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Functional effects of the hadal sea cucumber *Elpidia atakama* (Echinodermata: Holothuroidea, Elasipodida) reflect small-scale patterns of resource availability

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Abstract Holothuroidea represent the dominant benthic megafauna in hadal trenches (∼ 6,000–11,000 m), but little is known about their behaviour and functional role at such depths. Using a time-lapse camera at 8,074 m in the Peru–Chile Trench (SE Pacific Ocean), we provide the first in situ observations of locomotory activity for the elasipodid holothurian *Elpidia atakama* Belyaev in Shirshov Inst Oceanol 92:326–367, (1971). Time-lapse sequences reveal 'run and mill' behaviour whereby bouts of feeding activity are interspersed by periods of locomotion. Over the total observation period (20 h 25 min), we observed a mean (±SD) locomotion speed of 7.0 ± 5.7 BL h^{-1}, but this increased to 10.9 ± 7.2 BL h^{-1} during active relocation and reduced to 4.8 ± 2.9 BL h^{-1} during feeding. These observations show *E. atakama* translocates and processes sediment at rates comparable to shallower species despite extreme hydrostatic pressure and remoteness from surface-derived food.

Introduction

Deposit feeding invertebrates, such as the Holothuroidea, dominate benthic megafaunal communities in the deep sea in

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terms of abundance and biomass (Rice et al. 1982; Ohta 1983; Sibuet 1985; Billett 1991). A consistent feature of holothurian communities, irrespective of location, is the marked increase in diversity at abyssal depths (3,000–6,000 m) (Billett 1991) relative to bathyal (1,000–3,000 m) (Hansen 1975) and hadal depths (>6,000 m) (Hansen 1957; Belyaev 1989). Frequently observed mass abundances of holothurians, particularly in trenches associated with high productivity in temperate and sub-Antarctic latitudes, have led some authors to refer to the hadal zone as "the *kingdom of Holothuroidea*" (*sensu* Belyaev 1989), a view that has been reinforced by trawl-catch frequencies of 88% at depths >6,000 m (comparable only to Polychaeta) and high levels of dominance (75–98% in number of all organisms retrieved, >90% biomass) at depths >7,500 m (Belyaev 1989). Although such high returns tend to be associated with trawls confined to the bottom of the axial part of the trenches, where the greatest quantity of organic matter accumulates (Otosaka and Noriki 2000; Danovaro et al. 2003; De Leo et al. 2010; Jamieson et al. 2010), it follows that the cumulative contribution of the Holothuroidea to deep ocean benthic process and functioning must be considerable (Amaro et al. 2010).

Despite such high levels of abundance, intra- and interspecific competition is thought to be low because individual species of holothurians adopt different feeding strategies, including preferential feeding on nutritionally rich patches (Hauksson 1979; Hudson et al. 2005) and/or subtle differences in mobility or feeding behaviour (Hudson et al. 2005; Godbold et al. 2009) that allow them to utilise different fractions of the same detrital food source (Uthicke and Karez 1999; Miller et al. 2000). It is also known that differences in feeding rates (compare, for example, Hudson et al. 2005; Godbold et al. 2009) alter the gut residence time of a food parcel, leading to more efficient digestion and rates of assimilation (Hiratsuka and

Uehara 2007). Whilst these physiological and behavioural adaptations influence holothurian activity, much of the ingested material is of low nutritional value (Lopez and Levinton 1987), leading to foraging activity that results in significant levels of surficial bioturbation that has seldom been quantified (Sibuet and Lawrence 1981; Bett and Rice 1993; Uthicke 1999; Roberts et al. 2000; Bett et al. 2001). Indeed, a recent review of invertebrate bioturbation (Teal et al. 2008) indicates a paucity of such data from bathyal or abyssal depths (maximum depth data obtained = 5,654 m, Yang et al. 1986) and a complete absence of information from hadal depths. Hence, it is clear that the ecological consequences of particle redistribution following holothurian foraging and feeding activities are not known despite the importance of this group in deep ocean ecosystems.

In contrast to shallower environments, where species can be caught and returned to the laboratory, carrying out controlled experimental manipulations on hadal specimens is difficult. Direct in situ experimental manipulations are possible using remotely operated vehicles (ROVs), but progress is slow as there is only one vehicle capable of sampling >6,000 m (Fletcher et al. 2010). A more practical solution is the use of free-fall baited cameras (Jamieson et al. 2009a, b) which allow time-lapse or continuous video recordings of benthic faunal behaviour. Here, we use such technology to present the first detailed in situ account of the locomotion and feeding behaviour of the holothurian *Elpidia atakama* (Belyaev 1971) (family Elpidiidae) at 8,074 m in the Richards Deep area of the Peru–Chile trench. This species has never been seen alive and appears to be endemic to the Peru–Chile trench. We compare locomotion speed and feeding behaviour with abyssal analogues and conclude that the observed patterns of activity are consistent with the view that the behaviour of *E. atakama* reflects exploitation of patchily distributed resources. We contend that the ability to exploit environmental heterogeneity in this way explains, at least in part, why the holothurians are so abundant and outcompete other deposit feeding species at abyssal and hadal depths.

Materials and methods

Study site

The Peru–Chile Trench (SE Pacific Ocean) is the longest trench in the world (5,900 km × 100 km, Angel 1982) and runs parallel to the west coast of South America from Ecuador to central Chile. The trench lies below the Humboldt Current and the Peruvian upwelling system (Echevin et al. 2008), a region of high surface productivity (averaging 269 g C m^{-2} year^{-1}, Longhurst et al. 1995) with values reported as high as 3,613 g C m^{-2} year^{-1} (Fossing et al. 1995).

Equipment

We deployed Hadal-lander B (Jamieson et al. 2009b), a free-falling lander equipped with a 5 megapixel digital still camera (OE14-208; Kongsberg Maritime, UK) and a Conductivity, Temperature and Depth (CTD) sensor (SBE-19*plus* V2; SeaBird Electronic Inc. USA), at 8,074 m in the Richards Deep, Peru–Chile trench (23° 22.470′S, 71° 19.973′W) on the 13 September 2010. The camera was mounted vertically (altitude 1 m) providing a visible area of 62 × 46.5 cm (0.29 m^{-2}). We attached a bait (∼1 kg of Tuna, *Thunnus* sp.) to a 1-cm-diameter scaled bar in the centre of the field of view (FOV) and positioned to intersect the sediment–water interface. Time-lapse images were taken at 60-s intervals. The CTD probe recorded temperature (°C), salinity, and pressure (dbar) every 10 s. Lander recover was achieved by acoustically jettisoning ballast weights to initiate the ascent to the surface. CTD data were averaged, and pressure was converted to depth (m) following Saunders (1981).

Image analysis

Motion paths of *E. atakama* were tracked using ImageJ 1.42q, a Java-based public domain program developed at the USA National Institutes of Health (available at, http://rsb.info.nih.gov/ij/index.html). Images were calibrated and analysed in chronological order. We used the X–Y coordinates at the base of the central feeding tentacle as a location marker and calculated the distance (cm) an individual travelled per time step to determine the absolute locomotion speed (cm h^{-1}) as follows:

$$a = \frac{d}{t} = \frac{\sqrt{(X_2 - X_1)^2 + (Y_2 - Y_1)^2}}{t} \tag{1}$$

where $\tilde{a}$ = absolute locomotion speed, cm h^{-1}; d = distance, cm; and t = time interval (here, 60 s).

We also explore how differences in time-lapse interval alter ecological interpretation by re-calculating the absolute locomotion speed (and percentage deviation in error relative to the highest resolution of observation) for *E. atakama* at 1-, 2-, 5-, 10-, 20- and 60-min intervals and place our results within the context of other findings published in the scientific literature.

In order to account for body size, we divided $\tilde{a}$ by body length (BL = longest axis of specimen) to provide a size-specific speed (BL h^{-1}).

Results

We recorded 1,225 images (20 h 25 min) at a calculated depth of 8,072 m (=8,276 dbar). At this depth, water temperature was 2.25°C and salinity was 34.68. Sequences included observations of the holothurian, *Elpidia atakama*, and three species of scavenging gammarid amphipods: *Eurythenes gryllus*, (Thurston et al. 2002), *Hirondellea* sp.nov. (Perrone et al. 2002) and an unidentified species. After 20 h, the bait remained present but had been significantly reduced by scavenging amphipods (Fig. 1).

E. atakama was observed (starting at 48 min elapsed time) on three occasions (Period A, 218 images or 3 h 38 min; Period B, 138 images or 2 h 18 min; and Period C, 219 images or 3 h 44 min; total = 9 h 40 min; Fig. 1), which were separated by periods of time when the individual moved out of the field of view (2 h 18 min and 20 min, respectively). Within these sequences, the number of images in which *E. atakama* was present varied, ranging from 76 images (1 h 16 min) in Period B, 140 images (2 h 20 min) in Period A, to 203 images (3 h 23 min) in Period C. The individual was not always fully visible within the field of view; hence, only images where the head was clearly visible were used to track holothurian activity. We matched exit to entrance positions between sequences and checked body size measurements (~5.1 × 2.3 cm) and confirmed that all appearances were the same individual.

The distance that *E. atakama* traversed varied over time, but the rate of movement did not appear to be related to the length of time the individual was observed. Maximal locomotion speed was attained during Period A (96.5 cm in 140 min, = 41.36 cm h^{-1} or 8.1 BL h^{-1}), with lower rates of movement observed in Periods B (37.3 cm in 76 min, = 29.45 cm h^{-1} or 5.8 BL h^{-1}) and C (133 cm in 203 m, = 33.6 cm h^{-1} or 6.6 BL h^{-1}). When averaging these together, $\tilde{a} = 35.5 \pm 29.3$ cm h^{-1} (7.0 ± 5.7 BL h^{-1}), giving a mean swept area rate ($\tilde{a}$ × body width × distance/t) of 81.6 cm^{-2} h^{-1}. The speed and direction of movement was neither constant nor unidirectional (Fig. 2), reflecting a 'run and mill' movement pattern (Kaufmann and Smith 1997), i.e. relatively large distances are achieved with minimal changes in speed and direction (routine locomotion) and are interspersed with bouts of localised, closely spaced turns that allow sediment processing and feeding (milling activity, *sensu* Smith et al. 1993; Fig. 2). Closer examination of our images suggests that feeding does not take place during routine locomotion (all feeding tentacles protrude forward clear of the sediment–water interface), rather feeding tentacles only contact the sediment–water interface during milling activity (Fig. 3). This demarcation of behaviour alters the locomotion ability of the organism and leads to temporally distinct activity periods. For example, following its first appearance (Period A), *E. atakama* exhibited a locomotion speed of 59.3 cm h^{-1} for 26 min (11.6 BL h^{-1}) before it began a bout of feeding (or milling) activity for 55 min in a localised area, characterised by irregular but short-distance movements at 17.4 cm h^{-1} (3.4 BL h^{-1}). On the cessation of any obvious feeding activity, locomotion speed increased to 61.7 cm h^{-1} (12.1 BL h^{-1}) for 53 min before feeding started again at a speed of 15.4 cm h^{-1} (3.0 BL h^{-1}) for 6 min. Similar observations were also observed in the second period (Period B), where *E. atakama* fed for the first 49 min at a speed of 23.0 cm h^{-1} (4.5 BL h^{-1}) before relocating at a speed of 43.6 cm h^{-1} (8.5 BL h^{-1}) for 27 min until exiting the field of view. In the third appearance (Period C), *E. atakama* fed for the majority of time (152 min) with two small periods of routine movements (31 and 20 min). The locomotion speed during bouts of relocation was 54.0 cm h^{-1} (10.6 BL h^{-1}), but during feeding, reduced to 27.1 cm h^{-1} (5.3 BL h^{-1}). In total,
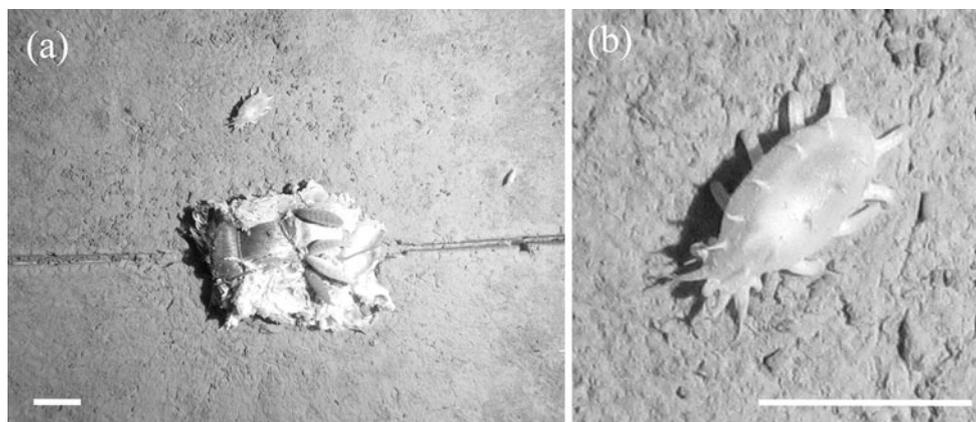

Fig. 1 a Full field of view image from 8,075 m showing the tuna bait parcel in the centre with four scavenging amphipods (*Eurythenes gryllus*) beginning to feed. In the centre, middle is the holothurian *Elpidia atakama*. **b** Close-up of *E. atakama*. *Scales bars* = 5 cm

Fig. 2 Absolute speed (cm min^{-1}) over time and the X–Y track for the three appearances of *E. atakama* (**a**, **b**, **c**). Periods of feeding (milling) activity are *shaded*. Trend *lines* are 10 min moving averages. In the *right hand panels*, *S* marks the start position and *E* the end position
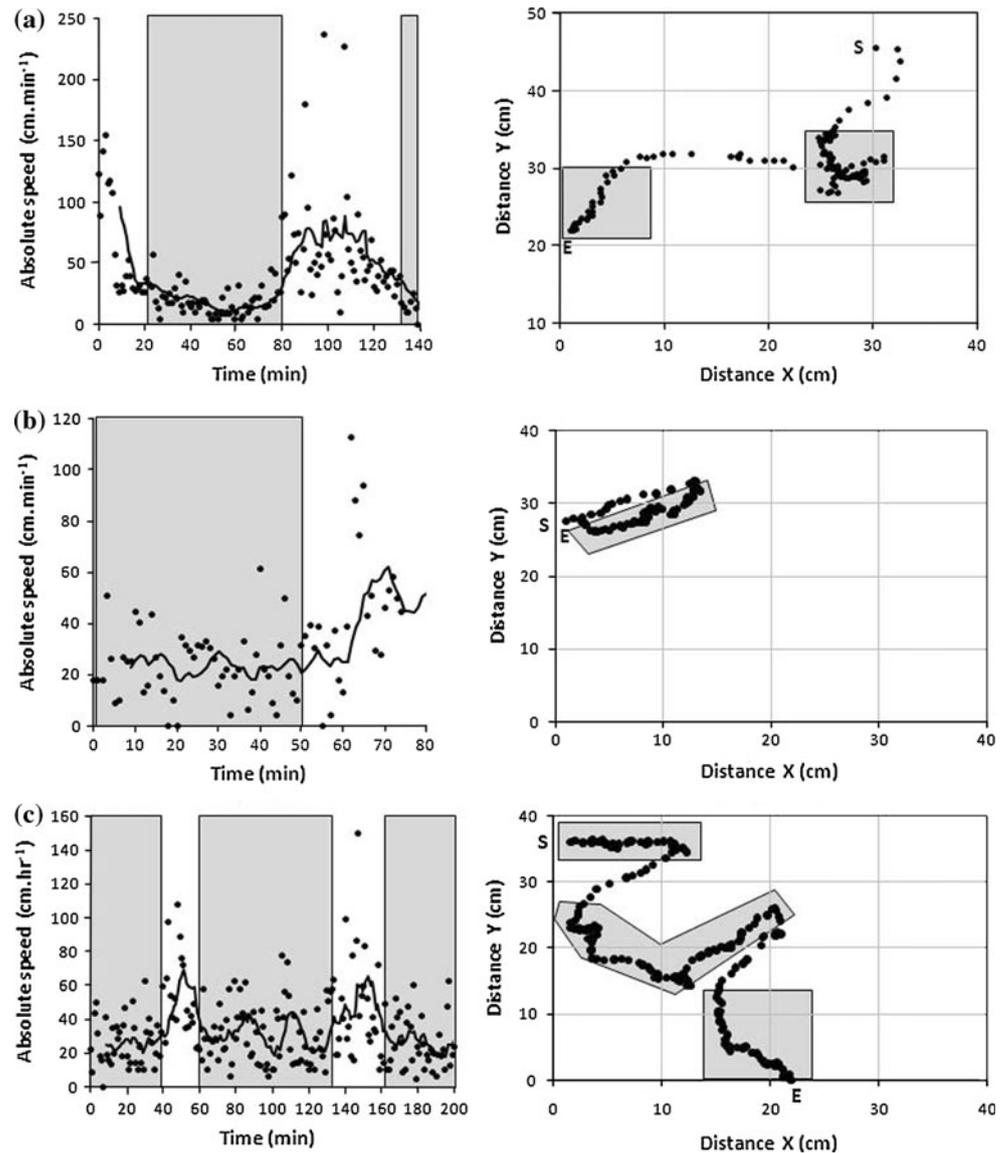
E. atakama spent 150 min relocating and 267 min feeding (a ratio of 1:1.8). By distinguishing between routine locomotion and feeding locomotion, mean locomotive speeds were 55.7 ± 36.7 cm h^{-1} (10.9 ± 7.2 BL h^{-1}) and 24.3 ± 14.8 cm h^{-1} (4.77 ± 2.9 cm h^{-1}), respectively.

It is important to place the current observations within the context of other known observations of holothurian behaviour (Table 1). Whilst it is clear that the rate of locomotion in *E. atakama* is faster than many other species, these differences relate only poorly to increasing depth (Fig. 4a) or to body size (Fig. 4b). An alternative explanation may be that the rate of locomotion relates to the quality and reliability of food supply, although this hypothesis has not been tested explicitly and we acknowledge that comparisons between studies are difficult

to make given the lack of available data and differences in methodology (Fig. 5). Re-analysis of our own data showed that increasing the time-lapse interval over the observation period results in a rapid (logarithmic) increase in error, resulting in >55% estimate error when images are taken at 60-min intervals (decreases from 7.0 ± 5.7 BL h^{-1} to 3.2 ± 0.9 BL h^{-1}; Fig. 5a), relative to the highest resolution of observations (1 min). Data using 60-min intervals from Kaufmann and Smith (1997) and Smith et al. (1993) and 1-min intervals from (Smith et al. 1997) are in good agreement with our predictions (Fig. 5b). Furthermore, the measurements of the rate of movement of *Elpidia minutissima* (Smith et al. 1993; Kaufmann and Smith 1997) are almost equal to those of *E. atakama* based on a theoretical 60-min interval.
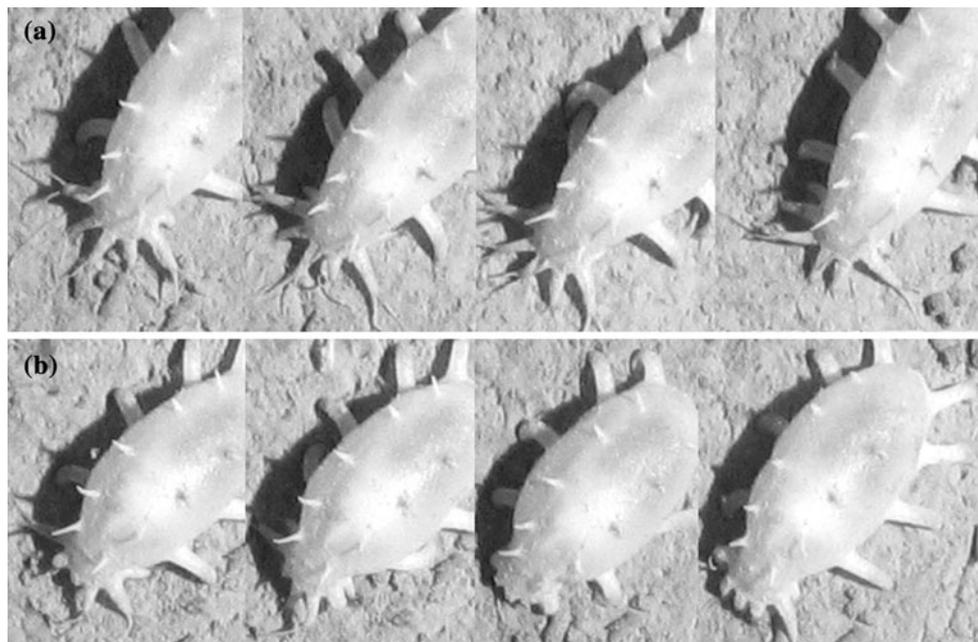
Fig. 3 The **a** locomotion and **b** feeding behaviour of *E. atakama*. Feeding tentacles are **a** positioned to the anterior (the *bottom* of each image) and raised above the sediment–water interface during locomotion and **b** lowered to intersect the sediment–water interface during bout of feeding. Frames were selected at random from successive bouts of locomotion and feeding

Table 1 Summary of measured body length (BL), absolute ($\bar{a}$) and size-specific locomotion speeds for holothurians at a range of depths

Species	Depth (m)	BL (cm)	$\bar{a}$ (cm h^{-1})	Size-specific speed (BL h^{-1})	Source
Laetmogone violacea	1,000	14.0	102.6	7.3	Smith et al. (1997)
Benthogone rosea	2,012–2,019	17.0	89.0	5.0	Billett (1991)
Staurocucmuis abyssorum	4,100	12.9	12.8	1.0	Kaufmann and Smith (1997)
Staurocucumis abyssorum	4,100	9.7	17.8	1.8	Smith et al. (1993)
Elpidia minutissima	4,100	4.4	11.9	2.7	Kaufmann and Smith (1997)
Elpidia minutissima	4,100	4.1	14.8	3.6	Smith et al. (1993)
Peniagone vitrea	4,100	8.6	10.1	1.2	Kaufmann and Smith (1997)
Peniagone vitrea	4,100	7.3	8.1	1.1	Smith et al. (1993)
Scotoplanes globosa	4,100	9.5	16.3	1.7	Kaufmann and Smith (1997)
Synallactes profundi	4,100	17.4	12.7	0.7	Kaufmann and Smith (1997)
Oneirophanta mutabilis	4,100	15.3	64.6	4.2	Kaufmann and Smith (1997)
Oneirophanta mutabilis	4,100	14.3	84.8	5.9	Smith et al. (1993)
Oneirophanta mutabilis	4,844	16.2	128.9	8.0	Smith et al. (1997)
Elpidia atakama	8,074	5.1	37.3	7.3	Present study

Discussion

We have documented the feeding and locomotion behaviour of a hadal holothurian and shown that the behaviour is not exceptional; the run and mill pattern of *Elpidia atakama* exemplifies patterns of behaviour of functionally analogous abyssal species in the NE Pacific, including *Elpidia minutisima*, *Staurocucumis abyssorum*, *Synallactes profundi*, *Peniagone vitrea* and *Scotoplanes globosa*

(Smith et al. 1993; Kaufmann and Smith 1997), and locomotion and feeding rates are comparable to holothurians found at shallower depths. However, our findings provide compelling evidence that *E. atakama* is a functionally important species that is likely to change its behaviour in response to localised resource heterogeneity (Godbold et al. 2009, 2011) and the repackaging of organic matter (OM; Bett et al. 2001). Also, movement over the sediment surface associated with relocation constitutes

Fig. 4 Summary of observations of size-specific locomotion speed (BL h^{-1}) for **a** water column depth and **b** body size of individual holothurians. *Open circles* represent measurements for *E. atakama* in the present study, whilst *closed circles* represent the data listed in Table 1
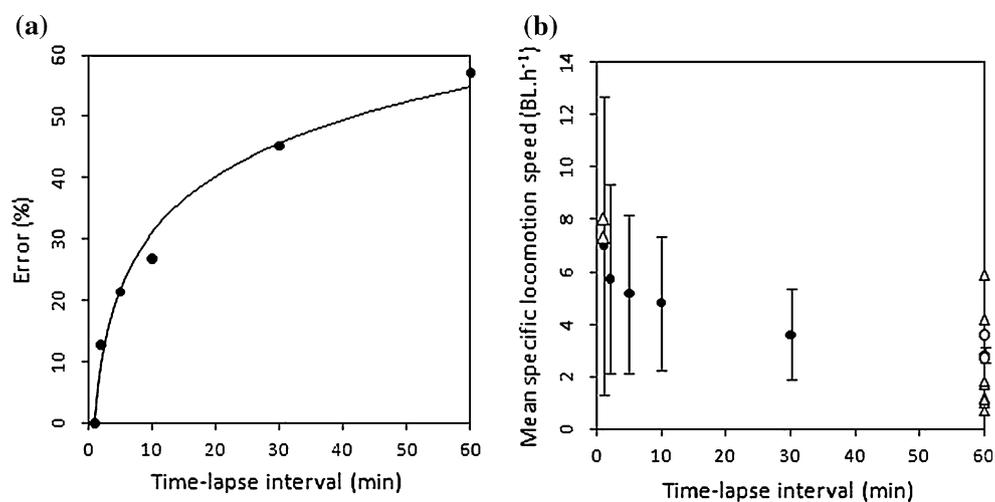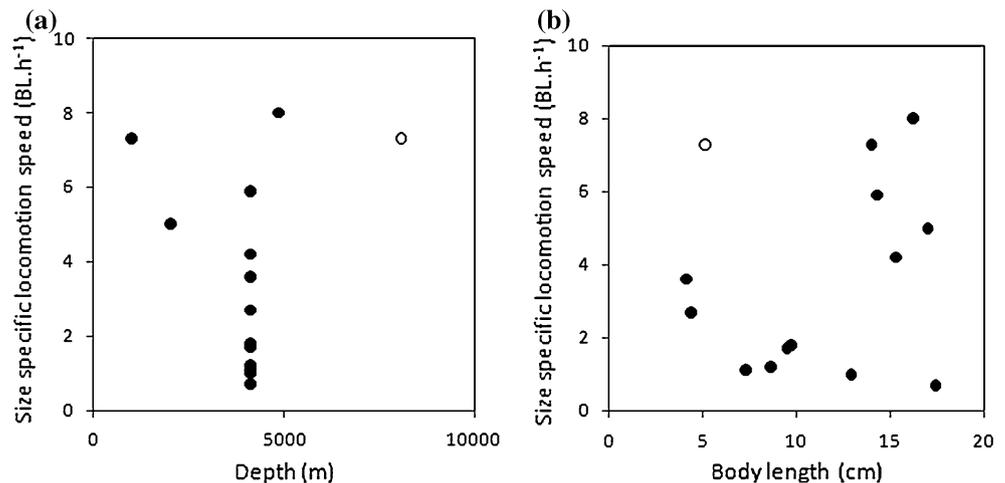

Fig. 5 The effect of increasing the elapsed time between successive time-lapse images on mean locomotion speeds for the holothurians listed in Table 1. In **a,** the degree of estimation *error* increases rapidly as time-lapse intervals are extended (recalculated from present study data). In **b**, data are shown for *E. atakama* at 1-, 2-, 5-, 10-, 30-, and 60-min time-lapse intervals (recalculated from present study data) alongside previously published data (*triangles*) for the abyssal species listed in Table 1. Estimates for *E. minutissima* are denoted by *grey circles*

bioturbation which is qualitatively distinct from bioturbation associated with feeding activity (Bulling et al. 2008), giving credence to the view that epifaunal species can have a substantial effect on the properties of the sediment profile (Solan et al. 2004). It is, however, difficult to assess the ecological contribution of *E. atakama* in the absence of information on the spatial extent and temporal persistence of this species. There are no abundance estimates for *E. atakama* (or any other holothurian) in the Peru–Chile Trench. However, a review of all-known hadal records up to 1989 found that the density of both *E. uschakovi* in the New Hebrides trench and *Elpidia* sp. from the Palau trench was 0.1 ind. m^{-2} (=1,000 ind. ha^{-1}), whilst the density of *E. solomonensis* from the New Britain and Bougainville Trenches ranged from 0.03 to 0.1 and 0.01 ind. m^{-2}, respectively (300–1,000 ind. ha^{-1} and 100 ind. ha^{-1};

Belyaev 1989). In general, however, the density of the Elpidiidae family (*Elpidia glacialis ushakovi, E. glacialis solomonensis, Elipida sp., Peniagone purpurea, P. azorica and Scotoplanes globosa*) at hadal depths can range from 0.5 to 10 ind. m^{-2} (5,000–100,000 ind. ha^{-1}) (Lemche et al. 1976). More recent reports from the Orkney trench (Vinogradova et al. 1993; Gebruk 1993) suggest for *E. decapoda,* a density of 15 ind. m^{-2} (150,000 ind. ha^{-1}) at 6,160 m and 30 ind. m^{-2} (300,000 ind. ha^{-1}) at 5,580 m. These estimates are considerably higher than those reported for the abyssal plains; most reports indicate 15.5–193.3 ind. ha^{-1}, although there are some exceptions, e.g. 370.8 ind. ha^{-1}, *E. minutissima* in the NE Pacific (Kaufmann and Smith 1997) and in the NE Atlantic, 8.77–337.92 ind. ha^{-1} for *Amperima rosea,* and 43,949 ind. ha^{-1} for *Elpidia echinata,* although there are instances of mass occurrences

of *Kolga hyaline* at 501,701 ind. ha^{-1} (Billett and Hansen 1982; Billett 1991; Billett et al. 2001). Nevertheless, using the calculated sweep area and observations of feeding activity obtained here, we estimate that a single individual of *E. atakama* may process 1 m^2 of surficial sediment every 5.1 days, or a population of 123 individuals will turnover 1 m^2 of surficial sediment every hour.

When considered together, the available estimates of holothurian density provide anecdotal evidence that holothurians are found in greatest abundance at hadal depths, rather than at adjacent abyssal areas. Mass abundances of hadal holothurians are thought to occur at the trench axis where elevated levels of organic material are likely to accumulate (Otosaka and Noriki 2000; Danovaro et al. 2003; Jamieson et al. 2010; Itoh et al. 2011). This appears to reflect a general relationship with topography (Rowe 1971) as concentrations of elpidiids are a common feature of underwater canyons and other depressions which are known to contain elevated levels of organic matter and deposit feeding benthic biomass (De Leo et al. 2010). It has been shown that density of benthic assemblages in trenches tends to be related positively to productivity in surface waters: highest densities in trenches that occur at high latitudes and/or close to continents (Belyaev 1989). Whilst it is tempting to speculate that the behaviour we have observed here is a response to the spatio-temporal variability in the extent and intensity of food supply (Ruhl 2007; Smith et al. 2009), the study region is eutrophic, and food resources are plentiful, albeit complicated by interannual phenomena of the region, including the El Nino Southern Oscillation and the development of oxygen minimum zones (Thiel et al. 2007). Furthermore, interannual and seasonal variation in abundances of abyssal holothurians is known to occur (Billett et al. 2001, 2010; Ruhl 2007; Smith et al. 2009) and will also be likely at hadal depths. Under these circumstances, it is unlikely that competition for resources will lead to behavioural differences in feeding strategy (Godbold et al. 2009). In the present study, *E. atakama* spent 150 min relocating and 267 min feeding (a ratio of 1:1.8), suggesting that resource supply is indeed abundant and that the distance between patches is relatively short (20–40 min travel time, or approximately 10 body length distance). This pattern of movement suggests considerable sensitivity to food concentration (McClintic et al. 2008) and implies that the dynamics and organisation of hadal communities are intimately linked to habitat structure and the distribution of resources in ways similar to those found in shallower benthic communities (Levinton and Kelaher 2004; Dyson et al. 2007; Bulling et al. 2008; Nogaro et al. 2008; Godbold et al. 2011). Thus, the cumulative response of hadal species to such small-scale variation is likely to

influence species contributions to ecosystem properties at much larger scales (Godbold et al. 2011).

Whilst we have been able to describe the likely ecological role of *E. atakama* at hadal depths, the high-resolution time-lapse sequences also enabled us to highlight some procedural difficulties that are likely to hinder progress in understanding the structure and functioning of hadal communities (Jamieson et al. 2010). Reanalysis of our time-lapse sequences at progressively lower temporal resolution suggests that the extended time-lapse intervals used in long-term observatories (Kaufmann and Smith 1997) are likely to miss the subtleties of holothurian behaviour and grossly underestimate the locomotion/feeding rates of individual species, because rest periods and alternative bouts of behaviour can occur between successive images (typically <1 h). This source of error makes pairwise comparisons between different studies, locations or seasons difficult and hinders generic understanding of ecological phenomena (Benton et al. 2007). If we are to fully appreciate the functional role of organisms that inhabit the deepest parts of our oceans, extended observations are now needed that appreciate the temporal and spatial scales at which species-environment interactions occur and which aim to test unambiguously ecological theory.

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