



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



Charlotte Berkström^{*,1}, Geoffrey P. Jones, Mark I. McCormick

ARC Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, Queensland 4811, Australia
School of Marine and Tropical Biology, James Cook University, Townsville, Queensland 4811, Australia

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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

* Corresponding author. Tel.: +46 8 16 36 70; fax: +46 8 15 84 17.

E-mail address: charlotte.berkstrom@su.se (C. Berkström).

¹ Department of Ecology, Environment and Plant Sciences, Stockholm University, SE-106 91 Stockholm, Sweden.

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

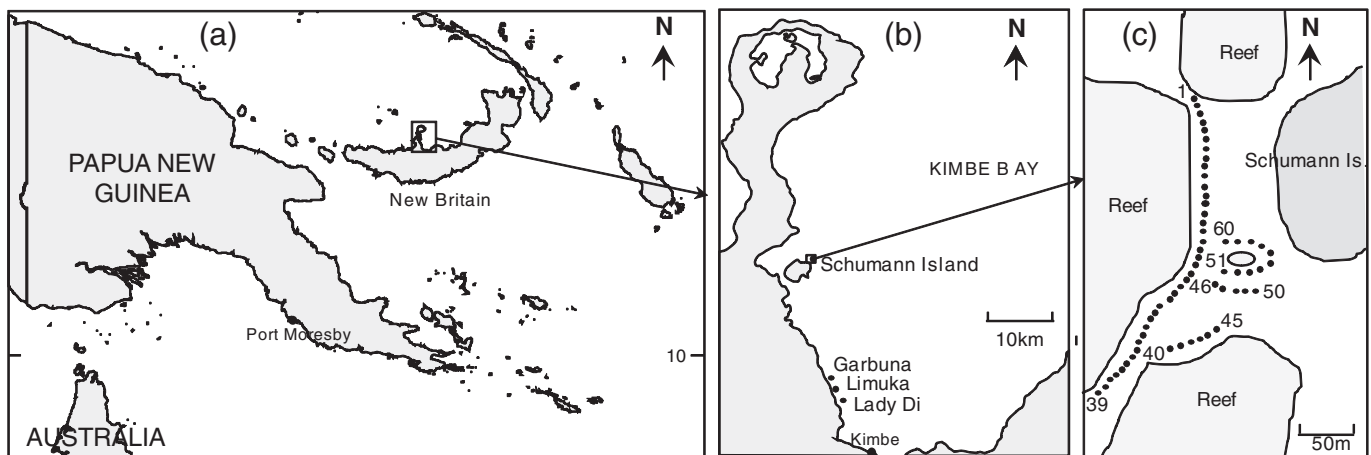


Fig. 1. Map of study site in (a) Papua New Guinea, showing (b) Kimbe Bay where habitat use and habitat availability for four species of juvenile wrasses (two habitat specialists and two habitat generalists) were collected on Garbuna, Limuka, and Lady Di coral reefs, and (c) site where experiments were 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.

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