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Critical evaluation of sediment turnover estimates for Callianassidae (Decapoda: Thalassinidea)

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Abstract: Members of the decapod family Callianassidae influence sediment dynamics and ecosystem function via their bioturbation activities. The latter is currently assessed by measures of sediment turnover rates which are collected, calculated and expressed by different methods. Some estimates, particularly extrapolations which do not consider the influence of temperature, population structure and expulsion behaviour, are likely to be significantly over/under estimates of sediment turnover. Therefore, published values of sediment turnover by the Callianassidae need to be treated with caution and are not strictly comparable. In view of the need for assessing the relative importance of callianassid bioturbation, it is suggested that attempts should be made to standardize the measurement of sediment turnover rate to allow future comparisons to be made with confidence.

Key words: Bioturbation; Callianassidae; Comparison; Sediment turnover; Standardization

Introduction

Members of the crustacean, decapod family Callianassidae, often referred to as "mud" or "ghost" shrimps, are distributed widely in tropical and northern temperate waters (Saint Laurent & Bozic, 1972; Manning & Felder, 1991). Callianassids occupy burrows, of varying complexity and design, in intertidal and subtidal soft sediments (Griffis & Suchanek, 1991). Unwanted sediment, produced during the course of burrow construction/maintenance and feeding (principally deposit feeding), is ejected from the burrow and forms mounds on the substratum surface (Dworschak, 1983). Such bioturbation activities of callianassids has important consequences for the structural and geotechnical characteristics of the substratum (Bird, 1982; Tudhope & Scoffin, 1984). The presence and activity of *Callianassa* species is also linked to significant sediment and radioactive particulate resuspension (Roberts et al., 1981; Colin et al., 1986). In addition to physical manifestations, sediment turnover by the Callianassidae controls the associated plant and animal populations of lagoon and reef sediments (Suchanek, 1983; Alongi, 1986) and the occurrence of chemical elements (Abu-Hilal et al., 1988; Vaugelas & Buscail, 1990). Such influences affect a variety of important

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ecosystem functions, including nutrient exchange, faunal community structure and biogeochemical cycling (e.g. Koike & Mukai, 1983; Waslenchuk et al., 1983; Posey, 1986). The principal method of assessing such biogenic activity is to estimate sediment turnover rates (see reviews, Lee & Swartz, 1980; Thayer, 1983). Unfortunately, the validity and usefulness of these estimates, as a means of comparing the relative role of callianassinds in ecosystem functioning, is constrained by the lack of a rigorous and unambiguous method of calculation and expression of sediment turnover. The present paper summarizes the various methods used to estimate sediment turnover rates, emphasizes that such estimates are not strictly comparable, and recommends a standard approach for the future measurement of sediment turnover estimates.

Methods of Measuring Sediment Turnover

Table I summarizes the various methods of measuring sediment turnover for callianassids. *Direct Entrapment* is the most widely used method and involves placing a simple trap over the site of sediment ejection (usually a mound) and collecting the expelled sediment after a given time (e.g. Roberts et al., 1981). The sampling is performed mostly in situ, although some sediment collections have been carried out in the

TABLE I

Comparison of sediment turnover rates for Callianassidae N.B. This table is intended to be illustrative and not exhaustive. (Key: ? = unknown; D = Direct Entrapment; L = Leveling; T = Tracer Particles; i = in situ; l = laboratory).

Species	Sediment turnover rate	Scaling	Method	Source
Neotrypaea californiensis	20–50 ml(wet)/ind./day	?	?, ?	Mac Ginitie, 1934
Callianassa sp.	6–7 cm/wk	?	L. & T., i	Aller & Dodge, 1974
Callianassa sp.	0.1–0.2 cm/wk	?	L. & T., i	Aller & Dodge, 1974
Calianassa tyrrhena	25 cm^3(wet)/ind./day	?	?, ?	Ott et al., 1976
Callianassa sp.	3.395 kg(dry)/m^2/day	1	D., i	Roberts et al, 1981
Callianassa sp	0.819 kg(dry)/m^2/day	1	D., i	Roberts et al, 1981
Callianassa sp.	0.004 kg(dry)/m^2/day	1	D., i	Suchanek, 1983
Neocallichirus rathbunae	2.59 kg(dry)/m^2/day	1	D., i	Suchanek, 1983
Glypturus laurae	3.0 kg(dry)/mound/wk	0	?, i	Vaugelas &Saint Laurent, 1984
Glypturus laurae	1.5 kg(dry)/mound/wk	0	?, i	Vaugelas & Saint Laurent, 1984
Callianassa sp.	240.1 cc(wet)/m^2/day	1	L., i	Suchanek et al, 1986
Callianassa sp.	56.0 cc(wet)/m^2/day	1	L., i	Suchanek et al, 1986
Callianassa sp.	800 cc(wet)/m^2/day	1	D. & L., i	Suchanek & Colin, 1986
Glypturus armatus	1660 g(dry)/mound/wk	0	D., i	Vaugelas et al, 1986
Glypturus armatus	500 g(dry)/mound/wk	0	D., i	Vaugelas et al, 1986
Neotrypaea californiensis	18 ml(wet)/ind./day	0	L., i	Swinbanks & Luternauer, 1987
Callianassa kraussi	12.14 kg(wet)/m^2/day	3	T., i	Branch & Pringle, 1987
Callianassa subterranea	3.5 kg(dry)/m^2/yr	2	D., l.	Witbaard & Duineveld, 1989
Callianassa subterranea	11 kg(dry)/m^2/yr	2	D., l.	Rowden et al., unpubl. data

laboratory from shrimps recovered at sites below SCUBA-diving working depth (e.g. Witbaard & Duineveld, 1989).

A second method, *Levelling*, involves the removal of all surface sediment features from a delineated area to a recognised datum, usually a flat plane, or to a clearly marked surface horizon. Mounds of sediment which then appear after a prescribed time are assumed to result from callianassid expulsion activity and their dimensions are measured either in situ or they are carefully collected for weight/volume determination (Suchanek et al., 1986; Swinbanks & Luternauer, 1987).

The *Tracer Particle* method utilises labelled sediment (usually coloured with fluorescent dye/paint) which is placed at depth(s) in the study area. Cores are taken after a prescribed time, sectioned, and the relative depth occurrence of labelled particles is quantified. Sediment turnover is estimated from the extent of the subsequent net redistribution of the labelled particles. The technique has been used extensively for calculating the sediment turnover rates for bioturbators such as polychaetes (Gordon, 1966; Gerino, 1990), but it is rarely applied to callianassids (Branch & Pringle, 1987) (Table I).

Expressing Sediment Turnover Rate

The expression of sediment turnover for callianassids usually involves the three parameters of quantity, space and time and Table I illustrates the diversity of units applied to these parameters by various authors. When the Direct Entrapment method is used, the quantity of collected sediment is expressed usually by weight (wet or dry) or volume (by displacement) (e.g. Vaugelas et al., 1986). The Levelling method also uses weight/volume when the sediment is collected directly, or a volume approximation, based on the measured dimensions of height and breath of each mound converted to a volume using the formula for a cone (Suchanek & Colin, 1986). The use of Tracer Particles results in the sediment turnover estimate being expressed initially in terms of sediment deposition depth (Aller & Dodge, 1974), however, conversions are sometimes made (e.g. depth to weight; Branch & Pringle, 1987).

The quantity of sediment determined by the Direct Entrapment method is derived generally from collections of individual mounds/shrimps. The sediment expelled (weight/volume) may be expressed per individual mound/shrimp or scaled to a surface area by taking into account population or mound density (Suchanek, 1983). The results of the Levelling method of sediment collection may be related to the surface area of the study plot or scaled to a standardized area such as no./m^2 (Vaugelas et al., 1986). Sediment turnover estimates derived from the Tracer Particle method, expressed as depth of deposition, are independent of area and thus require no spatial unit.

The length of time over which the sediment expelled is collected is the usual time unit incorporated into the final estimate of sediment turnover, although sometimes there is scaling of the temporal unit up or down (e.g. week to year; Witbaard & Duineveld, 1989).

Problems Associated with Making Comparisons

Methodology and estimate reporting

Each of the three measurements of the quantity of sediment turned over (weight, depth and volume) have different attributes. Weight is likely to be measured with the most accuracy (there is an accepted procedure), depth is essentially an artificial measure (there is rarely an even deposition of sediment), whilst volume is open to criticism because determinations involve the error-inducing concept of "settling time" which may be defined (e.g. Suchanek & Colin, 1986 [1 h]) or undefined (Swinbanks & Luternauer, 1987). It is thus difficult to make meaningful comparisons between the various sediment turnover estimates for Callianassids as the quantity parameter is calculated, and expressed, by three very different methods (Table I). Even those estimates using the same parameters may not be compared directly as they often incorporate possible errors related to different degrees of scaling. An example of the problem is demonstrated by the results of Branch & Pringle (1987) and Suchanek (1983) for two different *Callianassa* species. The former workers estimated a sediment turnover rate of 12.14 $kg/m^2/day$ using the Tracer Particle method and compared it with the latter's estimate of 2.59 $kg/m^2/day$ based on the Direct Entrapment method. Branch & Pringle's (1987) estimate was arrived at by scaling (i) a calculated sediment depth deposition to an approximate weight (using a density measure for wet sediment), (ii) the area of study (490 cm^2) to m^2 and (iii) from one week to a day. On the other hand, Suchanek (1983) used only one scaling factor (individual mound measurements to natural mound density/m^2).

The above example illustrates two other concerns. Firstly, the validity of comparing data collected by two different sampling methods. Suchanek & Colin (1986) utilised two techniques at the same location and found that the mean sediment turnover estimate obtained by Levelling was nearly twice as much as that determined by Direct Entrapment. The second concern is that ambiguity of reporting parameters can result in unlike comparisons being made. For the estimates of sediment turnover detailed in Table I we have indicated whether the specific quantity unit is dry or wet weight. Unfortunately, clarity of reporting units is not always available from the original paper. This problem resulted in Branch & Pringle (1987) unknowingly comparing their wet with a dry weight estimate of Suchanek (1983). Another example of ambiguity which hampers meaningful comparisons is that more than one form of the sediment turnover estimate is sometimes reported. Vaugelas et al. (1986) reported that *Glypturus armatus* was estimated to move 1660 g/mound/wk, or 76.8 kg/100 m^2/wk, or the equivalent of a layer of sediment 1 cm thick taking 12–16 wks to pass through the burrow. MacGinitie (1934), who provided the first estimate of sediment turnover rate for a callianassid, not only expressed the value in three different ways, but in addition failed to report the details of sediment collection method and turnover calculation.

Precision and accuracy of calculation

The value of any comparison between sediment turnover estimates is reduced by differences in the degree of precision and accuracy incorporated into the final calculation. Some estimates of sediment turnover are based on a small number of single observations (e.g. Ott et al., 1976), whilst others are from extensive and replicated studies (e.g. Swinbanks & Luternauer 1987). Even the more extensive studies, however, sometimes fail to incorporate fundamental information into the final estimate. For example, the deep-burrowing habit of callianassids makes population density difficult to determine using normal shallow-penetrating sampling gear; density is usually inferred indirectly from the number of ejection mounds (i.e. 1 mound = 1 shrimp) (Vaugelas, et al., 1986). Even when attempts have been made to relate mounds (and/or other surface openings) more precisely to actual numbers, there is a degree of error attached to the apparent ratio, which will be transmitted into the extrapolation (Dworschak, 1983). In addition to the problem of an accurate measurement of population density, the size-frequency structure of the population at the study site, and its effect on sediment turnover, is frequently ignored. For example, Suchanek & Colin's (1986) Direct Entrapment estimate of sediment turnover was obtained only from mounds greater than a defined size (Table I). Lack of account for the influence of population size structure imposes error on the final estimate of sediment turnover (i.e. if sediment quantity is expressed per total mound density then this will result in an over estimate; if expressed per defined size mound density then this will give an under estimate). The less-frequently adopted Levelling method is likely to reflect more accurately the sediment turnover rate, as it presumes to collect all the sediment expelled by the entire shrimp population within a given area. However, the effect of the physical disturbance of levelling on the activity of the shrimps is not known. Thus, it is possible that error will be incorporated into the subsequent estimate of sediment turnover, especially as the effect of disturbance will probably be size specific (e.g. smaller individuals may take longer or never recover from the disturbance).

Influence of behaviour and environment

The frequency of sediment ejection by callianassids does not appear to follow any diurnal pattern (Suchanek, 1983). Few studies have elucidated temporal changes in sediment turnover rates and those that have, fail to include any differences in their final estimate. For example, differences in sediment expulsion rates between two sampling occasions, separated by more than 2 months (tropical region) and a 4 °C change in temperature (temperate region), have been observed by Suchanek & Colin (1986) and Swinbanks & Luternauer (1987) respectively. Although a trend was demonstrated in each case, and its possible importance recognised, the authors expressed their final estimate of sediment turnover as a *mean daily,* rate. Only Vaugelas & Saint Laurent (1984) measured long-term sediment turnover rates (weekly determinations over nearly eight months) for *Glypturus laurae* and demonstrated a distinctive pattern of sediment expulsion behaviour such that the amount of material expelled was different even between successive months. Unfortunately, the differences were not incorporated into their final *weekly* estimate (Table I).

STANDARDIZATION OF SEDIMENT TURNOVER ESTIMATES

At present it is impossible to make valid and straightforward comparisons because of the diversity of the collection, calculation and expression methods of sediment turnover estimates. Previous attempts to compare turnover rates converted data to a common format, but such conversions introduced error as they were neither standard, equally applied, nor verified by the original authors (e.g. Vaugelas, 1985, 1990). The ability to compare sediment turnover rates with confidence requires standardization of methods and reporting. As a first step towards this goal, the following recommendations are made:

(1) Whenever possible, the Direct Entrapment method should be adopted as the most accurate and practical method for collecting expelled sediment.
(2) Dry weight, rather than volume or depth, should be used as the most exact and appropriate unit for expressing the quantity of sediment turned over.
(3) The remaining two units of the turnover expression (space and time) should be constrained by the confidence of their measurement.

As an illustration of the last recommendation, our recent studies of the temperate species *Callianassa subterranea* have demonstrated the influence of body size and temperature upon the amount of sediment expelled by individuals. In addition, our experiments were conducted over sufficient time to illustrate that sediment expulsion activity was not continuous, but a complex of active and inactive periods. Combining these experimental data with field information on seawater temperatures and population dynamics (density, size frequency), it has been possible to produce an annual sediment turnover budget of 11 $kg/m^2/yr$ for a site in the North Sea (Rowden et al., unpub. data). This estimate is approximately three times higher than the value reported previously for the same species at this location (Witbaard & Duineveld, 1989). Possible reasons for the discrepancy between these estimates may be that Witbaard & Duineveld (1989) extrapolated from a weekly estimate, derived from four individuals in a single experimental tank, to an annual expression of sediment turnover. Although the latter authors acknowledged that their findings were preliminary, their estimate has, nonetheless, been used for comparative purposes (Vaugelas, 1990).

Thus, to reduce possible error and to allow comparison of reported estimates, if there is no, or little, information on population dynamics or total mound (including small) density, then only the unit of individual shrimp/mound should be utilised in the final expression of sediment turnover. In addition, a similar constraint should be applied to the temporal unit of the estimate. The length of time over which expelled sediment was collected should be the standard unit, with alternative values being utilised only if account has been taken of possible variability within that time (e.g. influence of expulsion behaviour and of changes in productivity and temperature in tropical and temperate regions respectively). Therefore, whilst it is often preferable to have a final value of sediment turnover expressed as quantity per m^2/year, extrapolation to these, or other units, should not be undertaken unless the estimate incorporates sufficient confidence in the spatial or temporal unit quoted. In addition, all of the original values and calculations used to obtain the sediment turnover estimate by extrapolation must be reported.

Sediment turnover rates, expressed as suggested, would enable direct comparison of estimates of bioturbatory activity for callianassids. Until such standardization, the relative importance of callinassids in sediment dynamics and ecosystem function will not be accurately identified.

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