade-offs in coral feeding butterflyfishes. The more specialised species did not outperform the more generalised species.

A number of factors may explain why generalists did not outperform specialists on at least some habitats. A close inspection of the selection ratios revealed that *T. lunare* selects for live coral and avoids rubble, while it uses dead coral in proportion to its availability. *T. lunare* may therefore not be as “general” as first thought based on observational data from Berkström et al. (2012) and may explain why some of the predictions for generalists did not hold. Furthermore, performance in this study was measured as the presence of fish remaining on reefs. Losses may be due to mortality or movement of fishes away from patches. It is widely assumed that the disappearance of fish in a colony represents mortality (Nanami and Nishihira, 2001). However, some movement of juveniles between patches and surrounding reefs was discovered for generalist species with a few tagged juveniles ($n = 4$) found on surrounding reefs. Movement rather than mortality may therefore, to some extent, explain why generalists did not outperform specialists in terms of survival on less preferred habitats. Generalist species may be more prone to move than specialist species due to the fact that they can persist on a wider range of microhabitats. By being general in microhabitat usage, a generalist will explore more habitats than a specialist and by doing so will be more likely to move around. However, large sand gaps are known to impede fish movements between reefs (Chapman and Kramer, 2000; Turgeon et al., 2010) due to the low structural complexity of sand offering few refuges from predation (Shulman, 1985; Sweatman and Robertson, 1994), and sand

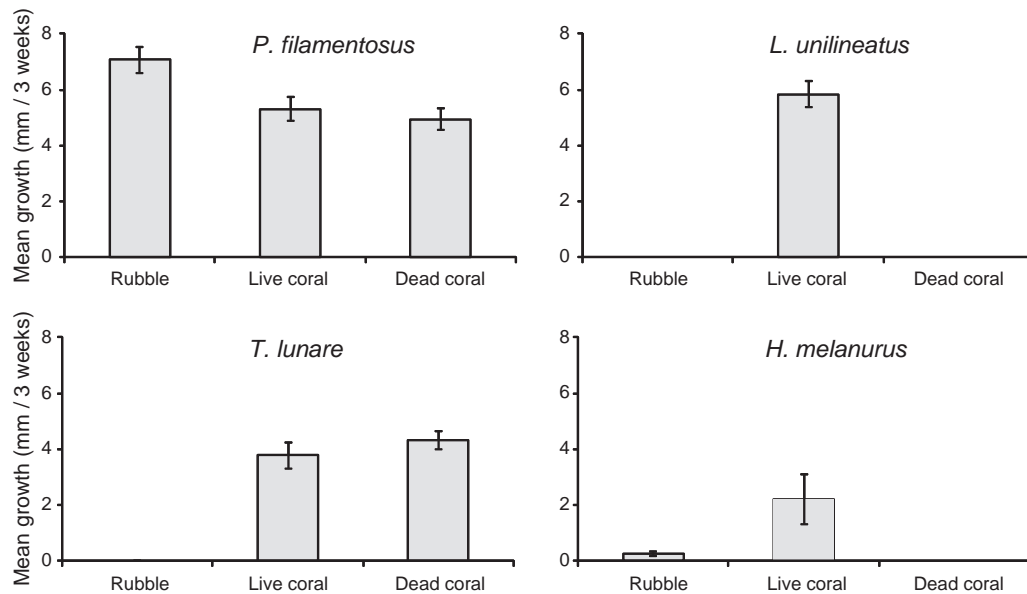


Fig. 6. Mean growth over a period of 3 weeks on three different types of patch reefs (100% dead coral, 100% live coral, and 100% rubble) for two habitat specialists (*Paracheilinus filamentosus* and *Labrichthys unilineatus*) and two habitat generalists (*Halichoeres melanurus* and *Thalassoma lunare*) in Kimbe Bay, Papua New Guinea.

should have been sufficient enough to isolate patches from each other for the two generalist species.

Another explanation to why generalists did not conform to the predictions that generalists would outperform specialists on non-preferred habitats may be that the trade-off is expressed in terms of growth and not survival. Another study comparing a habitat specialist with a habitat generalist (depth in this case) found that survival for the generalist differed between habitats, but growth did not (Srinivasan, 2003). In the present study, growth could not be compared between all habitats for generalists as they did not remain on all 3 habitats, and hence the presence of a trade-off may have been missed. Moreover, a trade-off may exist in some other, untested, characteristic not measured in the present study (Futuyma and Moreno, 1988).

Whether a species is a microhabitat generalist or a specialist may have both short- and long-term effects throughout a fishes' life, e.g. determining its mobility and local home range. A generalist species with a broad use of microhabitats may increase its mobility by being able to survive and feed in multiple habitats, allowing it to move and explore larger areas. In contrast, a specialist species would be restricted by its ability to survive and feed in only one or few habitats. Mobility may explain why the generalist species (*H. melanurus* and *T. lunare*) were the species with most juveniles disappearing within the first week. These fish may have been more prone to move and, hence, be susceptible to predation by transient predators if the patch which they were transplanted to did not supply them with enough food. In contrast, the specialist species (*P. filamentosus* and *L. unilineatus*) may have had a higher tendency to stay on a patch if food was available. The rubble specialist *P. filamentosus* mainly feeds on planktonic copepods (calanoids and cyclopoids) while the generalist species *H. melanurus* and *T. lunare* mainly feed on benthic copepods (haracticoids) (Berkström et al., 2012). Planktonic copepods may be more available for a species to feed on within a restricted area (such as a 1 × 1-m patch reef) due to currents supplying patch reefs with these copepods. Benthic copepods on the other hand are not supplied on a constant rate by currents and hence food availability may explain the pattern (opposite to our predictions) with *P. filamentosus* staying on all habitats although being a specialist and *H. melanurus* and *T. lunare* disappearing from most habitats although being generalist species.

In conclusion, the present study provides some evidence for and some evidence contradicting the trade-off hypothesis. Specialists conformed to predictions while generalists did not. The hypothesis

that generalists are potentially more mobile species requires further investigation. Because growth rates between habitats could not be compared for generalists, the presence of a trade-off in fitness expressed in growth may have been missed. Thus, it is premature to reject the trade-off theory based on these results. We suggest a greater range of specialist and generalist species to be examined in the future, under conditions in which the fate of all individuals can be more accurately determined.

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