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Utilization of organic matter by invertebrates along an estuarine gradient in an intermittently open estuary

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ABSTRACT

In intermittently open estuaries, the sources of organic matter sustaining benthic invertebrates are likely to vary seasonally, particularly between periods of connection and disconnection with the ocean and higher and lower freshwater flows. This study investigated the contribution of allochthonous and autochthonous primary production to the diet of representative invertebrate species using stable isotope analysis (SIA) during the austral summer and winter (2008, 2009) in an intermittently open estuary on the south-eastern coast of Australia. As the study was conducted towards the end of a prolonged period of drought, a reduced influence of freshwater/terrestrial organic matter was expected. Sampling was conducted along an estuarine gradient, including upper, middle and lower reaches and showed that the majority of assimilated organic matter was derived from autochthonous estuarine food sources. Additionally, there was an input of allochthonous organic matter, which varied along the length of the estuary, indicated by distinct longitudinal trends in carbon and nitrogen stable isotope signatures along the estuarine gradient. Marine seaweed contributed to invertebrate diets in the lower reaches of the estuary, while freshwater/terrestrial organic matter had increased influence in the upper reaches. Suspension-feeding invertebrates derived large parts of their diet from freshwater/terrestrial material, despite flows being greatly reduced in comparison with non-drought years.

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1. Introduction

Estuaries are often characterised by soft-sediment habitats that receive spatial subsidies, which fuel extensive ecosystem food chains (Canuel et al., 1995; Constable and Fairweather, 1999). These organic matter subsidies can be derived from autochthonous estuarine primary production or subsidised by allochthonous marine or freshwater sources (Deegan and Garritt, 1997; Cook et al., 2004; McLusky and Elliott, 2004; Doi et al., 2005, 2009; Elliott and Whitfield, 2011). Determining the relative importance of different organic matter sources for estuarine consumers can be complicated by several factors. These include the spatial complexity of estuaries, variability of available sources (e.g. seasonal primary producers) and shifts in source dominance caused by exchange of organic matter with adjacent habitats and spatial and temporal variations in water exchange (e.g. tides and flow, Deegan and Garritt, 1997; Kwak and Zedler, 1997). Accordingly, when collecting samples or making observations, previous studies have focussed on longitudinal estuarine gradients such as salinity or distance from estuary mouth, and recorded various degrees of mixing of *in situ* estuarine production and allochthonous subsidies (Owens, 1985; Canuel et al., 1995; Deegan and Garritt, 1997; Bucci et al., 2007).

Stable isotope analysis (SIA) can be used to quantify the input of primary production (sources) into ecosystems and to gain information about consumer diets and trophic position. Generally, previous studies in permanently open estuaries have found gradual longitudinal enrichment in $\delta^{13}C$ signatures from the upper to the lower estuary in particulate organic matter, seston and invertebrate consumers (Thornton and McManus, 1994; Canuel et al., 1995; Deegan and Garritt, 1997; Doi et al., 2005; Bucci et al., 2007; Kanaya et al., 2008). This is caused by increased diet contribution of marine organic matter sources; particularly those derived from macroalgae with enriched $\delta^{13}C$ (Smith and Epstein, 1971; Moore and Suthers, 2005). Terrestrial sources, particularly C_3 plants with depleted $\delta^{13}C$ signatures, contribute more to particulate organic matter and consumer diet towards the estuary head (Park and Epstein, 1960;; O'Leary, 1981). Consequently, gradual downstream enrichment of $\delta^{13}C$ signatures suggests changes in the relative importance of allochthonous terrestrial and marine organic matter subsidies along the estuary.

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Similar longitudinal trends have been shown for $\delta^{15}N$ signatures. Freshwater invertebrates often exhibit depleted $\delta^{15}N$ signatures compared to their marine counterparts, reflecting the assimilation of predominantly terrestrial-derived material that has atmospheric nitrogen ($\delta^{15}N = 0$) as a major nitrogen source (Schoeninger and DeNiro, 1984; Owens, 1985). This has also been detected in estuarine suspended organic matter (Mariotti et al., 1984; Owens, 1985). As a result, France (1994) assumed the presence of a linear trend in $\delta^{15}N$ along an estuarine gradient and recommended using $\delta^{15}N$ signatures as a marker of ecotonal coupling in coastal environments to measure the dietary proportion of food from different environmental sources.

While many studies using stable isotopes have been conducted in permanently open estuaries (Haines, 1977; Haines and Montague, 1979; Rainer, 1982; Peterson et al., 1985; Guest et al., 2004; Doi et al., 2005; Connolly et al., 2005a; Winemiller et al., 2007), information on intermittently open or seasonally-closed systems is scarce (Hirst, 2004; Hastie and Smith, 2006). These systems are typically located in semi-arid areas with high-energy, microtidal coastlines (Perissinotto et al., 2000; Elliott and McLusky, 2002; Moreno et al., 2010). Low river discharge in summer leads to the formation of a temporary sand barrier disconnecting the estuary from the ocean (Fairbridge, 1980; Kench, 1999; Haines et al., 2006). During mouth closure, input from the marine environment is blocked, while due to variable flow, contributions from freshwater are limited as well (Nozais et al., 2001). These circumstances can result in spatial subsidies being added or interrupted rapidly and greatly during the hydrodynamic cycle and it remains to be investigated whether the assimilation of organic matter by estuarine invertebrates is affected.

Furthermore, southeastern Australia experienced a marked reduction in rainfall between 2000 and 2010, which resulted in severe drought and reduced flows in riverine systems (Matthews, 2006; Murphy and Timbal, 2008; Timbal, 2009). Despite heavy rainfall associated with a strong La Niña event during 2010 and 2011, projections of climate change strongly predict a reduction in rainfall across southern Australia in the future (Hughes, 2003). In intermittently open estuaries, reduced freshwater flow might cause greatly altered hydrodynamic patterns (Sherwood, 1988; Teske and Wooldridge, 2001), thereby potentially affecting spatial subsidies and consumer diets.

The primary aim of the present study was to determine dominant organic matter sources for benthic invertebrates along an estuarine gradient in an intermittently open estuary. Also, there is only limited information about trophic interactions for most species (Ponder, 1965; Lucas, 1980; Wells and Threlfall, 1982; Matthews and Fairweather, 2008). The extent to which spatial subsidies influence the diet of different invertebrate feeding types is unknown. A further aim of this study was to investigate which feeding groups were affected most by potential changes in spatial subsidies. Specific objectives were to: (1) interpret carbon and nitrogen SI signatures and diet contributions for invertebrates with a range of feeding modes, and (2) characterise temporal and spatial patterns in $\delta^{13}C$ and $\delta^{15}N$ of common primary producers and consumers along an estuarine gradient in an intermittently open estuary.

2. Material and methods

2.1. Study area

The Hopkins River estuary is an intermittently open estuary of approx. 10 km length near Warrnambool, on the south-western coast of Victoria, Australia (Fig. 1). The Hopkins River originates at 240 km north at Mount Langi Ghiran, and its catchment comprises 8651 km^2. Within 1 km of major tributes, 99% of the area has been cleared for pasture and cultivation (Sherwood, 1988; Matthews, 2000; Nicholson et al., 2008). The estuary occupies a limestone canyon (Sherwood, 1988) with a well-defined channel of a maximum depth of 13 m (Newton, 1996), contributing to strong oxygen and salinity stratification during low-flow conditions (Sherwood, 1985). Larger wetland areas are absent (Sherwood, 1988) apart from narrow littoral stands of the reed grass *Phragmites australis* (Ierodiaconou and Laurenson, 2002) and the sea rush *Juncus kraussii* as well as intertidal and subtidal sand- and mudflats hosting communities of benthic invertebrates and seasonal seagrass beds. Non-drought winter flows between the years 1955 and 1996 comprised approx. 84% of the total yearly discharge in the

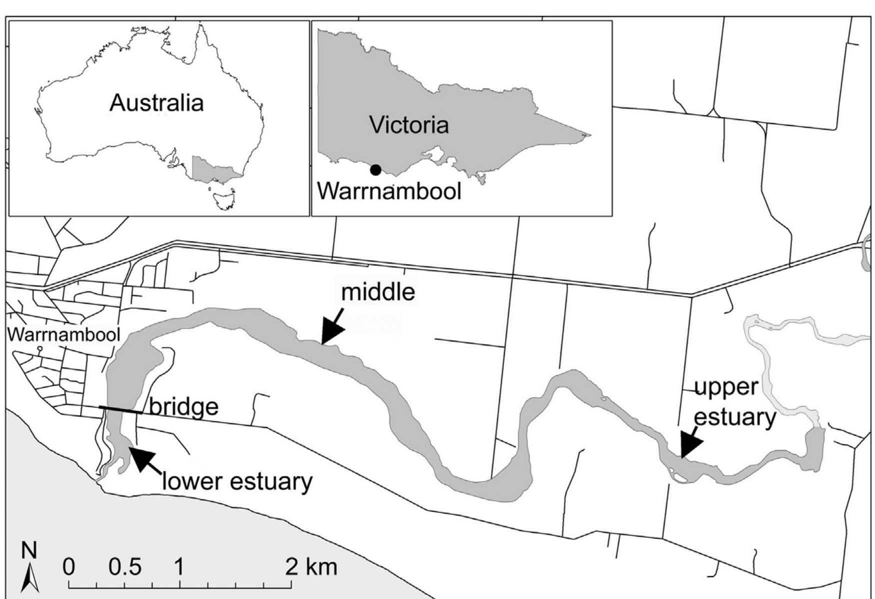

Fig. 1. Hopkins River estuary, Victoria, Australia. Arrows mark the upper, middle and lower estuary sampling sites.

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