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Carbon isotope signatures reveal that diet is related to the relative sizes of the gills and palps in bivalves

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ABSTRACT

In marine bivalves, the relative sizes of the gills and palps appear to be a useful functional trait that reflect feeding mode, i.e. suspension feeders have relatively larger gills than palps for pumping, whereas deposit feeders have relatively larger palps than gills for sorting. Also, within a species, the relative sizes of the gills and palps are related to changes in local food conditions. However, there is still no firm evidence showing that differences in the relative gill and palp sizes between species are related to diet selection. Based on the knowledge that carbon and nitrogen isotope signatures of an animals tissues reflect past diet, we compared the relative gill and palp sizes of bivalves from Roebuck Bay, northwestern Australia with their carbon and nitrogen isotope signatures. The carbon isotope signatures distinguished clear differences in diet between bivalves along a gradient from suspension to deposit feeding, and strikingly this pattern was closely followed by the relative sizes of the gills and palps of the bivalves. This study confirms that relative gill and palp sizes in bivalves are a functional trait that can be used to compare resource use between species. Furthermore, these data may suggest that morphospace occupation, as determined by relative gill and palp sizes of bivalves, could reflect a gradient of resource use between species.

1. Introduction

Functional traits have been proposed as necessary building blocks needed to provide insights into species adaptations and interactions including ecosystem properties (McGill et al., 2006). A trait is defined as any morphological, physiological or phenological feature measurable at the level of the individual, and a functional trait is a trait that impacts fitness indirectly via its effects on growth, reproduction or survival (Violle et al., 2007). It is expected that the most predictive functional traits will be those that relate directly to resource acquisition (McGill et al., 2006), e.g. beak size and shape in birds (Schoener, 1971) and feeding morphology in fishes (Bellwood et al., 2006). A revival of trait comparisons in community ecology should be useful (McGill et al., 2006); as previously, morphological traits have provided insights both as direct and indirect measures of an organism's performance and/or resource use (Wainwright, 1994).

Contrary to the expectation that benthic bivalve species indiscriminately select their diet based solely on the size of food particles (see review by Ward and Shumway, 2004), there is evidence to show that bivalve species have the potential to select their diet based on particle quality via their feeding processes (Levinton et al., 1996; Ward and Shumway, 2004; Ward et al., 1997). Feeding processes, i.e. food uptake and selection, are optimized by the finely–tuned cooperation between the gills (ctenidia) and labial palps of the bivalves. The main role of the gills is to trap particles from a self–generated water current, and transfer these particles to the labial palps (Jones et al., 1992; Meyhöfer, 1985; Møhlenberg and Riisgård, 1978). The labial palps predominantly sort the organic from inorganic particles (Pohlo, 1967; Yonge, 1949). Organic particles are then accepted into the alimentary canal, whereas inorganic particles are rejected as pseudofaeces. Depending on the gill type in some suspension feeders sorting and rejection of particles can take place on the gill and the role of the labial palps can be reduced (Barille et al., 2000; Dutertre et al., 2007; Shumway et al., 1985; Ward et al., 1998). Interestingly, the way in which bivalves deal with food quantity and quality appears to be species dependent (Ward et al., 2003).

The capability of the gills and palps to respond to food conditions and distinguish bivalve feeding modes, suggests that these organs are a unique functional trait. Within a species, the size of the gills and labial palps are

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Table 1
Species names, their authority name (authority) and their phylogenetic classification (subclass, order, superfamily, family)

species	authority	subclass	order	family	MGS	silt	description of habitat	latitude	longitude
Suspension feeders									
Anadara granosa	Linnaeus 1758	Pteriomorphia	Arcoida	Arcidae	96	28	DF: fine sediments	−17°58′36″	122°16′16″
Anomalocardia squamosa	Linnaeus 1758	Heterodonta	Veneroida	Veneridae	168	8	DF: sandy sediments	−17°58′43″	122°15′22″
Barbatia pistachio	Lamarck 1819	Pteriomorphia	Arcoida	Arcidae	NA	NA	DF: rocky outcrop	−17°58′54″	122°16′05″
Gafrarium tumidum	Röding 1798	Heterodonta	Veneroida	Veneridae	163	8	DF: mangrove roots	−17°58′50″	122°16′12″
Placamen berryi	Menke 1843	Heterodonta	Veneroida	Veneridae	103	23	DF: fine sediments	−17°58′47″	122°16′47″
Deposit feeders									
Tellina capsoides	Lamarck 1818	Heterodonta	Veneroida	Tellinidae	88	30	DF: fine sediments	−17°58′47″	122°16′47″
Tellina sp.		Heterodonta	Veneroida	Tellinidae	23	85	One Tree: silt	−17°59′24″	122°22′58″
Tellina piratica	Hedley 1918	Heterodonta	Veneroida	Tellinidae	168	8	DF: sandy sediments	−17°58′43″	122°15′11″
Lucinid bivalve									
Divericella irpex	Smith 1885	Heterodonta	Veneroida	Lucinidae	117	22	DF: sandy sediments	−17°58′47″	122°15′14″

The sediment characteristics measured at the sample site of each species are included: median grain size (MGS) and silt (<63 μm fraction of sediment, %) and a description of the habitat (DF is Dampier Flat). The geographical coordinates of collection are also included. NA indicates data was not available.

known to be flexible (Drent et al., 2004; Piersma and Drent, 2003) and related to changing food conditions over time (Honkoop et al., 2003) and space, e.g. turbidity and silt (Barille et al., 2000; Drent et al., 2004; Essink et al., 1989; Payne et al., 1995a; Payne et al., 1995b; Theisen, 1982). Furthermore, the relative size of the gills and labial palps reflect different functional roles in suspension and deposit feeding bivalves. In suspension feeders, the relatively larger gills than labial palps suggest pumping is important for food collection (Jones et al., 1992; Møhlenberg and Riisgård, 1978), whereas in deposit feeders the relatively larger labial palps than gills suggest sorting is important for purging inorganic material (Pohlo, 1967; Reid and Reid, 1969; Yonge, 1949). Interestingly, the relative size of the gills versus the labial palps in multiple bivalve species form a gradient between suspension and deposit feeders within two tidal flat systems, suggesting that bivalves can fill a wide spectrum of feeding niches (Compton et al., 2007). Thus, relative gill and palp sizes of bivalves are known to relate to food acquisition. However, there is no direct evidence showing that the relative gill and palp sizes reflect diet selection.

Previously, it was not easy to identify how feeding morphology was related to diet in bivalves because: (1) assimilated food sources were difficult to determine (Hummel, 1985; Kamermans, 1994), and (2) some bivalve species easily switch feeding mode, e.g. facultative deposit feeders (Brafield and Newell, 1961; Hughes, 1969; Ólafsson, 1986; Peterson and Skilleter, 1994; Thompson and Nichols, 1988). For example, stomach content analysis suggested that a suspension (*Cerastoderma edule*) and a deposit (*Macoma balthica*) feeder were eating similar proportions of the same food sources, i.e. benthic and pelagic algae (Kamermans, 1994). More recently, carbon and nitrogen stable isotopes have shown a clear–cut separation between bivalve species in their assimilated carbon sources (viz. dietary sources) (Decottignies et al., 2007b; Herman et al., 2000; Riera, 2007; Riera and Richard, 1996; Riera et al., 1999), such that the suspension feeder (*Cerastoderma edule*) was observed to assimilate carbon from plankton, whereas the deposit feeder (*Macoma balthica*) assimilated carbon from a mixed diet of benthic microalgae and plankton (Rossi et al., 2004). Within individual bivalve species, carbon isotopes have also shown that there is differential diet selection along estuarine gradients (Riera and Richard, 1996; Yokoyama and Ishihi, 2003), and that bivalve diets reflect changing food conditions over time (Decottignies et al., 2007a; Decottignies et al., 2007b).

In this study, the gill and palp size of bivalves were related to the carbon and nitrogen isotope signatures of the bivalves from Roebuck Bay, northwestern Australia. We aimed to test whether the relative sizes of gills and palps of bivalves reflect diet, and thus can be used as a functional

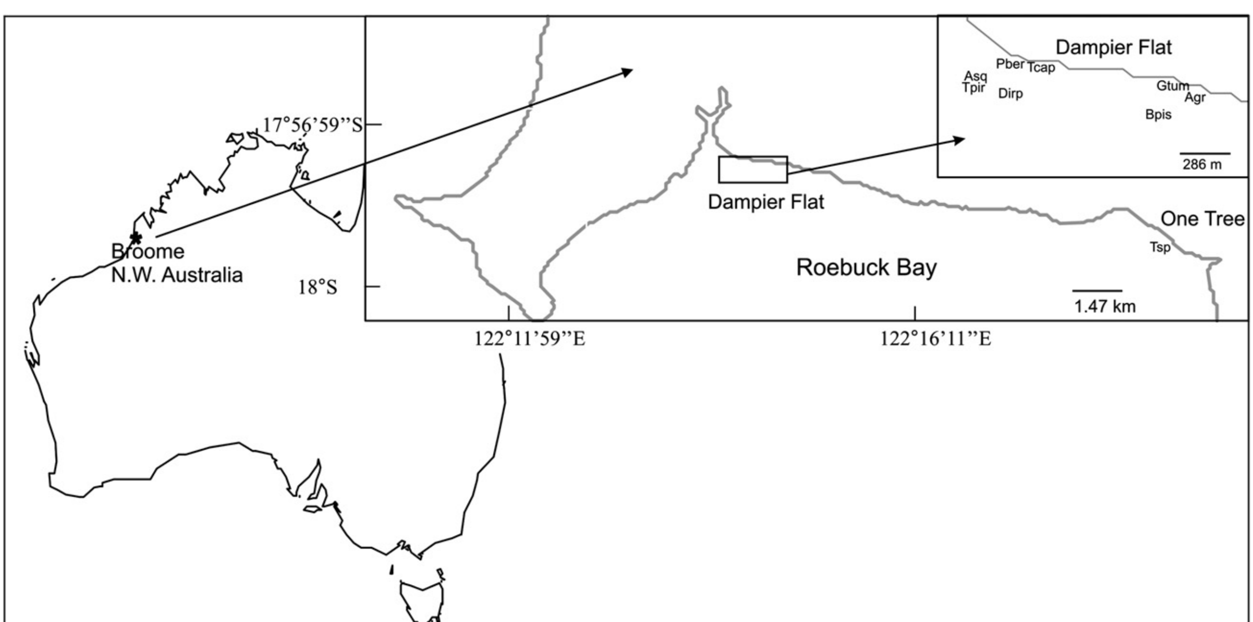

Fig. 1. Roebuck Bay is situated near the town of Broome. Within Roebuck Bay the study sites were Dampier Flat and One Tree. Within the sample site of Dampier flat, the sample spot of each bivalve species is indicated. The species names are abbreviated: Asq – *A. squamosa*, Gtum – *G. tumidium*, Pber – *P. berryi*, Agr – *A. granosa*, Bpis – *B. pistachia*, Tsp – *T.* sp., Tcap – *T.capsoides*, Tpir – *T. piratica*, Dirp – *D. irpex*.