The Trophic and Spatial Ecology of Rabbitfishes (Perciformes, Siganidae) on Coral Reefs

Thesis submitted by
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The research presented and reported in this thesis was conducted within the guidelines for research ethics outlines in the *James Cook University Policy on Experimentation Ethics: Standard Practices and Guidelines* (2001), and the *James Cook University Statement and Guidelines on Research Practice* (2001). The proposed research methodology received clearance from the James Cook University Experimentation Ethics Review Committee (approval number A1321).

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STATEMENT ON THE CONTRIBUTION OF OTHERS

This thesis is the result of collaborative work with my supervisor, Prof. David Bellwood. While undertaking these collaborations, I was responsible for project concept and design, data collection, analysis and interpretation and synthesis of results into publication format. My supervisor provided intellectual guidance, access to laboratory equipment, financial support and editorial assistance for the writing up of each thesis chapter. Whilst conducting this research I was supported by a James Cook University Postgraduate Research Scholarship.

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Abstract

On Indo-Pacific coral reefs rabbitfishes (Perciformes, Siganidae) represent one of the main families of roving herbivorous fishes. Yet their ecology is little-studied and the exact nature and extent of their role in reef ecosystem processes is currently unknown. This thesis examines the trophic and spatial ecology of abundant species of rabbitfish on the Great Barrier Reef (GBR), Australia and considers the implications of this ecology for ecosystem function.

Variation in the diet, feeding rate, alimentary tract structure and patterns of digestion of two reef-associated species of rabbitfish, *Siganus doliatus* and *Siganus lineatus* were examined in relation to ecosystem function. Despite their similar morphology, the two species exhibited distinct feeding behaviours, with significantly different feeding rates, diets and movements of digesta through the alimentary tract. *S. doliatus* displayed feeding behaviour typical of a diurnal herbivore, taking an average 9.7 bites min^{-1} over the main part of the feeding day and had a diet dominated by red thallate algae (primarily *Laurencia* spp., *Eucheuma* sp., *Halymenia* sp, and *Gracilaria* sp.), and red and green filamentous algae. In contrast, the stomach contents of *S. lineatus* were dominated by amorphous organic matter (detritus). *S. lineatus* could not be observed feeding during diurnal hours and the movement of digesta through the gut suggested that *S. lineatus* was feeding nocturnally or during crepuscular periods. The observed differences in trophic ecology suggest distinct functional roles for these

morphologically similar species, with *S. doliatus* a grazer of reef turf algae and *S. lineatus* primarily a sucker of detrital aggregates.

With underwater observations unable to resolve the location and extent of the functional impact of *Siganus lineatus*, acoustic telemetry (manual acoustic tracking) was used to investigate the movement patterns and spatial ecology of *S. lineatus*. This represented the first time such technology had been used with rabbitfish. Over 550 hours of tracking data were collected on the behaviour of 7 individuals: 4 from a reef habitat and 3 individuals living along a mangrove-shoreline habitat. The average home-range area of *S. lineatus* was found to be 3.2 ha (± 0.35 SE) and, within this total, activity was highly concentrated around core areas (average core area of just 0.39 ± 0.07 ha). Remarkably, the temporal distribution of activity pattern for individuals from the two habitats was diametrically opposed. Those *S. lineatus* inhabiting the mangrove-shoreline site foraged during the day over sandy substrata and remained stationary in rest holes during the night, whereas individuals from the reef-based populations foraged only during nocturnal hours over neighbouring sand-aprons, and remained at the edge of favoured coral bommies during the day. This represents the first documented example of a wholesale intraspecific shift in diel activity rhythm for a tropical marine fish. The results suggest that *S. lineatus* may be an estuarine or dark-water species whose physiological capabilities enable it to feed nocturnally on reefs. This flexibility may simply represent a temporary "masking" effect of external biological stimuli such as predation or competition, or a permanent evolutionary widening of trophic mode that has enabled a species with the ability to feed in dark conditions to expand its habitat range into nocturnal feeding on coral reefs. Either way, the species may have the

potential to provide insights into the impact of biological rhythm plasticity on ecosystem functioning at both the ecological and evolutionary level.

The spatial ecology of the most abundant rabbitfish on inshore reefs of the GBR, *Siganus doliatus*, was also explored in a study of its long-term movement patterns. The degree of mobility and site-attachment displayed by the species was investigated relative to other numerically dominant, so-called "roving" herbivorous fishes, the parrotfishes *Scarus rivulatus* and *Chlorurus microrhinos*. Using remote acoustic telemetry (passive tracking), movements of individuals of the three species were tracked along a 3km stretch of fringing reef on the inner GBR over a period of 12 months. Despite differences in their functional ecology and body size, the three species exhibited similarly small home ranges and high levels of site fidelity over the study period. On average, *S. doliatus* moved along just a 180 m stretch of reef (± 3 m SE), compared to the 220 m (± 10 m) length of reef covered by the excavating parrotfish *C. microrhinos* and the 225 m (± 2 m) covered by *Sc. rivulatus*. Analysing the movement patterns of individuals in terms of organisational network theory revealed that all three species exhibited highly directed movements with "ultra small-world" dynamics of the kind that are characteristically vulnerable to targeted attack. Looking at the movements of reef herbivores through the lens of network topography highlights an inherent vulnerability in the overall process of herbivory, one of the key drivers of coral reef health and resilience.

Having found that the spatial dynamics and site-attachment of rabbitfishes was similar to other reef herbivores, the question remained as to whether the reef-dwelling

algal-feeding species represent an element of functional redundancy on reefs. The feeding behaviour of three rabbitfish species from the clade most closely tied to coral reef habitats: *Siganus corallinus, S. puellus* and *S. vulpinus*, was examined in relation to representative species of the two other main families of roving herbivores (the surgeonfishes and parrotfishes). Observations across four sites showed strong evidence of feeding niche separation at small (<10 cm) spatial scales, with rabbitfishes foraging to a greater degree in reef crevices and interstices. When substratum accessibility (measured as depth of snout penetration) at this micro spatial scale was taken into account, rabbitfishes occupied a broader feeding niche than either parrotfish or surgeonfish and overlap in feeding location between rabbitfishes and the other two families was less than 70%, compared to the 98% overlap observed between parrotfishes and surgeonfishes. Rabbitfishes also showed a significantly greater degree of feeding selectivity than the other herbivore families, taking fewer bites and swimming further between forays. Analysis of the external morphology of the head of representative species of the three families revealed a morphological basis for this behavioural distinction with rabbitfishes displaying a relatively longer, narrower snout and narrower head than the surgeonfish and parrotfish. Sympatric coexistence of rabbitfishes and other roving reef herbivores therefore appears to be facilitated by segregation along a spatial feeding axis. The resulting differentiation in feeding behaviour is based on morphological and, potentially, social specialisations and results in those reef-dwelling species of rabbitfishes examined here performing an ecosystem function unique among roving reef herbivores, that of "cryptic-browser", a group that specifically feeds on cryptic, crevice-dwelling algal communities.

By examining aspects of the trophic and spatial ecology of individual species of rabbitfish, this thesis begins the process of unravelling what has previously been considered a relatively homogeneous functional grouping on reefs ("algal croppers"). It presents evidence of a special ecosystem function for rabbitfishes on reefs, challenges the assumption that morphological similarity equates to functional equivalence, and uncovers unexpected flexibility in the chronoecology of one particular species of rabbitfish as a potential mechanism for expansion of habitat range. Although neither as numerically abundant nor as dominant in terms of biomass as other species of roving herbivore on reefs of the GBR, the unique role of rabbitfish may mean that they are no less deserving of protection in terms of their contribution to key reef ecosystem processes.

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