Reworking activity of the thalassinidean shrimp *Trypaea australiensis* Dana, 1852 (Decapoda: Pleocyemata: Callianassidae) in an Australian estuary: A pilot study

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ABSTRACT

Trypaea australiensis Dana, 1852 is the predominant bioturbating thalassinidean shrimp on the east coast of Australia. It is, like other large bioturbators, generally considered an important ecosystem engineer. The sediment particle reworking rate of thalassinideans, a key parameter in benthic biogeochemical modelling, nevertheless remains unknown. We have for the first time quantified particle reworking by a population of *T. australiensis* living in fine estuarine sand. The particle reworking rate was monitored for 18 days using coarse sand as a new tracer approach followed by analyses of grain-size distribution in the sediment to a depth of 24 cm. Burial depth (BD, cm) over time (t, days) followed the relationship $BD = 0.3002 \times t$ for an average population density of 96 individuals m^{-2}, equivalent to a sediment displacement of 1.1 m^3 m^{-2} yr^{-1} (11.4 liters individual^{-1} yr^{-1}). The individual-specific particle reworking by this thalassinidean is higher than that reported for most other key bioturbators, and its engineering impact on estuarine sediments therefore has potentially large consequences for biodiversity and ecosystem functioning.

Key Words: bioturbation, Crustacea, ecology, reworking rate, seagrasses

INTRODUCTION

Infauna that intensely rework sediment particles are considered ecosystem engineers, having a major influence on sediment processes and community structure (Jones *et al.*, 1994; Pillay & Branch, 2011; Kristensen *et al.*, 2017). The particle reworking activities of these animals dramatically affect the physical and chemical conditions of the surrounding sediment (Cadée, 2001; Pillay & Branch, 2011; Kristensen *et al.*, 2017). These effects include vertical displacement of organic matter, altered sediment sorting by burial of large particles, increased porosity, raised redox conditions, and fine particle resuspension (D'Andrea & DeWitt, 2009; Li *et al.*, 2017; Dunn *et al.*, 2019; Cozzoli *et al.*, 2020, 2021). As a consequence, reworking affects the benthic sediment community by changing living conditions for other benthic animals and macrophytes (Pillay & Branch, 2011; Kristensen *et al.*, 2017). Typical examples of bioturbating ecosystem engineers that may affect the distribution of both macrophytes and smaller animals are thalassinidean ghost shrimps (Atkinson & Taylor, 2005; Pillay & Branch, 2011), the lugworm, *Arenicola marina* Linnaeus, 1758 (Philippart, 1994; Volkenborn *et al.*, 2007; Eklöf *et al.*, 2015), and

mangrove crabs such as sesarmid and fiddler crabs (Kristensen *et al.*, 2008; Lee *et al.*, 2014). Studies have shown that expansion of eelgrass (*Zostera marina* Linnaeus 1753) is prevented when lugworms bury seeds and seedlings below their recovery depth (Valdemarsen *et al.*, 2011; Govers *et al.*, 2014). Also, small polychaetes, such as *Hediste diversicolor* Müller, 1776, may entirely disappear because of the constant sediment disturbance (Volkenborn & Reise, 2006; Kristensen *et al.*, 2014). The extent of the negative, or in some cases even positive impacts, however, strongly depends on the population size, reworking intensity, and species of the bioturbator in question.

The thalassinidean shrimp, *Trypaea australiensis*, Dana 1852 (or the marine yabby), is a dominant bioturbating crustacean in many shallow sandy marine sediments along ~5,000 km of the eastern coast of Australia from Cape York Peninsula, Queensland to Port Phillip Bay, Victoria (Fulton & Grant, 1906; Rotherham, 2004). Population densities can reach 500 individuals m^{-2}, depending on individual size and environmental conditions (Hailstone & Stephenson, 1961; Rotherham, 2004). It has a maximum body length of 8 cm and an average body wet weight of 4–5 g, with males being slightly larger than females (Hailstone & Stephenson,

1961; Dunn *et al.*, 2019). *Trypaea australiensis* is a subsurface deposit-feeder (Pillay & Branch, 2011) and upward conveyor that live in Y-shaped and open-ended burrows with about two burrow openings per individual (Butler & Bird, 2008; Kristensen *et al.*, 2012), extending 1 m into the sediment (Cadée, 2001). The shrimps use their first and second pairs of legs for digging and pulling the sand backwards (MacGinitie, 1934; Pillay & Branch, 2011). The sediment is carried afterwards to the opening of the burrow and pushed outside creating volcano-like mounds on the sediment surface (MacGinitie, 1934; Pillay & Branch, 2011).

Thalassinideans have the potential to be important ecosystem engineers due to their continuous burrowing and burrow maintenance (Grigg *et al.*, 2007; Pillay & Branch, 2011). Because the magnitude of sediment particle reworking by *T. australiensis* is currently unknown, the extent of their ecosystem engineering impact cannot be assessed. The purpose of this preliminary study was to quantify, for the first time, the *in-situ* reworking potential of *T. australiensis*. We investigated populations inhabiting soft sediment in an estuary in Queensland, Australia. Reworking was assessed using a new particle tracer method (Maire *et al.*, 2010) and results were evaluated in the context of sediment reworking rates known for other bioturbating infauna in soft sediments.

MATERIALS AND METHODS

The study was performed in the estuary of Tallebudgera Creek (28.10984°S, 153.44888°E), Queensland, Australia. The tidal range in the area is 1.8 m (Abdullah & Lee, 2016) and salinity varies between 29 psu and 36 psu, dictated by tidal state and rainfall (Morton, 1992). Sediment consisted of fine sand with a median grain size of 0.16 mm; silt + clay content of 7.4 % and organic content of 0.56 % (Wendländer *et al.*, 2019).

The study site is inhabited by a large and long-standing population of *T. australiensis*. The population size at the study site was assessed by Wendländer *et al.* (2019) from counts of burrow openings within six haphazardly placed circular frames (41 cm diameter, 0.13 m² area) at multiple sampling times. Based on an average of 2.1 burrow openings per individual for *T. australiensis* (see Butler & Bird, 2008), we estimated that this species had an average density of 96.4 individuals m⁻² (± 6.9 SD) at the study site.

Sediment reworking was quantified by tracing the short-term burial of coarse sand added to the surface of the otherwise fine-grained sandy sediment. A 2 ×1 m plot was marked with poles and a 1–3 cm layer of coarse sand was spread on top of the sediment surface. Exclusion controls were not applied for *T. australiensis* since sediment erosion by water currents at the study site is limited (Wendländer *et al.*, 2019) and similar studies with coarse sediment added on top of fine sediment showed no mixing between layers and at the sediment-water interface (Bruhn *et al.*, 2020; Flindt *et al.*, 2021; NSO *et al.*, unpublished data). Five sediment cores (5 cm diameter, 30 cm deep) were sampled at the plot immediately after adding the coarse sand to assure that a distinct layer was present at the surface. These cores were sectioned into 0–1, 1–2, 2–3, 3–4, 4–6, 6–8, and 8–12 cm intervals. Core sampling and sectioning were repeated in a similar way 11 and 18 d after the initial set-up, except that the cores were sliced into different and deeper intervals (0–1, 1–2, 2–4, 6–8, 10–12, 14–16, 18–20 and 22–24 cm) for capturing all subducted coarse sand. Every alternate slice below 4 cm depth was discarded due to logistical constraints.

To determine the intrusion of coarse sand into the original fine sediment by shrimp reworking, the grain-size distribution of the coarse sand and surrounding sediment was analysed at all depth intervals obtained from the core sectioning. Grain size was determined using a laser diffraction particle size analyser (Malvern Mastersizer 3000; Malvern Instruments Ltd, Malvern, UK) according to the manufacturer's guidelines.
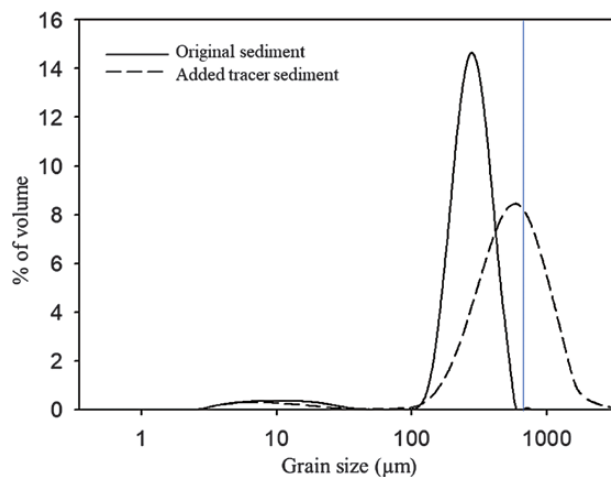

Figure 1. Grain size distribution of the original fine sediment at Tallebudgera Creek, Queensland, Australia and the added coarse sand tracer. The blue line marks the grain size fraction of 666 μm.

The presence of coarse sand was detected by tracing the 666 μm grain-size fraction, because particles of this size were the smallest in the added sand that were highly abundant and not present in the original sediment (Fig. 1). Only measurements of this fraction were used for further analyses. The 666 μm fraction of coarse sand displaced into the sampled sediment layers was quantified from the grain-size analysis. The coarse sand content in the unused 2-cm sediment sections were estimated as the average of slices immediately above and below. To compensate for potential horizontal loss due to displacement of added tracer sand into other burrow shafts during the experiment (Maire *et al.*, 2010), the sum of coarse sand in the entire depth of each core was considered the total initial amount. The subsequent calculations for each depth interval were undertaken according to their tracer content as a fraction of the total.

The burial depth of the 666 μm grain-size fraction over time was used as a measure of reworking rate. The burial depth at any sampling day was defined as the deepest layer where the 666 μm grain-size fraction was significantly higher than the background level (pairwise t-test at a significance level $P = 0.05$). The background level was defined as the average 666 μm grain-size content in the lower 10 cm of the cores (14–24 cm). Values slightly above zero were probably caused by passive transport of sand by gravity through the burrow shafts as described by Kristensen *et al.* (2012). To determine the volume of sediment handled, the burial depth was corrected 1–3 cm upwards to compensate for the thickness of the initially added coarse sand. A linear regression model of burial depth over time was applied to estimate the burial (or reworking) rate. This model was chosen because the reworking activity within upper 10 cm of *T. australiensis*-bioturbated sediment is assumed constant with time and depth, as also reported for *A. marina* by Delefosse & Kristensen (2012).

RESULTS

Over the duration of the 18-d experiment, the added coarse sand tracer was incorporated into the top 10 cm of the sediment profile by infaunal particle reworking activity. Only individuals of *T. australiensis* appeared to be involved since the core slicing revealed no traces of other bioturbating animals. Immediately after addition, the 666 μm grain-size fraction was restricted to a narrow layer in the upper 2–3 cm of the sediment (93–100 % of the total) with only traces below this depth (Fig. 2). After 11 d, the 666 μm particles extended deeper into the sediment with 93–100 % of the total pool present in a band to 6 cm depth. The
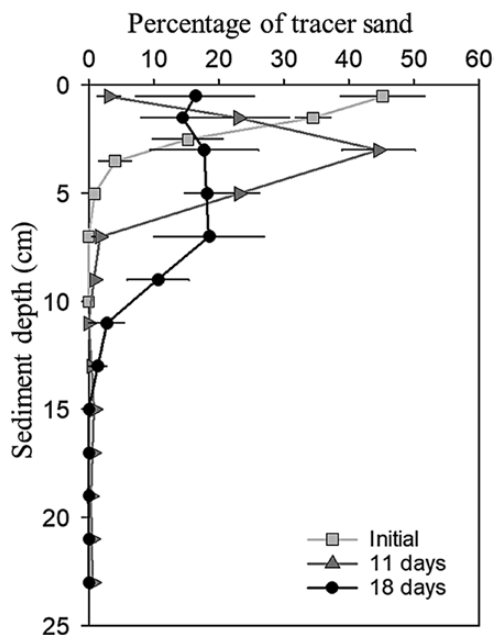
Figure 2. Depth distribution of added coarse tracer sand over the course of the experiment. Values are reported as average volumes (± SE, $N = 5$) of the total coarse sand volume (%) at different depths in the sediment. Sampling was conducted immediately after (Initial) as well as 11 and 18 days after addition of sand.

remainder was evenly dispersed as a low-background level below this depth. The coarse sand was dispersed even deeper after 18 d but now as a homogeneous layer with lower concentration in the upper 9 cm of sediment containing 80–100 % of the total pool. The background level below 9 cm depth was at this time slightly higher than after 11 d. Burial depth of 666 μm particles (BD, cm) over time (t, days) was expressed by a significant linear regression model, BD = 2.5314 + 0.3002 t (Fig. 3). The t = 0 intercept of 2.53 cm corresponds to the average thickness of the added coarse sand. After correcting for this, the reworking rate of the examined population of *T. australiensis* was estimated from the regression slope to be 1.1 m^3 m^{-2} yr^{-1}, which is equivalent to 11.4 liters yr^{-1} for each individual in the population.

DISCUSSION

The sediment particle reworking determined for *Trypaea australiensis* was notably high. Although thalassinideans are generally considered amongst the most active bioturbating infauna (Cadée, 2001; D'Andrea *et al.*, 2004; Kneer *et al.*, 2013; Dunn *et al.*, 2019), the rate obtained in this study for single individuals of *T. australiensis* (11.4 liters individual^{-1} yr^{-1}) is well above estimates for other thalassinideans of the same body size, such as *Calocaris templemani* Squires, 1965 (8 liters individual^{-1} yr^{-1}; Gagnon *et al.*, 2013) and *Neotrypaea californiensis* (Dana, 1854) (7–18 liters individual^{-1} yr^{-1}; MacGinitie, 1934; Swinbanks & Luternauer, 1987). Among other infauna types, the rate for thalassinideans is comparable to that for the ecologically important lugworm *A. marina* (7.4–9.3 liters individual^{-1} yr^{-1}) from colder waters (Valdemarsen *et al.*, 2011). Thalassinidean reworking rates are, however, towards the lower end of the extreme range exhibited by enteropneusts of 7–292 liters individual^{-1} yr^{-1} (Thayer, 1983; Suchanek & Colin, 1986; D'Andrea *et al.*, 2004).

Intense reworking impacts sediment properties by, for example, increasing sediment porosity, raising redox conditions, translocating organic matter, and reducing nitrogen content (D'Andrea & DeWitt, 2009; Kristensen *et al.*, 2012,2017; Dunn *et al.*, 2019).
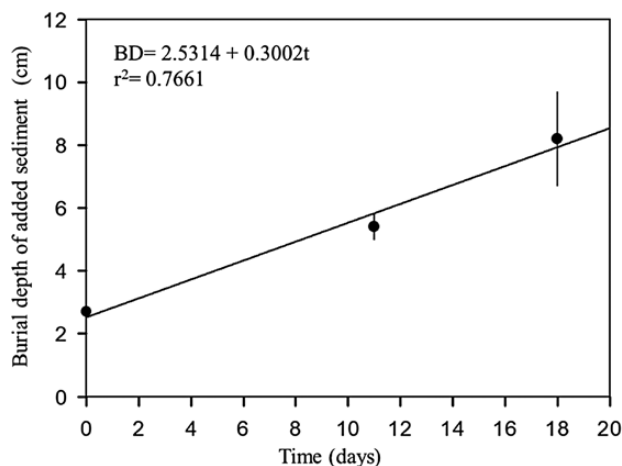

Figure 3. Reworking action of the populations of *Trypaea australiensis* as indicated by burial depth of added coarse tracer sand after t (time) of 0, 11, and 18 days. The line represents the linear regression model according to the equation indicated. Error bars represent SE (0.374, 0.400, and 1.500).

Trypaea australiensis physically disturbs the sediment continuously to at least 10 cm depth and would be expected to strongly affect co-occurring species. Several studies have described the negative impact of ecosystem engineering thalassinideans on other benthic organisms, including seagrasses (Berkenbusch & Rowden, 2007; Berkenbusch *et al.*, 2007; Siebert & Branch, 2007; Pillay & Branch, 2011), macrofauna (Cadeé, 2001; Pillay & Branch, 2011; Suchaneck, 1983), and meiofauna (Branch & Pringle, 1987; Pillay & Branch, 2011). Such effects are corroborated by the absence of any other bioturbating fauna at the study location. The potential negative consequences of the high bioturbation activity of *T. australiensis* for associated biota is also evident in the study by Wendländer *et al.* (2019), where transplanted seagrass (*Zostera muelleri* Irmisch ex Ascherson, 1867) in the Tallebudgera estuary grew more successfully when *T. australiensis* was excluded. It has been shown elsewhere that bioturbating activity of thalassinideans colonizing new areas can lead to a regime shift in the fauna community with potential loss of the native fauna (Suchaneck, 1983; Pillay & Branch, 2011; Berkenbusch *et al.*, 2007). For example, thalassinidean invasions in South Africa have resulted in a 25-fold reduction of bivalve abundance (Pillay & Branch, 2011). The high reworking rate and the creation of mounds of fine sand are also known to increase the erodibility of the sediment surface (Pillay & Branch, 2011). Consequently, small animals are likely to be more readily washed out of the sediment by even weak currents and waves, affecting both existing populations and colonization (Pillay & Branch, 2011).

Several factors limited our ability to scale up the influence of *T. australiensis*, either to annual rates or to other sites where they occur. The reworking estimates in the present pilot study were obtained in summer, and thus might overestimate when extrapolated to annual rates due to the temperature dependence of thalassinidean activities (Butler & Bird, 2008; Cozzoli *et al.*, 2021). Our population estimate based on 2.1 burrow openings per *T. australiensis* individual is also quite conservative as studies have shown that the number of openings per individual varies depending on environmental conditions (McPhee & Skilleter, 2002). Some of the added coarse sediment was apparently lost from our sampled plots during the study. One explanation may be that the missing tracer sediments were transported horizontally by activities of *T. australiensis* (Maire *et al.*, 2010), probably via secondary burrow shafts. Another possibility, albeit unlikely, is downward transport by *T. australiensis* to below the deepest sampling depth. Erosion of the added coarse sediment by currents is assumed

negligible at the study site as reported by Wendländer *et al.* (2019), particularly when considering the high erosion threshold of sediment with large grain sizes (Bruhn *et al.*, 2020; Flindt *et al.*, 2021). The impact of other particle reworking infauna is negligible since the present study and Wendländer *et al.* (2019) recorded no other larger infauna than *T. australiensis* at the study site. Passive mixing of coarse- and fine-grained sediment is also limited as indicated by the generally high stability of coarse sand-caps on top of muddy sediment despite exposure to relatively strong currents (Bruhn *et al.*, 2020; Flindt *et al.*, 2021; NSO *et al.*, unpublished data). Thalassinideans are known for their ability to actively sort sediment, which may potentially influence the present findings. If *T. australiensis* preferentially handles particles with diameters between 125 and 250 μm and eject them from the burrow openings (Bird *et al.*, 2004), our use of a larger grain size as a tracer may potentially bias the reworking estimate.

It is noteworthy that the 666 μm particles were dispersed homogeneously after 18 d in a relatively low concentration within the upper 9 cm of the sediment. This indicates that secondary mixing and dispersal of tracer particles by *T. australiensis* most likely occurred above the burial depth at this time. Similar secondary dispersal of particles has previously been observed for *A. marina* (Delefosse & Kristensen, 2012; Thomson *et al.*, 2020). A too long experimental period will probably lead to underestimated burial rates due to secondary mixing when the tracer reaches the excavation depth of *T. australiensis*. Since this preliminary experiment tested a new experimental setup, we made it of short duration to avoid secondary mixing and dilution of the tracer material over time. Our approach and timing fortunately proved to be suitable and provided reliable results as indicated by the linearity of tracer particle burial with time.

The relatively high sediment reworking rate of *T. australiensis* points to potentially strong negative effects on other benthic infauna and rooted vegetation. Furthermore, the rapid sediment turnover may affect ecosystem functionality related to vertical distribution of organic matter, redox conditions as well as sediment sorting, porosity and resuspension. Since this study primarily aimed at testing a new experimental approach, however, only the basic reworking rate of *T. australiensis* was obtained. Any impacts on the abovementioned ecosystem functionality by changes in reworking related to seasonality, changing environmental conditions, and interactions with other benthic organisms warrant further investigations. The use of coarse sediment as a tracer to quantify reworking of *T. australiensis* was successful and can be recommended for such future investigations.

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