Are tropical bivalves more specialized in their feeding morphology and habitat preferences than temperate bivalve species?

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The peak of species diversity in tropical areas has mystified temperate European scientists ever since the exploration of the New World led to the discovery of so many unknown new species. There are now more than 25 hypotheses that attempt to explain increased biodiversity in the tropics. But contrary to the many hypotheses, the common drivers that maintain tropical diversity are still not evident. To find the common drivers for species diversity, approaches are needed that compare adaptations of organisms within the context of their tropical and temperate environments. Such approaches have proven fruitful in the past. For example, shells are generally thicker in tropical than in temperate gastropod species, a phenomenon that is related to higher predation pressure. In this study we compared bivalve feeding morphology at a tropical (Roebuck Bay, Figs.1 and 2) and a temperate (The Dutch Wadden Sea) tidal flat to elucidate if morphological features could shed light on the relative competitive pressures in tropical and temperate systems. We also examined if the use of habitat space differed in highly diverse tidal flat systems from that in low diversity tidal flat systems.

Fig. 1 Roebuck Bay, Broome (top panel) and brooming for bivalves in Roebuck Bay (bottom panel).

Fig. 2. A bivalve from Roebuck Bay (*Tellina inflata*). Photo by R. Kentie.

In this study we examined bivalve species across different tidal flat systems. Bivalves are generally considered useful for examining diversity because (1) they have an extensive fossil record and (2) are found in a wide variety of marine habitats. In marine tidal flat systems, bivalves are useful to examine because they can form an integral part of ecosystem functioning, e.g. being a crucial link in food chains and/or maintaining water quality.

In biologically diverse tidal flats, it is expected that increased competition for food should promote increased resource specialization and thus increased morphological variation. Indeed, bivalve feeding morphology showed greater morphological variation at the tropical Roebuck Bay than the temperate Dutch Wadden Sea (Fig. 3). However, the greater morphological variation in Roebuck Bay was limited, as the Roebuck Bay bivalve species showed a larger degree of morphological similarity than the Wadden Sea bivalves. Morphological similarity of bivalve feeding organs could suggest that diet overlap is occurring in Roebuck Bay; especially because a direct correlation between bivalve feeding organs and diet, as determined by carbon isotope signatures, was observed. Morphological similarity between bivalves in Roebuck Bay might suggest that competition for food resources is not an important aspect maintaining species diversity in tropical Roebuck Bay.

Increased species diversity is expected to be associated with increased habitat heterogeneity. Increased habitat heterogeneity should either provide more niches and/or enable greater coexistence in diverse tidal flats. Although marine soft sediment environments are often considered to be vast and homogeneous, in reality sedimentary systems are complex environments with a variety of sediments and microhabitats. For example, shell debris and seagrass beds are known to be associated with increased species richness. In this study, increased species richness was not correlated with increased sediment heterogeneity across nine tropical and temperate tidal flats (Fig. 4). Instead of habitat differentiation, bivalve species showed distributional overlap within a local system (Fig. 5). Distributional overlap might suggest that species are facilitating their own coexistence via positive interactions and feedback loops.

In this study, we did not find that feeding morphology was differentiated or that bivalves have distinct habitat prefer-

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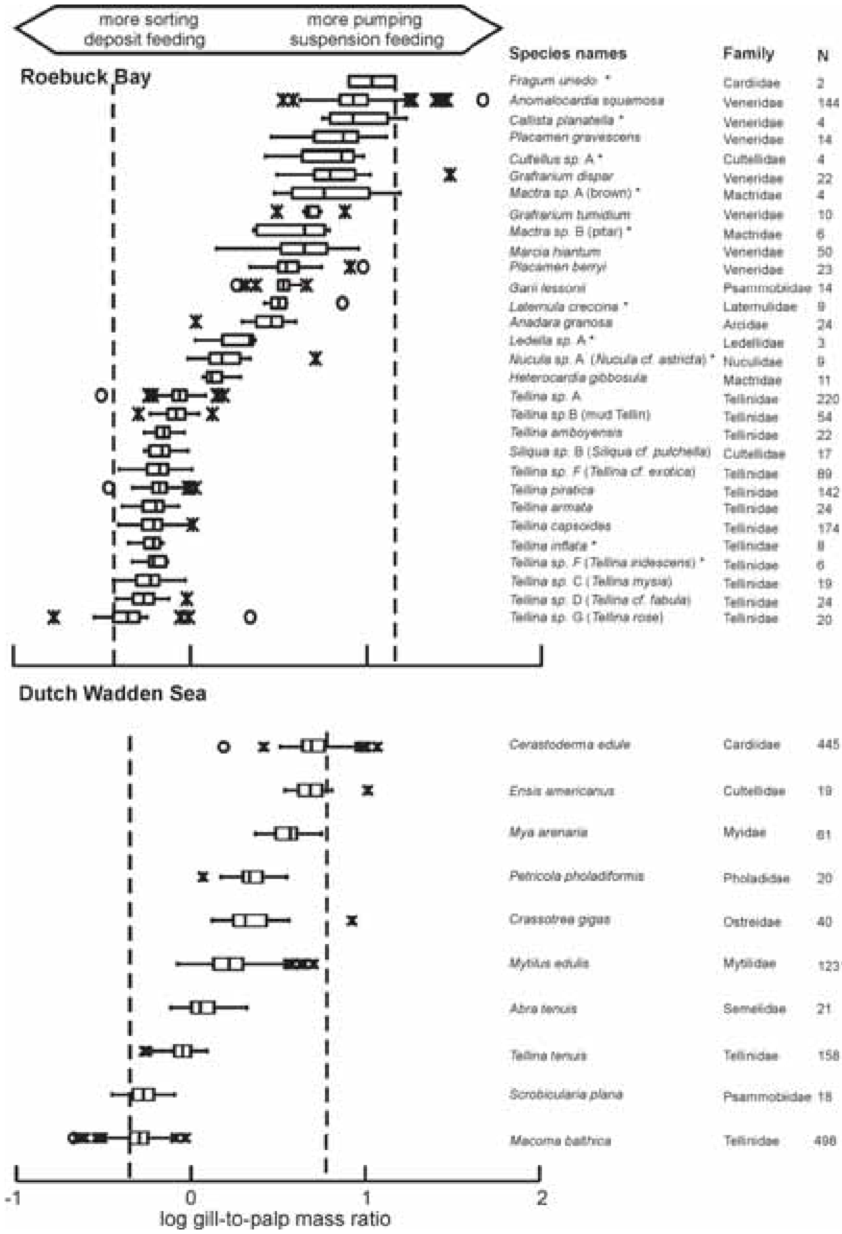

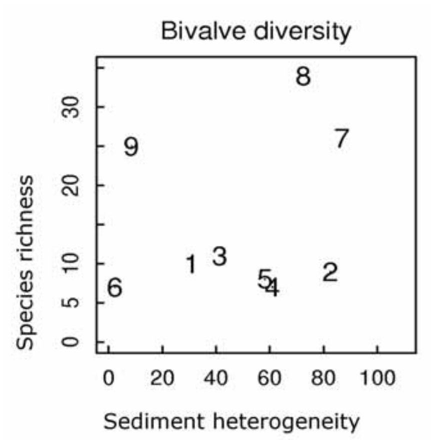

Fig. 3. Ranked sizes of the bivalve feeding morphology (log gill-to-palp mass ratios) in Roebuck Bay (top figure) and the Wadden Sea (bottom figure.). The bivalve feeding morphology displayed a gradient between mostly sorting (deposit feeding) and mostly pumping (suspension feeding), within the total morphological space at each location, as indicated by the stippled lines. The numbers of individuals (N) collected for each species are shown and the names of each species and their family are given.

Fig. 4. The species richness at three tropical and six temperate tidal flat systems was not correlated with sediment heterogeneity, determined as the interquartile range (IQR) of median grain size measurements (MGS). Tidal flats are indicated by numbers: 1 – German Wadden Sea, 2- Dutch Wadden Sea, 3 – The Wash, 4 – Mont Saint-Michel Bay, 5 – Marennes-Oléron Bay, 6 – Aiguillon Bay, 7 – Banc d'Arguin, 8 – Roebuck Bay, 9 – Eighty-mile Beach.

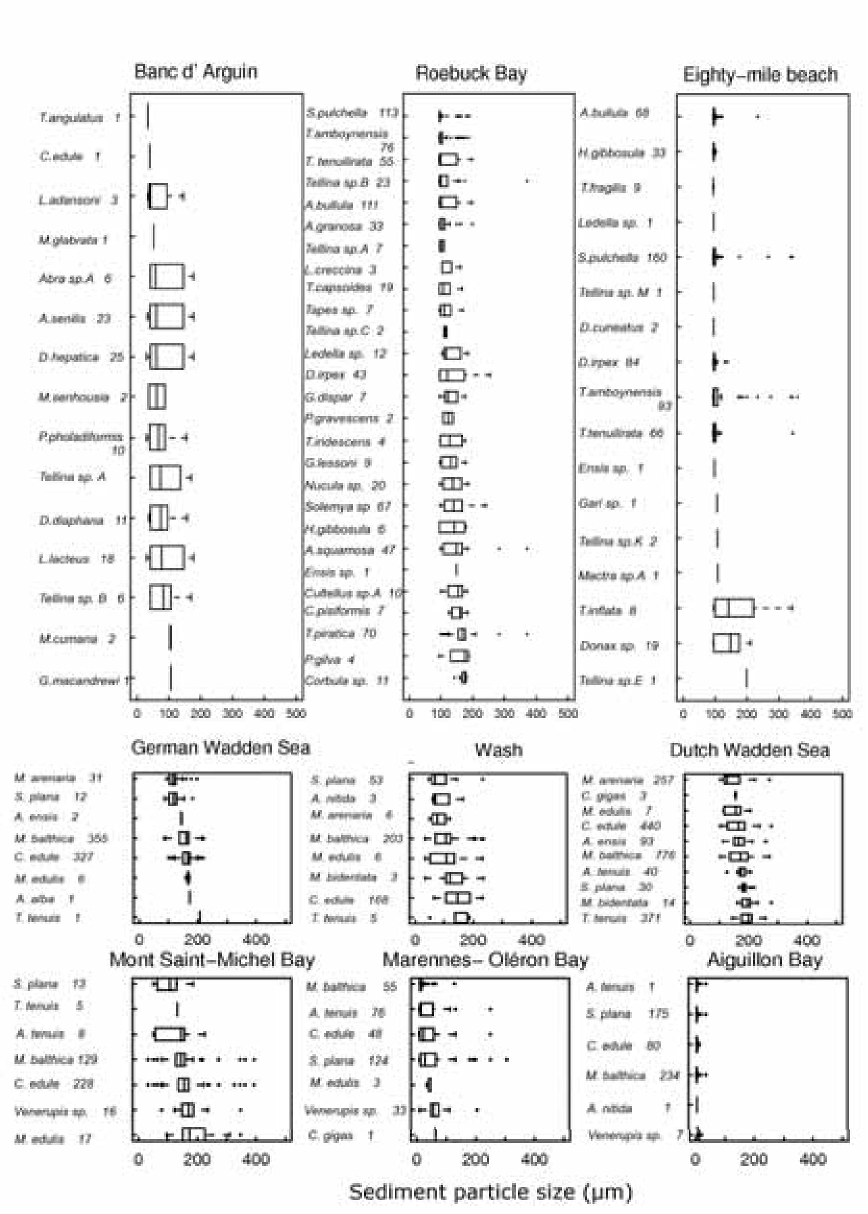

Fig. 5. Distributional overlap as shown by ranked boxplots of bivalve species distributions at three tropical (Banc d' Arguin, Roebuck Bay and Eighty-mile beach) and six temperate tidal flats (German and Dutch Wadden Sea, The Wash, Mont Saint-Michel Bay, Marennes-Oléron Bay and Aiguillon Bay). The name of the species and number of occurrences measured per species are shown next to each boxplot.

ences. These findings are contrary to our expectations that species in diverse bivalve assemblages would show specializations that enable them to coexist. A lack of feeding and habitat specializations could suggest that these aspects are not important factors driving diversity in tidal flat systems but that other parameters may drive differentiation, e.g. shell thickness in response to predation. Interestingly, some other studies have also shown morphological similarity in tropical systems, leading us to ponder how species then share a limited amount of resources. To identify factors influencing species differentiation in sedimentary systems an extensive set of functional traits and their related adaptive pressures should be measured across multiple systems in future studies.