Habitat specialisation, niche overlap and site fidelity in a vulnerable family of coral reef fishes – the cardinalfish (Apogonidae)

Thesis submitted by

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All data chapters of this thesis include collaborative work with my supervisor Prof. Geoffrey P. Jones. I was responsible for project concept and design, data collections, analyses, synthesis and the preparation of manuscripts. I obtained financial support from James Cook University (GRF and JCU-PRS) and the Nancy Vernon Rankine Award. My supervisor assisted with funds from the Australian Research Council and the ARC Centre of Excellence for Coral Reef Studies. I received considerable research support in the form of field accommodation, food, boating and diving facilities from Mahonia Na Dari and the Walindi Plantation Resort, Kimbe Bay, PNG. Logistical support for Chapter 4 was provided by Lizard Island Research Station, QLD, Australia. K. Winters, J. Stodart, M. Jonkers, M-E. Portwood, M. Cowlishaw, M. Giru and B. Pondi assisted me with data collection in the field. Statistical advice for Chapter 4 was provided by Prof. Phillip Munday. Four anonymous reviewers provided constructive feedback and editorial comments in Chapter 2 and Chapter 4 during the course of peer review for journal publications.

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DECLARATION OF ETHICS

The research presented and reported in this thesis was conducted within the guidelines for research ethics outlined in the *National Statement on Ethics Conduct in Research Involving Human (*1999*),* the *Joint NHMRC/AVCC Statement and Guidelines on Research Practice* (1997)*,* 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 A1028).

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It is the glory of God to conceal a matter;
to search out a matter is the glory of kings.
Proverbs 25:2

I dedicate this PhD thesis to my grandfather, Dr. John W. Gardiner.
Your scientific curiosity and passion for knowledge is an inspiration to us all.

GENERAL ABSTRACT

Habitat degradation is viewed as the most imminent threat facing coral reef fish assemblages. Reef fishes may have a low resilience to habitat change as a result of key ecological and behavioural traits, including extreme habitat specialisation, high levels of co-occurrence and strong home site fidelity. This thesis explores the levels of specialisation, co-occurrence and site fidelity (including homing behaviour) and their interrelationships in a speciose family of coral reef fishes - the cardinalfish (Family Apogonidae). The vulnerability of this family to habitat loss and degradation is examined by addressing the following five questions: (1) Do cardinalfish communities exhibit strong associations with particular substrata or do species vary in their micro-habitat use? (2) Do cardinalfish species differentially specialise on particular types of coral colonies and on specific areas within coral colonies? (3) Is the observed degree of habitat specialisation and niche overlap a result of behavioural preferences for habitat types, conspecifics or a combination of these? (4) Do cardinalfish individuals move amongst adjacent resting sites and can they home between isolated reef platforms? (5) Are cardinalfish constrained to using particular resting sites or can they relocate following habitat disturbance?

Chapter 2 describes the degrees of habitat specialisation and spatial overlap among 10 common cardinalfish species in Kimbe Bay, Papua New Guinea (PNG). Nine of the 10 common species were strongly associated with live scleractinian corals and the majority of individuals were associated with a single species of branching coral (*Porites cylindrica*). Cardinalfish used this coral much more than would be expected given its availability, indicating a high degree of apparent habitat specialisation. In addition, the nine coral dwelling apogonids exhibited a high degree of spatial overlap using the same depth ranges, the same species of corals and the same individual colonies. The high level of both specialisation and overlap in habitat use suggests that this reef fish assemblage is particularly susceptible to the loss of a single coral species.

Evidence for fine-scale habitat use and partitioning of a single coral species (*Porites cylindrica*) was examined in **Chapter 3**. There was considerable evidence of fine-scale specialisation and partitioning among seven common cardinalfish species in Kimbe Bay (PNG), both among *Porites* colonies and on refuge positions within *Porites* colonies. All species preferentially inhabited large coral colonies, despite their limited availability. Strong conspecific aggregation observed in six of these species lead to a high proportion of unoccupied corals. Within coral heads, three cardinalfish species showed a high degree of specialisation, inhabiting a small

proportion of the available space. A high level of habitat partitioning among species was also observed within colonies. Species differentiated between refuge areas deep inside coral colonies, within interstitial spaces at the colony surface and positions on the vertical edges of coral colonies. There was a positive relationship between the breadth of fine scale habitat use and the degree of species overlap both amongst and within coral colonies. Only two of the rarer, specialist species shared coral colonies and refuge positions. This study confirms that there is fine-scale habitat specialisation and partitioning in this common reef fish guild. Biodiversity of this group will be particularly vulnerable to the loss of large *Porites* colonies.

Chapter 4 explores the degree to which habitat and social preferences explain the association that three common cardinalfish species have with coral substrata. Three-way choice experiments were conducted to test fishes habitat preferences for living coral over dead substrata, for particular coral species and the influence of gregarious behaviour on these habitat choices. The strength of preferences for live *P. cylindrica* coral differed among species. All species were attracted to conspecifics and for some species attraction resulted in stronger associations with live *P. cylindrica* colonies. Conversely social preferences weakened associations with *P. cylindrica* when conspecifics occurred on marginal habitat. This chapter's results indicate that in the field, habitat preferences and conspecific attraction combine to reinforce the association between cardinalfishes and the narrow range of coral substrata seen in **Chapters 2** and **3**.

Under conditions of widespread habitat loss, strong bonds with home sites may restrict population connectivity and limit resilience to habitat change. **Chapter 5** examines the extent of site fidelity and homing behaviour for cardinalfishes of Kimbe Bay. It focuses on four species that are typically restricted to resting in large *P. cylindrica* colonies after nocturnal foraging migrations. Tagged individuals of two species remained faithful to particular colonies and to specific areas within these colonies. In contrast two other species moved between nearby colonies and/or away from the home reef area. Displacement experiments showed that all species exhibited strong homing behaviour up to 500m across continuous reef and deep open-water channels. A remarkable ability to home over long distances (2 and 5km) was also observed for one species.

Chapter 6 investigated whether cardinalfish species relocate from disturbed home sites or persist in the degraded habitat. Home coral colonies of two species were experimentally disturbed by draping them in netting to exclude cardinalfish access. Patterns of site fidelity and relocation of tagged individuals were compared with controls, before and after the disturbance. Most individuals remained faithful to home sites prior to the manipulation and on control sites

throughout the experiment. However, when access to home sites was blocked, most individuals either died (40%) or emigrated to nearby aggregation sites (50%). The majority of individuals resisted moving from home sites more than four days before emigrating. 25% of displaced individuals returned home after the disturbance had ceased. Results suggest cardinalfish associations with home sites are based on strong traditions and while some species can relocate to new homes, increased mortality may result. If traditional aggregation sites are permanently lost, long-term population decline is predicted.

In conclusion, the combination of extreme habitat specialisation, high levels of co-occurrence and strong site fidelity and homing behaviour indicate many cardinalfish species will be severely impacted by habitat loss. Cardinalfish in the Australia/PNG region will be highly vulnerable to declines in the availability, of not just a single branching coral species, *Porites cylindrica*, but to the loss of large coral colonies and to the damage of particular colonies sites that host large resting aggregations. Species exhibit a high dependence on particular coral colonies due to interactive effects of habitat specialisation preferences, social attraction to other cardinalfish and a limited capacity to relocate following localized disturbances. The family-level dependence on a single coral species provides a sobering example of how declining coral health may threaten biodiversity and re-shape the taxonomic structure of reef fish communities.

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