Disentangling the effects of macroalgae on the abundance of temperate reef fishes

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ABSTRACT

Habitat heterogeneity may mediate the relationship between organisms and their environment. However, the demographic and behavioural responses of organisms to different sources of habitat heterogeneity (*e.g.*, structural complexity and composition) may vary, and consequently, different sources of heterogeneity may interact to shape the abundance of individual species and composition of a species assemblage. We focused on habitat-forming macroalgae, and conducted a set of laboratory experiments to determine the macroalgal preferences of two species of temperate reef fish. In a subsequent field experiment, we manipulated macroalgal heterogeneity at two sites in Wellington, New Zealand, to determine the relative importance of different sources of habitat heterogeneity to the abundance of locally common reef fishes. Specifically, we manipulated three sources of habitat heterogeneity: (1) macroalgal species identities; (2) combinations of macroalgal species (*i.e.*, mixed stands); and (3) macroalgal density. Our laboratory experiments indicated that two common fishes readily distinguish and exhibit preferences for different forms of macroalgae. Our field experiment indicated that the abundance of reef fishes varied as a function of experimentally induced habitat heterogeneity. We detected within-species variation in responses to macroalgal composition (suggesting ontogenetic habitat shifts), and larger-scale influences on the abundance of reef fishes (effects attributable to location). Macroalgal identities affected the abundance of 7 of 15 reef fish species. Composition of macroalgal stands shaped the abundance of 5 of 7 reef fish species, and the overall structure of the local fish assemblage. Generally, heterogeneity in vegetative structures appeared to increase breadth of habitat use for reef fishes. This work suggests strong behaviourally mediated linkages between the abundance of reef fishes and the composition of vegetative structures in a temperate, macroalgal-dominated ecosystem.

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1. Introduction

Habitat heterogeneity is widely viewed as a precursor to biological diversity. Homogenization of ecological systems by human activities (*e.g.*, intensive fishing or farming) is often correlated with a progressive decrease in biodiversity (Loreau et al., 2004). This has led some workers to suggest that the protection and enhancement of habitat heterogeneity should form the basis for conservation and management of ecological communities (Fuhlendorf et al., 2006). However, "habitat heterogeneity" is a term that potentially encapsulates a wide range of environmental variables (*e.g.*, composition, patch or "grain" size, and structural complexity), and these individual variables may act separately or in combination to shape the behavioural and/or demographic responses of individual species. Moreover, individual species (or age-classes within a species) may vary in their responses to habitat heterogeneity. Consequently, a more sophisticated understanding of relationships between habitat heterogeneity and species responses may be desirable.

In temperate marine environments, brown macroalgal forests are known to influence the abundance and distribution of associated macrofaunal assemblages (Dayton, 1985; Schiel and Foster, 1986; Graham, 2004). The structure and composition of macroalgal stands (and the morphology of individuals for a given species of macroalgae) can vary considerably, often as a function of local environmental conditions (Schiel and Foster, 1986). Understanding how algal-associated organisms such as reef fishes respond to local-scale variation in the structure of macroalgal communities requires recognition of how different components of macroalgal habitats (*e.g.*, species identity, structural complexity, density) potentially interact to influence the abundance of a dependent species.

Vegetative structures of macroalgae may provide a range of "services" to fish, including food (or feeding sites) and refuge from potential predators. Fish and other organisms may use the same vegetative structures of an individual alga for different purposes, or they may partition their activities among different components of the alga (*e.g.*, fronds may be used for refuge/shelter and holdfasts for feeding sites; Steneck et al., 2002; Christie et al., 2007). In addition, the role and importance of specific vegetative features to fishes may vary with their ontogeny, and/or depend upon local environmental conditions (*e.g.*, degree of wave exposure and presence of predators, Taylor and Cole,

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1994; Christie et al., 2007). Specific macroalgal traits may act separately or in synergy with others to shape patterns of distribution and abundance of fishes.

Experiments that attempt to partition and explore the effects of different components of habitat heterogeneity (*e.g.*, the relative importance of habitat-forming species' identities, densities, and multi-species composition) are rare (but see Benedetti-Cecchi, 2004). Consequently, important complexities that may underlie relationships between temperate reef fishes and macroalgal habitats remain largely unexplored.

Given the strong effects of habitat attributes on fitness of dependent species (described above), we expect to find that reef fishes discriminate among different components of habitat heterogeneity (*i.e.*, presence/absence of macroalgae, macroalgal species identity, and the composition of algal stands). Consequently, we hypothesise that (1) habitat heterogeneity will shape the distribution and abundance of individuals over small spatial scales; (2) reef fishes may differ in their responses to particular sources of habitat heterogeneity (and these responses may depend upon local environmental contexts); and consequently, (3) different macroalgal habitats will support different species assemblages.

2. Materials and methods

2.1. Laboratory experiment — capacity for behaviourally mediated habitat preference

To determine whether common fish in our study system exhibit preferences for different macroalgal habitats, we conducted a choice experiment in a large outdoor recirculating tank ($9 \times 6 \times 1.2$ m depth) at the National Institute of Water and Atmospheric Research (NIWA), Wellington, New Zealand. We estimated behavioural preferences of two species of locally common reef fish (*Notolabrus celidotus* and *Notolabrus fucicola*) for five different benthic substratums.

N. celidotus (commonly known as the "spotty") and *N. fucicola* (the "banded wrasse") are reef fishes of the family Labridae, and among the most common inhabitants of reefs in the Wellington region. Both species feed upon invertebrates, with *N. fucicola* also consuming other small fishes (Russell, 1983; Denny and Schiel, 2001; Francis, 2001). *N. celidotus* and *N. fucicola* reach total lengths (TL) of up to 300 and 600 mm respectively

(Francis, 2001). We collected 10 small *N. celidotus* (TL < 150 mm), 10 large *N. celidotus* (TL > 150 mm), and 10 large *N. fucicola* (TL > 150 mm) using baited traps. All captured individuals were transferred to indoor concrete holding tanks and allowed to acclimatise for at least 48 h prior their use in experimental trials.

Initial field observations led us to identify and select three locally common species of macroalgae as potentially important habitats for reef fishes in our area: *Macrocystis pyrifera*, *Carpophyllum maschalocarpum*, and *Cystophora retroflexa*. These three algal species are abundant on shallow subtidal reefs of Wellington harbour (*e.g.*, Kau Bay) and the adjoining (and comparatively wave-exposed) south coast (*e.g.*, Island Bay, see Fig. 1a). In the study area, *M. pyrifera* (Fig. 1b) can reach up to 6 m in stipe length, and often forms large surface canopies aided by air-filled pneumatocysts; *M. pyrifera* provides shade and vertically-structured habitat through the water column. *C. maschalocarpum* (Fig. 1c) has flattened blades with ellipsoid vesicles. *C. retroflexa* (Fig. 1d) has a conical holdfast, a zig-zag stipe, rounded blades, and globose vesicles. Relative to *M. pyrifera*, *C. maschalocarpum* and *C. retroflexa* are smaller bushy-type macroalgae, reaching up to 0.5 to 1.5 m in stipe length (for further details see Adams, 1997). In the Wellington region, *M. pyrifera*, *C. maschalocarpum* and *C. retroflexa* reach mean densities of 3.8($\pm$1.6 SD), 4.1($\pm$2.4 SD), 1.0($\pm$1.5 SD) per m^2 respectively (A.P.M. *unpublished data*). We collected intact seaweed specimens (and associated epifauna) of all three species that were attached to small boulders using an open mesh collecting bag (0.5 mm mesh size). We attempted to minimise losses of associated epifauna by transferring seaweeds to tanks of seawater immediately after collection. We maintained specimens in outdoor tanks supplied with flow-through seawater, and these storage tanks were covered with black 0.5 mm mesh shade cloth to approximate light conditions from the sites of collection.

Our experimental design consisted of five treatments that we established within a single large tank: (1) four individuals of *M. pyrifera*, (2) six individuals of *C. maschalocarpum*, (3) six individuals of *C. retroflexa*, (4) 6–7 boulders (30 to 50 cm diameter) with no macroalgae, and (5) a control (an identified patch within the tank with no macroalgae or rocks). Different numbers of individuals per species were used to balance the biomass among treatments, and also reflected natural densities found in the field. Treatments were arrayed in a randomised order in a roughly circular pattern and separated from one another by 3 m. Experimental trials consisted of the release of a single focal individual of either
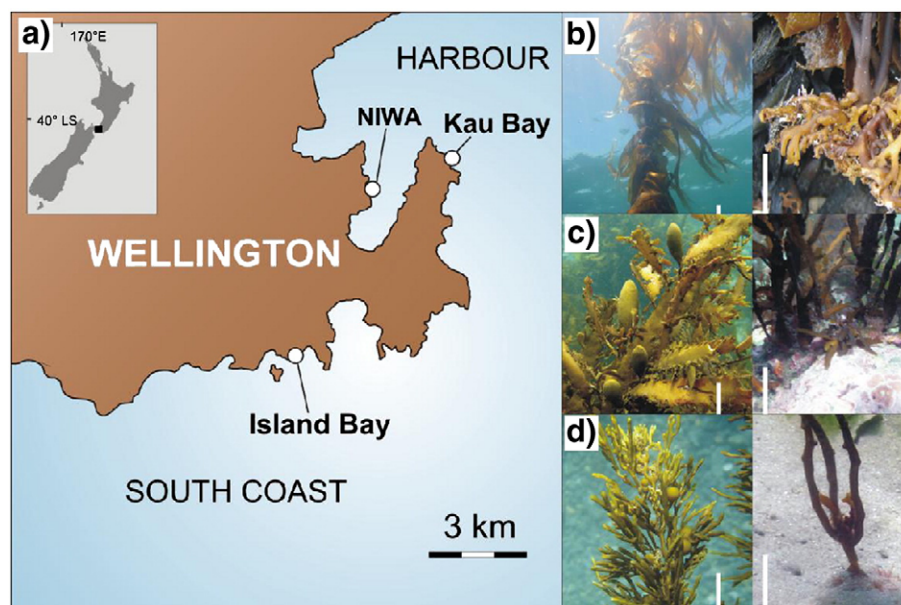

Fig. 1. a) Map giving locations of the study sites in Wellington Region, New Zealand; photographs of blades and their holdfasts for: b) *Macrocystis pyrifera* (Laminareales), c) *Carpophyllum maschalocarpum* (Fucales), and d) *Cystophora retroflexa* (Fucales). (*photo credits*: E. Macaya and A. Pérez-Matus).