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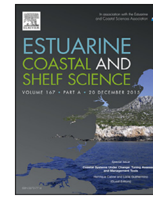

Trophic relay and prey switching – A stomach contents and calorimetric investigation of an ambassid fish and their saltmarsh prey

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ABSTRACT

Trophic relay is an ecological model that involves the movement of biomass and energy from vegetation, such as saltmarshes, within estuaries to the open sea via a series of predator-prey relationships. Any potential for trophic relay is therefore affected by water movements within an estuary and by the ability of a predator to "switch" prey in response to fluctuating abundances of those prey. Saltmarsh-dwelling grapsid crabs, which feed on saltmarsh-derived detritus and microphytobenthos, release zoeae into ebbing tides that inundate saltmarshes during spring-tide cycles within tidally-dominated estuaries, such as Brisbane Water Estuary, therefore providing an opportunity to examine whether prey-switching and/or trophic relay may occur in fish that feed on those zoeae (such as the highly abundant estuarine ambassid, *Ambassis jacksoniensis*). This model was examined by sampling *A. jacksoniensis* near saltmarshes in a large, temperate south-eastern Australian estuary during flood and ebb tides on days of saltmarsh inundation and non-inundation over four spring-tide events in 2012. Stomach fullnesses of *A. jacksoniensis* were generally highest during ebb tides on days of saltmarsh inundation, implying that feeding was most marked at these times. Caridean decapods dominated diets during flood tides and on days of no saltmarsh inundation, while crab zoeae dominated diets during ebb tides and on days of inundation, suggesting that, when saltmarsh-derived zoeae became abundant, *A. jacksoniensis* switched to feeding on those prey. Three potential zooplankton prey (calanoid copepods, caridean decapods and crab zoeae) did not differ calorimetrically, indicating that switching of prey by *A. jacksoniensis* is not directly related to their preying on energetically greater prey, but reflects opportunistic feeding on more abundant and/or less elusive prey. As *A. jacksoniensis* is able to switch prey from estuarine caridean decapods to saltmarsh-derived crab zoeae, this very abundant ambassid would be well-placed to promote any trophic relay, via further water movements or other predator-prey relationships, to the adjacent marine environment.

1. Introduction

'Trophic relay' is an ecological model in which the biomass and energy obtained by organisms feeding on and within estuarine vegetation, is transported by nektonic predators such as fish and mobile crustaceans, from the upper limits of estuaries down to their lower reaches and then out to the open sea (Kneib, 1997, 2000; Nagelkerken, 2009). The concept of trophic relay has important implications for the functioning of such estuarine ecosystems and, based on assessments of predator-prey relationships via stomach-content and stable isotope analyses in Australian estuaries (Vance et al., 1998; Fry et al., 1999; Adnan et al., 2002; Melville and Connolly, 2003), is likely to be a feature of those estuaries.

Although the process and extent of trophic relay is driven by predator-prey relationships, it would be affected by water movements within an estuarine system, which, in turn, are influenced by factors such as the volumes of freshwater flow, characteristics of the estuarine mouth and tidal movements (Kneib, 1997). In the context of tidal movement, the fauna within the saltmarsh vegetation that often fringes the shoreline of estuaries provides an important food source for estuarine fish when tidally inundated and would therefore promote trophic relay within such estuaries (Weisberg et al., 1981; Morton et al., 1987; Sumpton and Greenwood, 1990; West and Zedler, 2000; Laffaille et al., 2002; Platell and Freewater, 2009). However, the extent of any potential trophic relay via saltmarshes will be affected by the frequency of

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tidal inundation, which varies geographically. For example, saltmarshes in northern America are typically inundated up to twice daily, while those in Europe (with some exceptions; see Bakker, 2014), South America and eastern Australia, the last of which are often bordered by mangroves (Wilson and Whittaker, 1995), are typically inundated during only three to four days of each lunar cycle, i.e. during the spring-tide cycle (e.g. Laffaille et al., 2001; Thomas and Connolly, 2001; Costa et al., 2003; Hollingsworth and Connolly, 2006; Daleo et al., 2009).

Variations in the timing of inundation of saltmarshes (i.e. day or night) during the year in Europe and Australia, also have implications for any trophic relay driven by prey derived from those environments. For example, on the east coast of Australia, the semi-diurnal spring tides inundate saltmarsh during the day in summer, while such indundation occurs during the night in winter. In estuaries of this region during winter, a saltmarsh grapsid crab (*Helograpsus haswellianus*) that feeds primarily upon fine benthic organic material and microphytobenthos within saltmarsh vegetation (Mazumder and Saintilan, 2010; Alderson et al., 2013), releases zoeae into nightly ebb tides following saltmarsh inundation, with zoeae becoming particularly abundant within adjacent zooplankton assemblages (Mazumder and Saintilan, 2003; Hollingsworth and Connolly, 2006; Mazumder et al., 2006), and thus promoting any potential for trophic relay. Furthermore, the release of zoeae from other common saltmarsh-dwelling grapsids, such as *Heloecius cordiformis*, *Parasesarma erythrodactyla* and *Paragrapsus laevis*, from saltmarshes following tidal inundation during winter and at other times of the year (Mazumder et al., 2006, 2009) would also be likely to promote trophic relay during those times.

Any temporal and spatial variability in prey availability, such as zoeal release by crabs into the zooplankton, can provide an opportunity for "switching" of prey by estuarine predators (Murdoch et al., 1975; Ringler, 1985; Suryan et al., 2000; Siddon and Witman, 2004). For example, McPhee et al. (2015) found that, in autumn, the small ambassid *Ambassis jacksoniensis*, which is particularly abundant in estuaries of south-eastern Australia (Saintilan, 2009), switched feeding from thalassinid larvae to crab zoeae in a saltmarsh environment when those zoeae became abundant following saltmarsh inundation. Knowledge of prey-switching has implications for trophic relay and can also lead to insights into the feeding strategies used by various species (i.e. preferential *vs* opportunistic feeding; *sensu* Wassenberg, 1990), and may be linked to a maximisation of energetic gain among different available prey (e.g. Bittar et al., 2012). In the latter case, it is possible to determine, via calorimetry, the energetic density of different prey types and thus the potential energetic value of those prey to their likely predators (e.g. Robbins, 1983; Benoit-Bird, 2004; Wuenschel et al., 2006).

Despite the importance of zooplankton to the diets of estuarine predators, including both adult and their larval stages (Weisberg et al., 1981; Kneib, 1997; Loneragan et al., 1997; Laffaille et al., 2001; Hollingsworth and Connolly, 2006; Mazumder et al., 2006; Svensson et al., 2007; Platell and Freewater, 2009), little is known of the potential energetic contribution of different zooplankton prey to their predators, and particularly for those in estuaries, including saltmarshes. The collation of such information, along with understanding of the dietary composition of key predators, would allow for quantitative assessment of the potential energetic transfer within this type of environment.

This study aims to unravel the possible trophic pathways of the ambassid *A. jacksoniensis* within a large estuary and explore the potential contribution of saltmarsh, which is tidally inundated at only certain times of the year, to any trophic relay within this estuary. The specific objectives are to 1) determine the stomach fullnesses and dietary compositions, using stomach-content analyses, of *A. jacksoniensis*, focussing on any differences between seasons, tidal states (i.e. flood *vs* ebb) and taking into account whether or not the saltmarsh is inundated, and 2) ascertain the potential energetic contribution (calorimetric value) of possible zooplankton prey to the diets of *A. jacksoniensis*. With respect to the first objective, it is firstly hypothesised that the dietary compositions of *A. jacksoniensis* differ between varying tidal states and seasons (summer and winter). It is also predicted that saltmarsh-derived crab zoeae contribute greatly to diets of *A. jacksoniensis* at times when they are present in zooplankton (i.e. ebbing tides after saltmarsh inundation).

2. Materials and methods

2.1. Study site and environmental variables

Empire Bay Wetland (~33°29′25″S, 151°21′19″E) represents a saltmarsh habitat that is situated approximately 4–5 km from the entrance of the permanently-open Brisbane Water Estuary, on the temperate, south-eastern coast of Australia. Brisbane Water Estuary is a tidally-dominated shallow inlet, with a narrow entrance (~150 m wide) and a main tidal channel that separates into several basins/water bodies at distances of 6–8 km inland, and has maximum water depths of 5–6 m in the main water body (Ford et al., 2006; Cardno Lawson Treloar, 2008). The tidal range of Brisbane Water Estuary is approximately 1 m during most of the year and, like other estuaries in eastern Australia, such tides are semi-diurnal (Ford et al., 2006). The spring-tidal cycle in this environment, which includes tidal heights > ca 1.8 m Australian Height Datum (AHD), typically occurs over three or more consecutive days or nights in each lunar month, and results in the inundation of saltmarsh within Empire Bay Wetland where the study is conducted. Thus, the highest tides (and therefore saltmarsh inundation) occurred during the day in summer and at night during winter.

The catchment of Brisbane Water Estuary has a total area of 165 km^2 with land uses that range from urban to semi-rural, and is managed by the New South Wales state body, the Hunter Central Rivers Catchment Management Authority (Cardno Lawson Treloar, 2008). Much of the foreshore of this estuary has been urbanised, although there are still portions of foreshore that are reserves and National Parks, which includes the Empire Bay Wetland study site (Cardno Lawson Treloar, 2008). Freshwater output is derived from the nearby Kincumber Creek, which lies ca 4 km away (Cardno Lawson Treloar, 2008), as well as Erina Creek and Narara Creek.

Typical of south-eastern Australian saltmarshes, mangroves (*Avicennia marina* var. *australasica* and *Aegiceras corniculatum*) lie between the open water and the saltmarsh at Empire Bay Wetland (Cardno Lawson Treloar, 2008; NPWS, 2009). Low-lying saltmarsh plants such as *Sarcocornia quinqueflora*, *Sporobolus virginicus* and *Triglochin striatum* are prevalent in the low marsh, while taller plants (*Juncus kraussii* and *Suaeda australis*) are abundant in the high marsh (Harty, 1994; Roberts and Sainty, 2005; Cardno Lawson Treloar, 2008; NPWS, 2009). Intertidally, the substratum at Empire Bay Wetland consists largely of bare sand/mud-flats and mangrove pneumatophores and, within the adjacent subtidal area, the eelgrass *Zostera mulleri* subsp. *capricorni* is prevalent, while two other seagrasses (*Posidonia australis* and *Halophila* spp.) are also present (Cardno Lawson Treloar, 2008).

On each sampling occasion, the water temperature, salinity, dissolved oxygen concentration and turbidity were measured in the middle of the water column at the two sampling sites using a handheld Yeo-Kal 611 water quality meter.