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Factors influencing sediment turnover by the burrowing ghost shrimp *Callianassa filholi* (Decapoda: Thalassinidea)

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Abstract

Bioturbation by the burrowing thalassinidean shrimp *Callianassa filholi* (Milne-Edwards 1878) was studied at an intertidal sandflat in Otago Harbour, south-eastern New Zealand, over a period of 12 months. The amount of sediment expelled from shrimp burrows was measured each month (by direct entrapment over 24 h) and inhabiting shrimp were subsequently captured from the burrows. Rate of sediment expulsion was significantly related to seawater temperature, shore height of burrow and time, whilst the amount of sediment expelled from individual burrows was positively related to size of inhabiting shrimp but independent of sex. Annual sediment turnover for *C. filholi* was estimated at 96 kg (dry) m^{-2} $year^{-1}$ which accounted for the variability imposed by monthly changes in seawater temperature and the spatial and temporal dynamics of the shrimp population. The results demonstrate the need to take account of physical and biological factors when constructing sediment turnover estimates for callianassid shrimps, and inferring their bioturbatory significance.

Keywords: Bioturbation; *Callianassa filholi*; Ghost shrimp; Sediment turnover

1. Introduction

Thalassinidean shrimps construct and occupy burrows in a variety of soft-sediment environments in tropical and temperate regions, with their presence often evident in the form of conspicuous mounds of expelled material on the sediment surface (Dworschak, 1991). Construction and maintenance of their burrows have been linked to continuous

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mixing of deep and shallow layers of sediment, resulting not only in substantial sediment resuspension/transport (e.g. Roberts et al., 1981) but also in changes in organic content (e.g. de Vaugelas and Buscail, 1990) and grain size of the sediments (e.g. Tudhope and Scoffin, 1984). In addition to physical effects, thalassinideans have been demonstrated to profoundly impact the biogeochemical properties of sediments (e.g. Ziebis et al., 1996) and the community composition of their associated infauna (e.g. Posey, 1986). Consequently, thalassinidean shrimp, in particular members of the Callianassidae, can be considered important bioturbators with potentially the greatest effects over the largest depth range. Whilst various studies have been undertaken to assess sediment turnover activity by callianassids, inconsistent procedures and measurements for such assessments have resulted in ambiguous interpretations and make comparison of estimates difficult (see critique, Rowden and Jones, 1993). The present study examined bioturbation by the callianassid shrimp *Callianassa filholi*, a southern temperate species which occurs in both intertidal and subtidal sediments throughout New Zealand (Devine, 1966). The aim of the study was to calculate a sediment turnover estimate for an intertidal *C. filholi* population which accounted for the physical and biological factors influencing the shrimp's sediment expulsion activity.

Note: The systematic status of *C. filholi* is currently under review and will most likely be assigned to a different genus in the future (R.B. Manning, pers. commun.)

2. Materials and methods

The study site was situated at Otakou, Otago Harbour, south-eastern New Zealand (70° 42′ E, 45° 30′ S) and consisted of an uniformly sloping intertidal sandflat of well sorted sand, with a tidal range of 1.4–2.2 m (for site details see Fussell, 1979; Berkenbusch and Rowden, 1998). The amount of sediment expelled from shrimp burrows was measured over 24 h each month between October 1995 and September 1996 using a direct entrapment method. Sediment traps consisted of 11 cm diameter plastic containers with a 1-cm hole in the bottom and bolting mesh (110 micron) on top (to prevent water flushing out sediment). Twenty-five burrows were haphazardly selected on the sandflat and sediment traps were placed over flattened mounds and secured with wire stakes. An equal number of control traps was also deployed. The distance of each trap from the shore's high water mark was measured to the nearest metre (as a proxy measure for tidal height/inundation). After the collection period, sediment traps were removed and the shrimp inhabiting the burrow were captured using a yabby pump (Manning, 1975) and anaesthetised (7.5% magnesium chloride in freshwater) for 5 h prior to fixation in 10% formalin/seawater. (Note: On the first sampling occasion, in October 1995, 30 traps were put in place and on this and other occasions it was not always possible to retrieve all traps.)

In the laboratory, sediment collected from the traps was washed to remove salt, dried (70°C for 48 h) and weighed (±0.01 g). Shrimp were counted and sexed for each burrow, and their carapace lengths measured (CL; tip of the rostrum to the posterior margin of the carapace to the nearest 0.1 mm using a stereomicroscope with a measuring eye-piece). Only when single shrimp were captured from a burrow were they included in the subsequent analysis of amount of sediment expelled in relation to shrimp size. Seawater temperature in Otago Harbour was measured at the Portobello Marine Laboratory in close proximity (11 km) to the study site. Sediment grain size and organic content were examined as part of a previous study and no significant difference in these sediment parameters was detected over space or time (unpublished data). For this reason, sediment characteristics were not considered as part of the present study.

Statistical analysis included data from November 1995 to September 1996. Data were log-transformed (natural log) prior to applying General Linear Models. The first General Linear Model involved sediment weight (dry) collected from burrows and from control traps, distance down the shore, seawater temperature and time. This model included interactions between the difference of the former two factors with each, distance down the shore, seawater temperature and time. Due to less data available which included information on sex and size of shrimp inhabiting burrows, a second General Linear Model was applied. This involved sediment weight (dry) collected from burrows, size (carapace length) and sex of shrimp, seawater temperature, and time. It also included interactions between shrimp size and each sex, seawater temperature, and time. (Note: October samples were not included in the models due to the lack of data for shore height.)

3. Results

The amount of sediment expelled by *Callianassa filholi* appears to correspond to time and the annual pattern of seawater temperature (Table 1, Fig. 1). The relationship between the amount of bioejected sediment, seawater temperature and time (month) was statistically significant over the sampling period ($P < 0.001/F = 36.99$ and $P < 0.001/F = 7.24$, respectively, $n = 481$). At the beginning of the sampling period, the middle of

Table 1
Number of sediment traps, mean amount and standard error of sediment collected from *Callianassa filholi* mounds and control traps each month between October 1995 and September 1996

Month	Number of sediment traps (mounds/controls)	Mean amount of sediment from mound±S.E. (g dry weight trap^{-1} day^{-1})	Mean amount of sediment from control±S.E. (g dry weight trap^{-1} day^{-1})
October	30/29	33.22±5.10	6.81±1.24
November	17/17	63.19±9.18	9.11±1.95
December	26/24	34.11±6.92	8.58±2.70
January	24/24	41.11±6.28	6.8±0.73
February	24/22	44.11±10.85	5.92±1.02
March	24/21	61.61±9.11	14.5±2.21
April	24/22	19.10±4.78	9.66±1.51
May	23/23	17.15±3.73	12.22±1.84
June	22/22	16.70±5.29	4.33±1.67
July	20/25	7.23±1.71	4.87±0.87
August	24/22	10.53±1.19	9.16±1.19
September	23/20	17.32±2.42	4.40±0.92

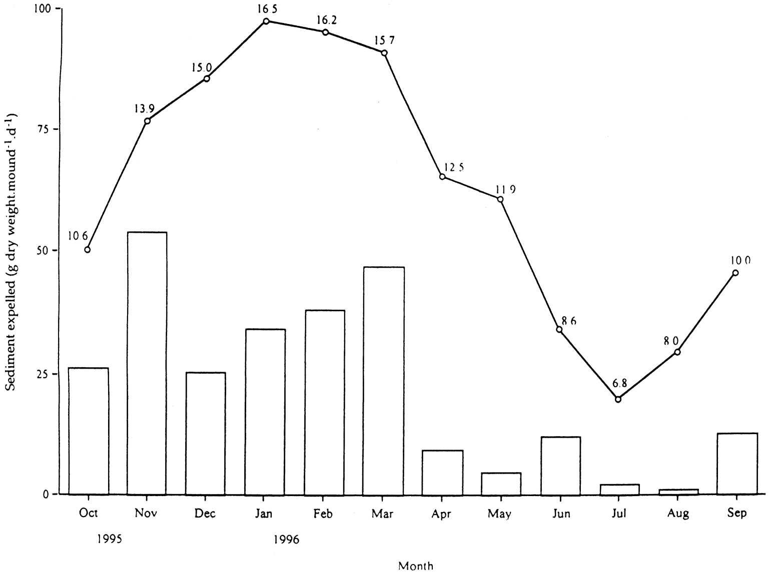

Fig. 1. Amount of sediment expelled (difference in mean dry weight between shrimp mounds and control traps; g day^{-1}) by *Callianassa filholi* and seawater temperature (on sampling day; °C) between October 1995 and September 1996.

spring 1995, the mean amount of sediment expelled by *C. filholi* increased as seawater temperature rose, reaching a peak in November. Despite a further rise in seawater temperature, the sediment expulsion rate dropped drastically the following month. Over summer, however, the shrimp's expulsion activity increased again and resulted in another peak in March. With decreasing seawater temperature, the expulsion rate showed a sharp decline in April and continued to drop to a minimum at the end of winter (August) corresponding to a minimum in seawater temperature the previous month. The amount of sediment increased again at the beginning of spring, corresponding to the rising seawater temperature (Fig. 1). The difference between mean amount of sediment from shrimp mounds and from controls was statistically significant ($P < 0.001/F = 86.10$) and was significantly related to seawater temperature ($P < 0.01/F = 9.11$) and time (months; $P < 0.05/F = 2.43$).

The amount of sediment expelled by *C. filholi* also varied with distance of individual mounds from the top of the shore (Fig. 2). With the relationship between expelled sediment collected from mounds and their position on the sandflat being statistically significant ($P < 0.01/F = 9.47$). Initially, the amount of expelled sediment increased with distance from the shore and resulted in the highest amount of sediment collected from burrows 50–70 m down the shore. With increasing distance down the shore, the amount of expelled sediment decreased to a minimum at a distance of 110–130 m. Any further increase in distance of burrows down the shore resulted in similar low levels of sediment activity. The difference between the amount of expelled sediment and that in control traps was independent of shore position ($P > 0.10$).

Size of individual *C. filholi* (carapace length, CL) also related significantly to the

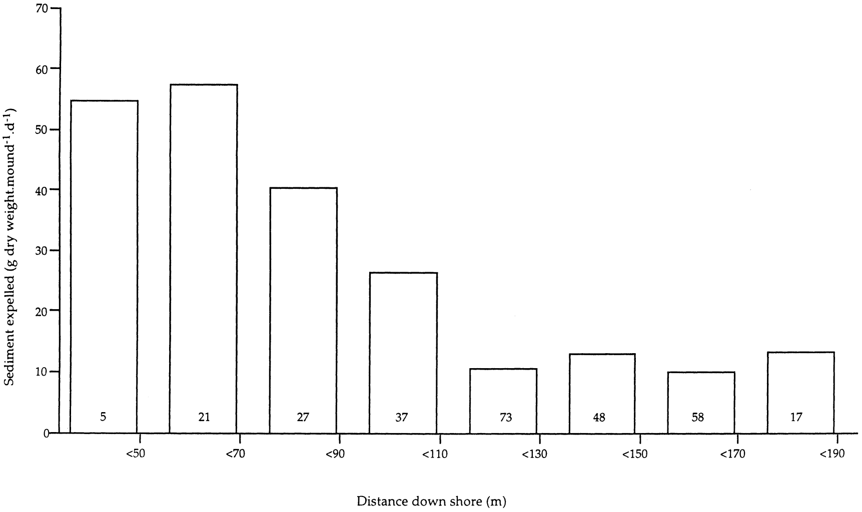

Fig. 2. Amount of sediment expelled by *Callianassa filholi* (difference in mean dry weight between shrimp mounds and control traps; g day^{-1}) in relation to shore position (arbitrary 20 m intervals) (n values = number in bars).

amount of sediment expelled ($P < 0.05/F = 6.73$, $n = 89$). Shrimp ranged in size from 6.0 to 13.2 mm CL reflecting the entire size range of the adult population (Berkenbusch and Rowden, 1998). An increase in CL resulted in higher amounts of sediment expelled, however, at apparently two different rates. These are a result of the above mentioned physical factors, i.e. seasonal difference accounts largely for both rates, with autumn/winter data representing the lower rate, and spring/summer data representing the higher one (Fig. 3). In contrast to size, sex and the interaction between sex and size did not have any significant effect on the amount of sediment expelled (both $P > 0.05$).

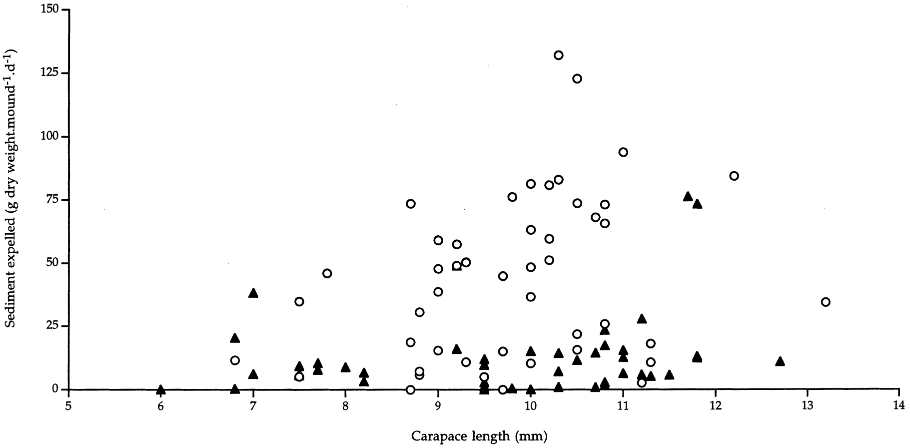

Fig. 3. Sediment expulsion rate in relation to size (carapace length) of *Callianassa filholi* between October 1995 and September 1996 (open circles: spring and summer data; solid triangles: autumn and winter data).

Table 2
Summary of data utilised for the calculation of annual sediment turnover estimate for *Callianassa filholi* at the study site between October 1995 and September 1996

Month	Mean amount of sediment (g dry weight) expelled per mound (total-control) day^{-1}	Mean shrimp density (number of individuals m^{-2})[a]	Shrimp/mound ratio	Mound m^{-2}	Mean amount of sediment (kg dry weight) expelled m^{-2}
October	26.41	12.0	1.0	12.0	9.82
November	54.08	15.0	1.5	10.0	16.22
December	25.53	13.0	1.4	9.3	7.35
January	34.31	23.0	1.3	17.7	18.82
February	38.19	15.0	1.1	13.6	15.10
March	47.11	11.0	1.2	9.2	13.39
April	9.44	16.0	1.1	14.5	4.12
May	4.93	25.0	1.3	19.2	2.94
June	12.38	18.0	1.7	10.6	3.93
July	2.36	21.0	1.6	13.1	0.96
August	1.37	13.0	1.3	10.0	0.42
September	12.93	15.0	2.0	7.5	2.91

[a] Data collected by direct coring, from Berkenbusch and Rowden, 1998).

From these results and information on the population structure it was possible to calculate an annual sediment turnover estimate for *C. filholi* at the Otakou study site (Table 2). To establish mound density m^{-2}, data from this study (number of shrimp captured from each mound after collection of the sediment trap) were used to establish a shrimp/mound ratio for each month. Given the shrimp/mound ratio and the mean population density each month (data from Berkenbusch and Rowden, 1998) it was possible to calculate monthly values for the number of mounds m^{-2}. Twenty-four hour data of mean amount of sediment expelled per mound minus mean amount of sediment collected in control traps each month was used to derive monthly averages. Multiplying the resulting value by the number of mounds m^{-2} allowed for the calculation of the amount of sediment expelled per m^{-2} each month, and subsequently the total annual sediment turnover estimate of 96 kg (dry) m^{-2} year^{-1} (Fig. 4).

4. Discussion

Results from this study illustrate the influence of physical and biological factors on sediment expulsion activity of an intertidal callianassid shrimp. Seawater temperature, burrow position on the shore and size of individual shrimp significantly affected sediment turnover by *C. filholi*.

A strong correlation between the amount of sediment expelled by shrimp and seawater temperature is consistent with findings for other callianassids. Rowden et al. (1998) reported *C. subterranea* to be relatively inactive at low temperatures (≤ 7°C) and observed significantly lower sediment expulsion activity by individuals exposed to

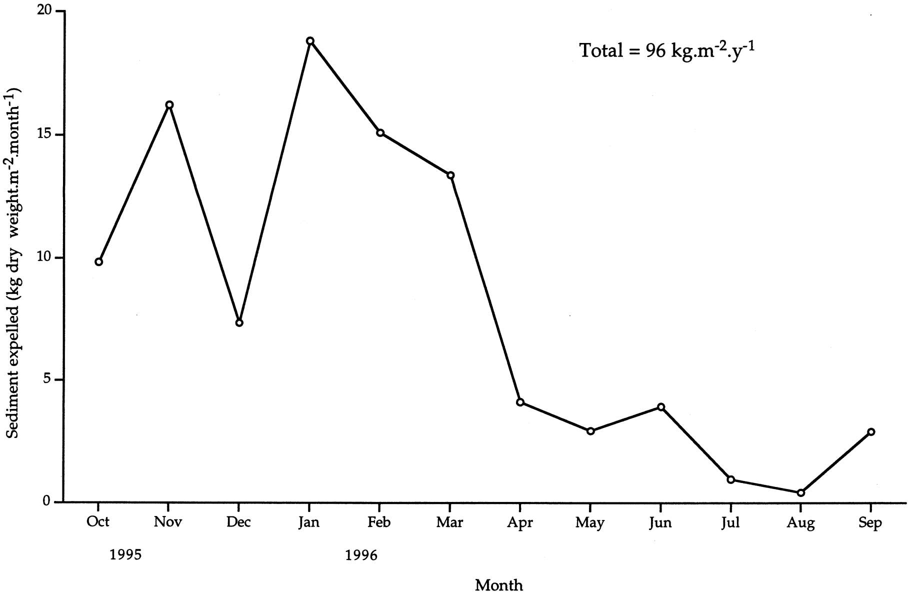

Fig. 4. Calculated annual sediment turnover estimate (kg dry weight m^{-2} year^{-1}) for *Callianassa filholi* at the study site between October 1995 and September 1996.

spring and winter temperatures compared with shrimp experiencing summer temperatures. Another temperate species, *Neotrypea californiensis* also exhibited a relationship between sediment expulsion activity and seawater temperature (Swinbanks and Luternauer, 1987). Low sediment expulsion activity of *C. filholi* in winter related to minimum seawater temperatures ($\approx$ 7°C), but sediment activity was also low in summer in spite of seawater temperature rising. The latter is possibly due to seawater in the burrow exceeding a temperature optimum, i.e. in the intertidal environment where changes in tide can result in rapid and drastic changes in temperature on the exposed shore. For example, Hill and Allanson (1971) found that *Upogebia africana* in an intertidal estuary irrigated burrows less frequently when temperatures rose above tolerance levels, resulting in partially closed off burrows as temperature continued to rise. This protection mechanism enables the shrimp to keep burrows cool in their exposed intertidal environment, and has been recorded for other burrowing crustaceans (e.g. Eshky et al., 1995). In addition to seawater temperature affecting its sediment turnover rate, *C. filholi* showed a decrease in sediment expulsion activity with increasing distance of burrows down the shore. Suchanek et al. (1986) speculated on a link between sediment turnover by callianassids and nutrient content in their environment, suggesting that rapid sediment turnover reflected the necessity to process larger volumes of sediment when nutrient content was low. This hypothesis was supported by Nickell et al. (1995), who recorded comparably lower ejecta mounds from *C. subterranea* burrows in areas of organically enriched sediments. Difference in shore height reflects the time in which shrimp burrows are covered by water and the time in which nutritive detritus can be deposited from the water column. As a result, burrows further down the shore which are covered by water for a longer period of time are probably in areas of higher food content. This in turn, could be reflected by the lower sediment expulsion rate of *C. filholi* low on the shore in comparison with shrimp found higher up the shore.

In addition to physical factors, the sediment turnover rate at the study site appeared to correspond to size of individual *C. filholi*; the amount of sediment expelled was significantly higher for large individuals compared with small shrimp. This significant relationship between the amount of sediment expelled and size of shrimp is intuitive and consistent with findings for *C. subterranea* (Rowden et al., 1998).

Taking account of the above physical and biological factors it was possible to calculate a robust annual sediment turnover estimate of 96 kg m^{-2} $year^{-1}$ for the intertidal *C. filholi* population. Paucity of the necessary information and the lack of standard methods for assessing sediment turnover estimates for callianassids make it difficult to compare the present turnover estimate with that of other species (see Rowden and Jones, 1993). However, two studies of *C. subterranea* which also accounted for changes in temperature and population dynamics established sediment turnover estimates of 15.5 kg m^{-2} $year^{-1}$ (Stamhuis et al., 1997) and 11 kg m^{-2} $year^{-1}$ (Rowden et al., 1998). The sediment turnover estimated for *C. filholi* is notably higher than that for *C. subterranea*, especially given a population density 2.5 times higher for *C. subterranea* than for *C. filholi*. Part of the difference in sediment turnover rate between these two similar-size deposit-feeding temperate species could be due to differences in the measurement of sediment expulsion activity. Both the above studies on *C. subterranea* were based in the laboratory where individual shrimp were kept under constant conditions which resembled as far as possible their subtidal habitat. In contrast, the present study examined a larger proportion of an intertidal shrimp population in situ and accounted for a number of physical factors. Even though small juvenile and post-larval shrimp were missed by the sampling effort, which could potentially result in an overestimate of sediment expulsion rate, it has been found that large animals represent the significant proportion of the population throughout the year (Berkenbusch and Rowden, 1998). It is also likely that adults account for most of the sediment expelled to the surface as small animals are not thought to be extensive burrowers (Witbaard and Duineveld, 1989). The present study did not directly assess the periods of inactivity which have been reported for *C. subterranea* (Stamhuis et al., 1997; Rowden et al., 1998). Whilst this could also potentially result in an overestimate of sediment expulsion rate for *C. filholi*, possible periods of inactivity would have been inadvertently incorporated by the sampling effort. The 6–9-fold difference observed between the sediment turnover estimates for *C. filholi* from this study and those of the analogous northern temperate species *C. subterranea* (Stamhuis et al., 1997; Rowden et al., 1998) might perhaps be explained with reference to the tidal habitat of the populations examined. A study by Bradshaw (1996) of tropical callianassid species revealed a difference in sediment turnover between an intertidal and a subtidal population (although the estimates were coarse and did not take account of physical and biological factors contributing to sediment turnover activity). Such an observation and the indirect evidence of the present study could indicate a substantial divide in the sediment expulsion activity of intertidal–subtidal callianassid populations, presumably resulting from the differing physical and biological factors encountered.

The importance of taking account of population aspects and physical factors when calculating sediment turnover estimates for callianassids has been demonstrated previously by Stamhuis et al. (1997). These authors re-calculated a sediment turnover estimate for *C. subterranea* which had originally been proposed by Witbaard and Duineveld (1989); accounting for population dynamics and seawater temperature they found the newly derived value was almost three times higher than the original estimate. This example and the results of the present study stress the crucial importance of considering physical and biological factors when assessing the sediment turnover estimate for callianassids, and thereafter inferring bioturbatory significance.

Whilst estimates of sediment turnover by callianassids (and other species of benthic macrofauna, e.g. Retraubun et al., 1996) are perhaps becoming more considered and robust, the authors suggest that a number of related aspects warrant future study. These include elucidation of – the relationship between sediment expulsion activity and both burrow maintenance and processing of sediment for food; the pattern of sediment expulsion activity and tidal/lunar cycles, particularly for intertidal populations; the contribution of juvenile/post-larval shrimp to estimates of sediment turnover; and the factors which may be responsible for any observed differences in sediment expulsion rates between intertidal and subtidal populations of burrowing ghost shrimp.

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