

## RESEARCH ARTICLE

# Locomotory activity and feeding strategy of the hadal munnopsid isopod *Rectisura* cf. *herculea* (Crustacea: Asellota) in the Japan Trench

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### SUMMARY

**Benthic fauna in the hadal zone (6500–11,000 m) rely on maintaining sufficient locomotory activity to exploit a low, patchy and uniquely distributed food supply while exposed to high pressure, low temperatures and responding to predator–prey interactions. Very little is currently known about the locomotory capabilities of hadal fauna. *In situ* video footage of the isopod *Rectisura* cf. *herculea* (Birstein 1957) (Asellota, Munnopsidae) was obtained from 6945 and 7703 m deep in the Japan Trench (NW Pacific Ocean). Measurements of locomotion revealed routine walking speeds of  $0.19 \pm 0.04 \text{ BL s}^{-1}$  (mean  $\pm$  s.d.), increasing to  $0.33 \pm 0.04 \text{ BL s}^{-1}$  if naturally perturbed by larger organisms. When immediately threatened by the presence of predators (decapod crustaceans), the isopods are capable of eliciting backward escape jumps and burst swimming escape responses of  $2.6 \pm 1.5 \text{ BL s}^{-1}$  and  $4.63 \pm 0.9 \text{ BL s}^{-1}$ , respectively. These data suggest no significant reduction in locomotory capability despite the extreme depths in which they inhabit. These observations also revealed the isopod to be a bait-attending and aggregative species and suggest that it may not be obligatorily selecting infaunal food sources as previously thought.**

Key words: Isopoda, locomotion, feeding behaviour, hadal zone, trench fauna.

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### INTRODUCTION

Deep-sea organisms, and in particular hadal organisms, inhabit an environment that forces a number of overwhelming challenges, such as extremely high hydrostatic pressure, low temperatures, remoteness from surface-derived food supply and the absence of solar light. Although the hadal zone (6500–11,000 m) (Wolff, 1960; UNESCO, 2009) is perhaps most conspicuously perceived as ‘deep’, the relative role of increasing hydrostatic pressure *versus* other environmental parameters such as low temperature and low food supply remains unresolved, although adaptations to high pressure are an undoubted prerequisite to survival in the deep trenches (Hazel and Williams, 1990; Somero, 1992; Childress, 1995; Samerotte et al., 2007; Pradillon and Gaill, 2007). Hadal fauna must also rely on maintaining sufficient locomotory activity to exploit a low, patchy and potentially uniquely distributed food supply whilst simultaneously partaking in predator–prey scenarios. Some marine species exhibit a relaxation of metabolic rate with depth; however, there is no consistent relationship between hydrostatic pressure and metabolic rate across taxa (Childress, 1995; Seibel and Drazen, 2007). Therefore, hydrostatic pressure is not a key physiological control and does not necessarily influence energy generation for locomotion. The observed declines in metabolism with depth are currently best explained by the ‘visual interaction hypothesis’ (Seibel and Drazen, 2007), whereby in complete darkness the spatial extent of predator–prey interactions is reduced, lessening the requirement for rapid pursuit and evasion (Childress, 1995). This light-sensitive hypothesis is supported by a decrease in metabolic rate of sighted taxa and no such relaxation observed in non-sighted taxa (Seibel and Drazen, 2007).

The isopoda is a very successful order of Crustacea occurring in terrestrial, freshwater and marine environments (see

<http://invertebrates.si.edu/isopod>). In terms of numerical abundance and species diversity, isopods are one of the most important macrofaunal benthic taxa in deep-sea communities (Hessler and Sanders, 1967; Hessler and Strömberg, 1989). Little is known about the behaviour of deep-sea isopods in general. Even less is known about isopods at hadal depths despite being a very characteristic component of the hadal community (Wolff, 1960; Wolff, 1970). Isopod species diversity at hadal depths is greater than any other order of Crustacea and any other class of multicellular organisms, and within the Isopoda there is a high degree of species endemism in each trench or group of neighbouring trenches (Belyaev, 1989).

In the present study, we provide the first insights into the general behaviour and locomotory activity (escape responses, walking and swimming speeds) of hadal Isopoda, based on *in situ* observations of *Rectisura* cf. *herculea* (Birstein 1957) (Asellota, Munnopsidae) from 6945 to 7703 m in the Japan Trench (NW Pacific Ocean). Whilst these new data are novel and represent one of the first studies on hadal fauna locomotion, there is still a lack of sufficient multi-species data to prove or refute hypotheses such as the visual interaction hypothesis. However, this is the first study into invertebrate locomotion and behaviour at hadal depths aimed at reducing the knowledge gap between the hadal and the shallower zones, thus contributing to hypotheses-based studies in the future as further data become available.

### MATERIALS AND METHODS

Observations were made using the free-fall baited video camera system Hadal-Lander A (Jamieson et al., 2009a; Jamieson et al., 2009b). The camera, a 3CCD colour video camera (HV-D30; Hitachi, Japan) was pre-programmed to record one minute of video

every five minutes in MPEG2 format (704×576 pixels, 800 TVL). The camera and two 50 W lamps were coupled 1 m above the seafloor facing vertically downward. The field of view of the seafloor was 0.35 m<sup>-2</sup> (68×51 cm). One whole non-filletted mackerel carcass (*Scomber scombus*) was tied to a stainless steel bar in the centre of the field of view. Salinity, pressure and temperature were recorded at 30 s intervals throughout the deployment using a SeaCat *plus32* CTD (SeaBird Electronics Ltd, Bellevue, WA, USA). Three 2-litre invertebrate funnel traps were attached to the base of the lander and were baited with one third of a mackerel carcass.

The lander was deployed by free fall to the sea floor and was not attached to the ship. Ascent to the surface was initiated by acoustic command from the ship, which triggered the jettison of steel ballast weights. On retrieval, the data were downloaded.

### Study site

Hadal-Lander A made 10 deployments in, or on the edge of, hadal trenches of the West Pacific Ocean (Japan, Izu-Ogasawara, Mariana, Kermadec and Tonga Trenches) at depths of 5469–9729 m. During two of these deployments, isopods were attracted to the bait (Table 1, Fig. 1).

### Data analysis

Each 1-min duration video sequence was viewed, the presence of isopods was noted and the number counted. Their behaviour was categorised into four types; stationary on bait, stationary off bait, walking towards bait and walking away from bait. For those that were walking, it was noted whether they entered or exited the illuminated field of view and at what angle (where 'north' on the image was 0°, east was 90° and west was -90°). These observations were noted to provide insight into resource (bait) location.

Body length was measured from the tip of the head between the 1st antennae to the base of the pleotelson in still frames. To avoid measuring the same individual twice, frame grabs were taken at ~30 min intervals throughout the deployment, which featured the highest number of individuals in one image to obtain a representative sample of the population. Only individuals walking off the bait were measured. Image analysis software (ImageJ 1.42q; National Institute of Health, USA) was used. A calibration was set using the horizontal scale bar which secures the bait in the centre of the field of view.

Walking speeds were analysed by selecting specific sequences in which an individual isopod walked in a relatively straight line for at least 5 s. The sequence was extracted and deconstructed into frame grabs at 1 s intervals (every 25 frames). Each image was analysed in chronological order and the X–Y coordinate of the tip of the head (between the antennae) was measured using the point selection tool. After the position in each image was measured, the data were exported to a Microsoft Excel spreadsheet. Using Pythagoras theory, the distance (cm) between each coordinate was calculated to provide an absolute speed (cm s<sup>-1</sup>). A further measurement was made of the body length (BL) using the segmented line tool (and added to the size frequency data). The absolute speed was converted to size-specific

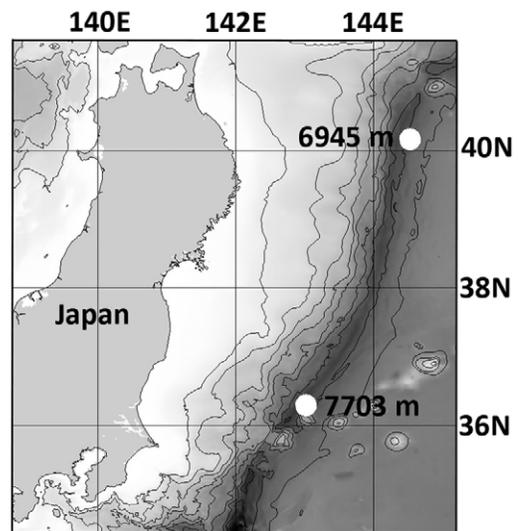


Fig. 1. Deployment locations at 6945 and 7703 m in the Japan Trench (NW Pacific) where isopods were observed.

speed (BL s<sup>-1</sup>) by dividing the absolute speed by the body length. To test the statistical significance for the relationship between walking speed and body size, linear regression analysis was performed in which response and explanatory variables were defined as walking speed and body size, respectively. The statistical analysis was performed using SPSS 18 (SPSS Inc.; www.spss.com).

For sequences featuring burst swimming activity, the sequences were analysed using the same method but with frame grabs at 0.2 s intervals (five frames).

Hydrostatic pressure (MPa) was converted to depth (m) following Saunders (Saunders, 1981). Salinity and temperature (°C) were averaged from data collected on the seafloor only and not during the descent or ascent of the lander.

### RESULTS

At 6945 m in the Japan Trench, the video camera recorded 103 one-minute sequences at one minute on, four minutes off, thus totalling 8 h 30 min on the seafloor. At 7703 m, 77 one-minute sequences were captured at the same intervals, thus totalling 6 h 40 min on the seafloor. Temperature and pressure were recorded as 1.8°C and 711.5 MPa and 1.9°C and 790.1 MPa, respectively (Table 1). The sediment surface was light siliceous ooze similar to that on the adjacent abyssal plains.

The isopods were the most numerous fauna at 6945 m, with 449 observations, whereas only 16 observations were made at 7703 m. The baited traps recovered a diverse collection of invertebrates, mostly small lysianassoid amphipods. None of the isopods were recovered; therefore, in the absence of voucher specimens it was not possible to unequivocally identify the species recorded in the videos; however, based on location, depth, body size and appearance it appears likely

Table 1. Details of the deployment sites in the Japan Trench (NW Pacific) where isopods *Rectisura cf. herculea* were present

Date	Latitude	Longitude	Pressure (MPa)	Depth (m)	Temp. (°C)	Number of video sequences*	Total time on seafloor
Oct. 2007	40°15.33'N	144°30.84'E	711.5	6945	1.8	103	8 h 30 min
Sept. 2008	36°14.96'N	142°49.01'E	790.1	7703	1.9	77	6 h 40 min

\*Time lapse sequence=1 min on, 4 min off.

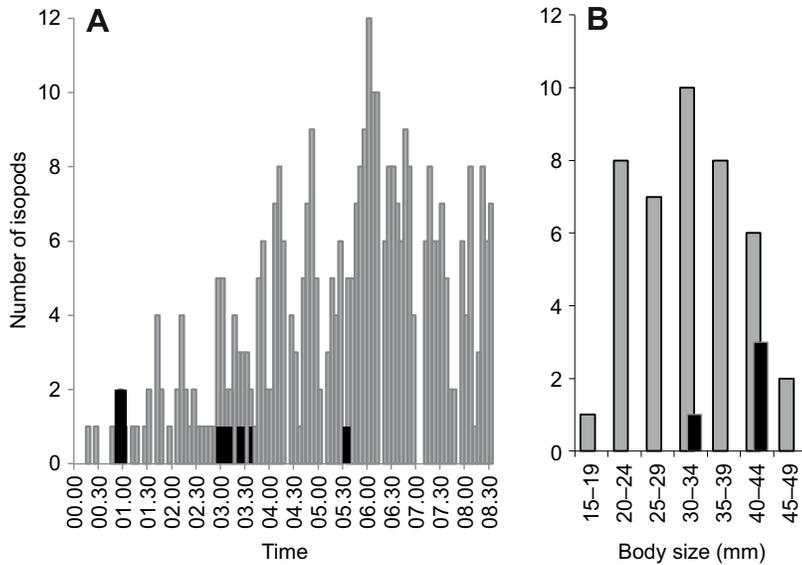


Fig. 2. (A) The number of *Rectisura cf. herculea* observed at the baited lander at 6945 m (grey bars) and 7703 m (black bars). (B) Body size frequency from 6945 m (black; mean=32±8.0 mm) and 7703 m (grey; mean=39±5.0 mm).

these isopods were *Rectisura cf. herculea* (A. Brandt, University of Hamburg, Germany, personal communication).

At 6945 m, in addition to the dominance of *R. cf. herculea*, the lander filmed small lysianassoid amphipods, fish (two occurrences of the liparid *Pseudoliparis amblystomopsis* and two occurrences

of the macrourid *Coryphaenoides yaquinae* (Jamieson et al., 2009c) and frequent appearances of the natantian decapod *Benthesicymus crenatus* (Jamieson et al., 2009d). At 7703 m, a large aggregation of fish, the liparid *P. amblystomopsis* and large lysianassoid amphipods dominated (Fujii et al., 2010).

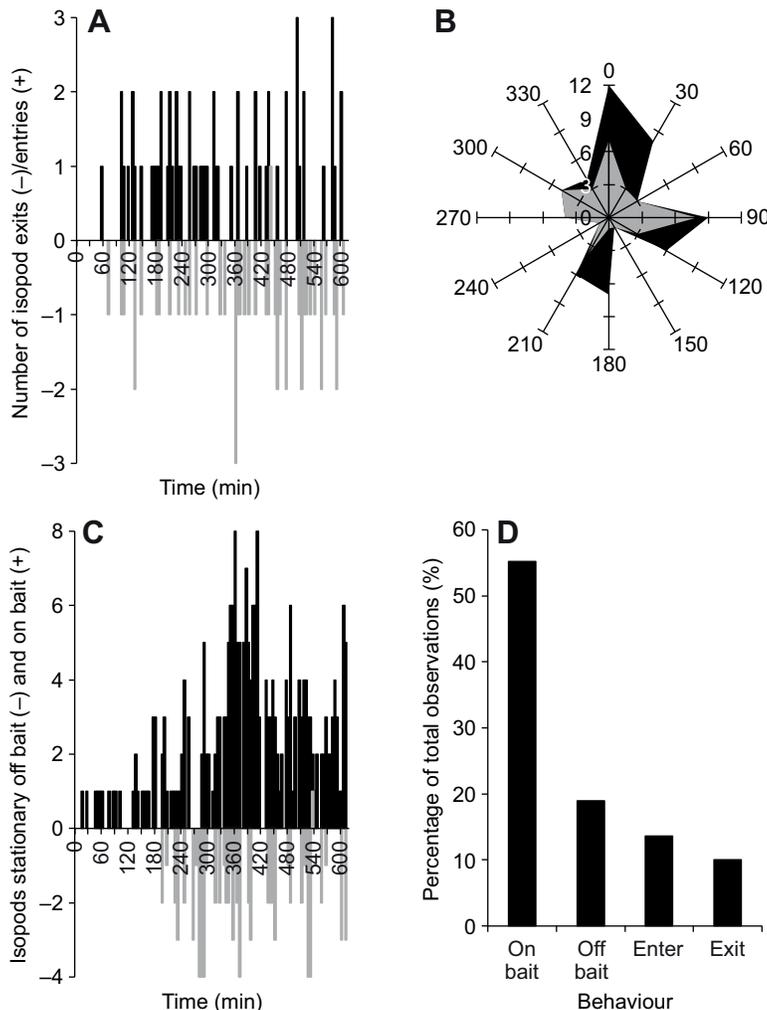


Fig. 3. Behaviour of the isopod *Rectisura cf. herculea* towards bait at 6945 m in the Japan Trench. (A) Number of isopods exits (grey; -) and entries (black; +) in the field of view, (B) the entry (black) and exit (grey) angles, (C) the number of isopods stationary on the bait (black; +) and stationary off the bait (grey; -) and (D) percentage of all four behaviour types of total number of observations ( $N=449$ ).

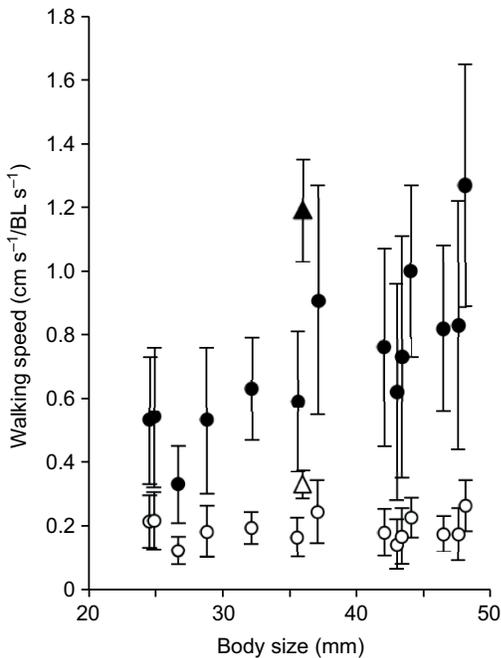


Fig. 4. Absolute walking speed (black circles) and size-specific walking speed (white circles) for the isopod *Rectisura cf. herculea* at 6945 and 7703 m in the Japan Trench. The triangle represents an aversion response to perturbation by a fish in close proximity.

#### General behaviour and body size

The first individual of *R. cf. herculea* at 6945 m arrived at 15 min, and the number of individuals increased to a maximum of 12 at 6 h, followed by a decrease in numbers to between 6 and 8 individuals at the end of the deployment (8 h 30 min) (Fig. 2A). At 7703 m, two isopods arrived at 50 min and stayed for three sequences (15 min). Solitary isopods were present at 2 h 55 min and 5 h 30 min (Fig. 2A).

Total body length of *R. cf. herculea* at 6945 m ranged from 18 to 47 mm, mean  $\pm$  s.d. =  $32 \pm 8.0$  mm ( $N=42$ ) (Fig. 2B). Only four

individuals were seen at 7703 m, measuring 32, 41, 41 and 43 mm. This low number is likely to be a result of the large aggregation of snailfish (see Fujii et al., 2010) rather than indicative of a lower abundance at this depth.

The 6945 m deployment did, however, provide a sufficient number of observations on which to analyse the isopods' behaviour towards the bait. Of the 449 observations made, 106 individuals were either entering or exiting the field of view (Fig. 3A). The ratio between entries and exits was 1.4:1, with 61 entering and 45 exiting (13.6 and 10.0% of the total observations, respectively), indicative of a gradual increase in number within the field of view but with a significant turnover of individuals. There was no distinct trend in the angle in which they entered or exited the field of view (Fig. 3B), although the majority entering were between  $0^\circ$  and  $30^\circ$ , coinciding with the down-current direction.

Of the 440 observations, 248 (55%) were observed stationary directly on top of the bait whereas 85 (19%) were observed sitting stationary on the seafloor away from the bait (Fig. 3C,D) which equates to an on:off bait ratio of 2.9:1.

#### Walking speeds

Routine walking speeds were measured for two of the isopods at 7703 m and 11 from the 6945 m deployment. Absolute walking speeds were recorded between  $0.33$  and  $1.27$   $\text{cm s}^{-1}$  (mean =  $0.7 \pm 0.2$   $\text{cm s}^{-1}$ ) and showed a significant increase with body size ( $R^2=0.609$ ,  $F=17.104$ ,  $P<0.01$ ; Fig. 4). Size-specific walking speeds were relatively constant with increasing body length, ranging from  $0.12$   $\text{BL s}^{-1}$  to  $0.26$   $\text{BL s}^{-1}$ , with an overall mean speed of  $0.19 \pm 0.04$   $\text{BL s}^{-1}$ .

A further walking speed was recorded for an individual in close proximity to a liparid fish that was beating its tail. The isopod appeared perturbed by this action and exited the area by walking at a higher pace; absolute speed =  $1.2 \pm 0.2$   $\text{cm s}^{-1}$ , size-specific speed =  $0.33 \pm 0.04$   $\text{BL s}^{-1}$ .

#### Escape responses

In four video sequences at 6945 m, the isopods exhibited three different escape responses in reaction to the presence of natantian

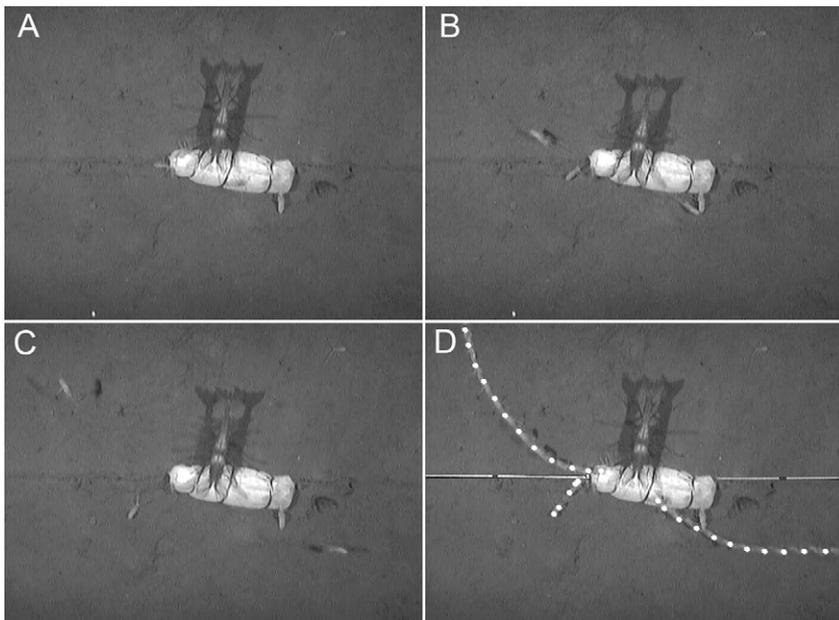


Fig. 5. Video frame grabs every 20 frames (0.8 s, A–C) of two burst-swimming escape responses and one backward jump of the isopod *Rectisura cf. herculea* in response to the presence of a natantian decapod at 6945 m. D shows the tracks of the three escapes marked at 0.2 s intervals (scale bar with 50 cm black markers is superimposed on D).

decapods approaching the bait (Jamieson et al., 2009d): five backward jumps, three horizontal swimming bursts and two vertical swimming bursts (Fig. 5).

The backward jump escape was initiated when a decapod was within ~80 mm from an isopod. The isopods jumped backwards and came to a rest an average of  $56 \pm 18$  mm away ( $1.9 \pm 0.8$  BL). The overall mean speed was  $7.8 \pm 4.2$  cm s<sup>-1</sup> ( $2.6 \pm 1.5$  BL s<sup>-1</sup>), and the maximum mean speed during a backward jump was  $12.0 \pm 2.6$  cm s<sup>-1</sup> ( $3.9 \pm 1.2$  BL s<sup>-1</sup>) (Fig. 6A,B). Maximum acceleration was  $49.5 \pm 12.7$  cm s<sup>-2</sup> ( $15.8 \pm 4.9$  BL s<sup>-2</sup>) (Fig. 6C,D).

The three horizontal swimming bursts were observed by isopods of 34, 34 and 41 mm long. The escape was initiated when the decapods were 47, 36 and 44 mm from the isopods. In all three instances, the isopods accelerated in the first 0.6 s and swam vigorously out of the field of view. One individual swam for ~280 mm until beyond the field of view and showed no sign of deceleration. The other two had travelled ~380 mm until out of view but were beginning to decelerate. All the escape responses were in a backwards position, paddling with pereopods V–VII whilst pereopods I–IV appeared tucked forward under the ventral surface towards the head. After the initial acceleration, at about 200–250 mm from the start of the burst, the isopods spiralled into an upside-down position. The mean absolute speed (including the initial acceleration) of the escape events was  $16.2 \pm 3.2$  cm s<sup>-1</sup> or  $4.6 \pm 0.9$  BL s<sup>-1</sup> (Fig. 7A,B). Mean maximum acceleration was  $25.0 \pm 19.6$  cm s<sup>-2</sup> or  $7.0 \pm 5.5$  BL s<sup>-2</sup> (Fig. 7C,D).

As an indicator of routine swimming speed, the absolute speeds of the escape after the initial burst (i.e. where acceleration decreases to around 0), the mean swimming speed was  $16.9 \pm 2.0$  cm s<sup>-1</sup> or  $4.8 \pm 0.6$  BL s<sup>-1</sup>.

Two instances of upward vertical escape response were observed. Owing to the viewing angle, measurements of speed and acceleration were not possible. On the first occasion, a pereopod of a decapod made contact with an isopod, which initiated a swimming burst at approximately 45° to the seafloor. The isopod, swimming backwards, spiralled 360° twice before exiting the field of view. The second event was again initiated by decapod contact, causing an isopod to swim vertically backward and awkwardly, using its pereopods until striking the camera housing (1 m above bottom). On contact with the camera, the isopod extended all of its pereopods and glided back to the seafloor, ventral side down as if ‘gliding’; therefore, the isopods are negatively buoyant. It took approximately 8 s to reach the camera and 8 s to glide back to the seafloor approximately 30 cm from the start position.

One other swimming behaviour recorded on video was of one individual swimming into the field of view, backwards and ventral side up, at an altitude of an estimated 30–40 cm and landing on the seafloor. It landed posterior first and ventral side up with its antennae extended backwards. It then took 2 s to right itself and a further 5 s to protrude its antennae forward.

## DISCUSSION

### Behaviour

The behaviour of *Rectisura cf. herculea* toward the bait indicates that these isopods were directly exploiting the bait, as the largest percentage of observations (55%) were of individuals aggregating directly on the bait itself.

Wolff studied the gut contents of 36 specimens of 19 asellote isopod species from the *Galathea* expedition and concluded that deep-sea benthic asellotes are primarily detritus feeders (Wolff,

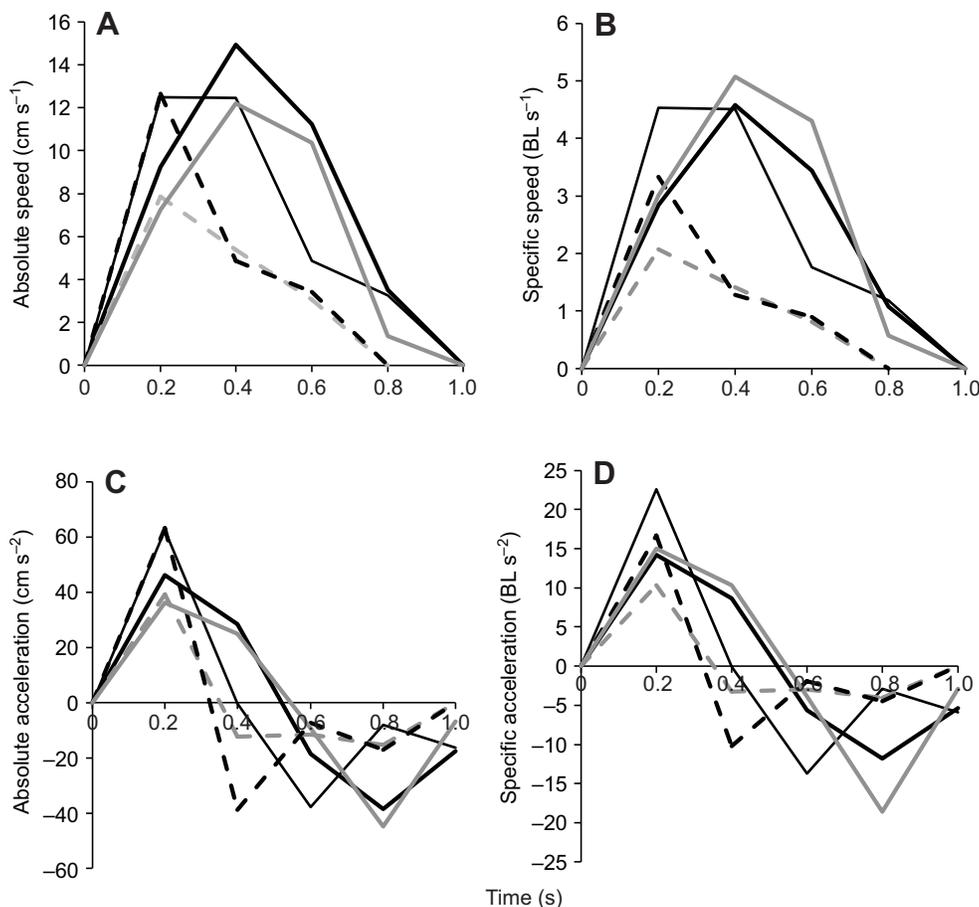


Fig. 6. Analysis of four backward-jump escape responses at 6945 m depth. (A) Absolute speed (cm s<sup>-1</sup>), (B) specific speed (BL s<sup>-1</sup>), (C) absolute acceleration (cm s<sup>-2</sup>) and (D) specific acceleration (BL s<sup>-2</sup>).

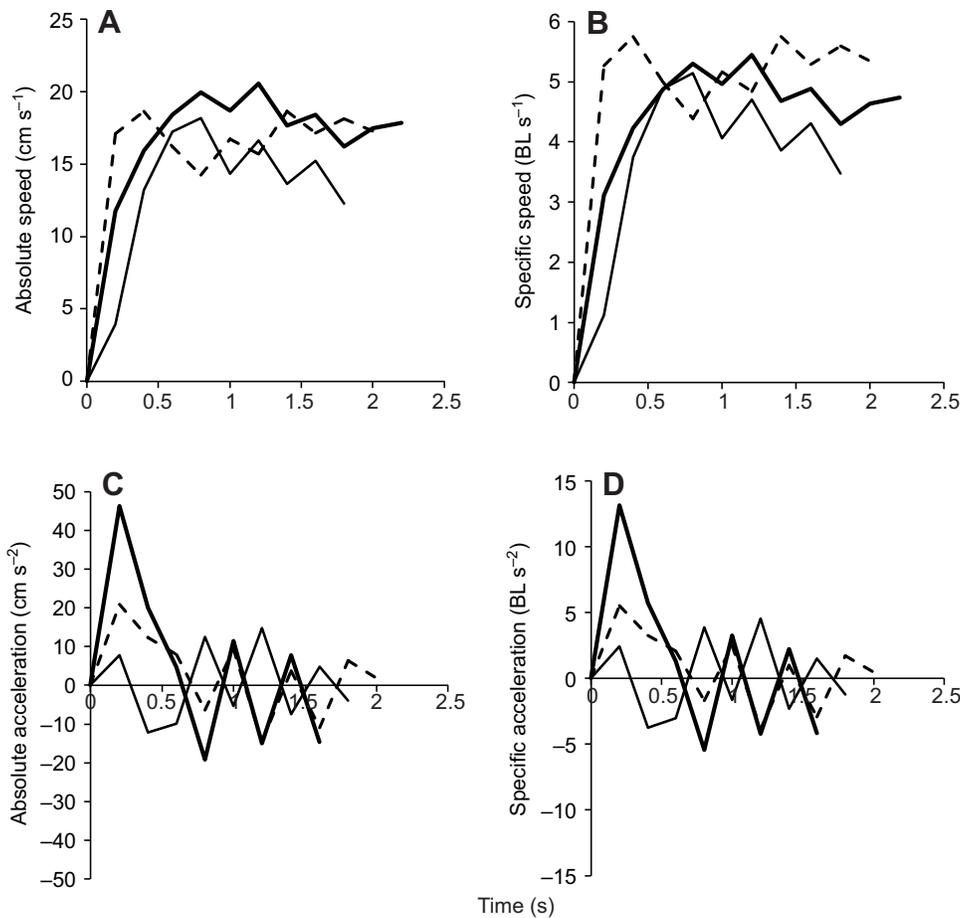


Fig. 7. Analysis of three backward-burst swimming events of the isopod *Rectisura cf. herculea* at 6945 m in the Japan Trench. Absolute speed and acceleration (A,C) and size-specific burst swimming speed and acceleration (B,D).

1962), although some species are known to directly consume plant debris (Wolff, 1976). Foraminifers have been reported in the guts of some asellote species, and were assumed to have been incidentally swallowed along with detritus (e.g. Wolff, 1962). However, Svavarsson et al. reported that *Ilyarachna hirticeps* and *Eurycope inermis* (Family: Munnopsidae) from 1200 to 2000 m were actually selectively preying upon benthic foraminifers rather than consuming detritus (Svavarsson et al., 1993), a strategy reiterated in mouthpart morphology (Wilson and Thistle, 1985). Scavenging is a feeding strategy used by some shallower isopod genera, notably *Natatolana* (Wong and Moore, 1995; Svane and Barnett, 2008), which also occur and scavenge as deep as 2500 m (Albertelli et al., 1992; Kaïm-Malka, 1997), and the giant isopod *Bathynomus giganteus* (Perry et al., 1995; Soong and Mok, 1994), which is known to occasionally consume fish and squid remains (Chamberlain et al., 1986; Barradas-Ortiz et al., 2003). However, these species belong to another suborder, Flabellifera, and the family Cirolanidae, which are a specialized group of sighted and active carnivorous scavengers.

In a low-food environment such as the hadal trenches, it is unlikely that the isopod feeding strategy is obligate (Kaiser and Moore, 1999). Previous studies such as that of Wolff (Wolff, 1962) and Svavarsson et al. (Svavarsson et al., 1993) may indicate that deposit-feeding and/or predation on foraminifers may be routine but the isopods are capable of exploiting the temporarily nutrient-rich presence of a carrion-fall, a strategy also found in lysianassoid amphipods (Blankenship and Levin, 2007). The observed stationary behaviour whilst in contact with bait and the absence of any kind of sudden movements or changes in direction in response to moving prey suggest they are consuming the bait carcass itself. Observations

from the Kermadec trench also reported the presence of two species of munnopsid isopod and bait between 7199 and 7561 m, and one specimen was recovered in a baited trap that did not contain sediment (Jamieson et al., 2011). Furthermore, unpublished observations (A.J.J. and T.F.) from 8000 m in the Peru-Chile Trench show not only the presence of munnopsid isopods attending bait but also an individual approaching a small piece of bait (tuna) that had broken off, holding onto it and dragging it out of the field of view (Fig. 8). These observations are further supported by anecdotal evidence of munnopsid isopods of the subfamily Bathyopsurinae approaching and feeding on bait at 4185 m in the Peru Basin (Brandt et al., 2004). It therefore seems appropriate to conclude that *Rectisura cf. herculea* is a bait-attending species, most likely of the facultative scavenging guild.

The sensory means of detection of bait by these isopods is unclear. Typically, scavenging fauna approach the bait up-current, having detected the odour plume through olfaction (Bailey and Priede, 2002). Although the greatest numbers of entries were between 0° and 30° (consistent with an up-current approach) there is no statistical evidence to prove a preferred angle of approach (or exit).

The relatively low number of isopods observed at 7703 m compared with 6945 m is likely an effect of the overwhelming presence of an aggregation of the snailfish *P. amblystomopsis* (Fujii et al., 2010) and not necessarily indicative of low density. However, the first arrival time at 7703 m of 50 min (prior to the snailfish first arrival at 75 min) and the arrival time of 15 min at 6945 m suggest that these isopods are of a reasonably high density at these depths. For comparison, reports of arrival times at hadal depths have been

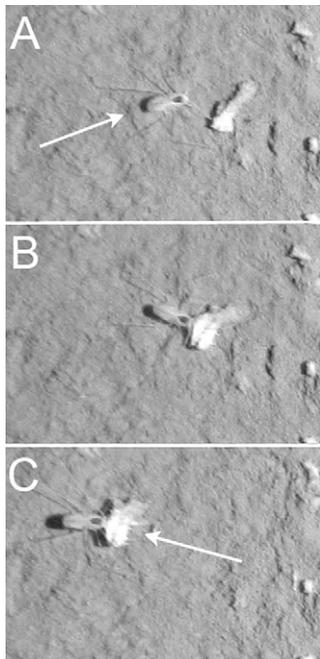


Fig. 8. Observations of a munnopsid isopod removing bait at 8000 m in the Peru-Chile Trench. The sequences are 1 min apart and show the approach (A), contact (B) and the backwards dragging of the bait out of the field of view (C). Arrows indicate direction of travel.

reported from 44 to 632 min for fish (Jamieson et al., 2011), 18–180 min for decapod shrimp (Jamieson et al., 2009d; Jamieson et al., 2011), 15–41 min for princaxelid amphipods (Jamieson et al., 2012), 5–21 min for lysianassoid amphipods (Jamieson et al., 2009c), 15–75 min for munnopsid isopods and 80 min for ophiurids (Jamieson et al., 2011).

### Locomotion

These observations provide the first measurement of locomotion of a hadal isopod. Unfortunately, there are no reported measurements of any other deep-sea isopod with which to compare it; however, the findings are comparable to the swimming speeds of the shallow-water isopods *Iodeta resicata* and *Iodeta vosnesenskii* ( $1.6\text{--}9.2\text{ BL s}^{-1}$ ,  $\text{BL}=31.4\text{--}35.2\text{ mm}$  and  $1.3\text{--}5.4\text{ BL s}^{-1}$ ,  $\text{BL}=47.8\text{ mm}$ , respectively) (Alexander, 1988). The general locomotive behaviour (backward jumping, swimming upside-down, etc.) is also similar to the behaviour of shallower-living janiroidean species observed in the laboratory (Hessler and Strömberg, 1989).

Burst swimming in the isopods was only observed in response to perturbation by decapods. The bulk of tissue devoted to swimming is often greater than that of their preferred locomotive mode, walking (Hessler, 1993). This seemingly contradictory trait is also found in caridoid malacostracans, where pleopods are used for routine swimming, although a larger bulk of tissue is devoted to caridoid escape responses (Hessler, 1981).

Although these observations are limited, some general locomotive trends can be construed (summarised in Fig. 9). The routine mode of locomotion of these isopods is walking using pereopods I–IV at a mean speed of  $0.19\pm 0.04\text{ BL s}^{-1}$ . If perturbed by the presence of a larger animal such as the liparids [or potentially the macrourids, which are known to prey on isopods (Percy and Ambler, 1974)], they can accelerate to  $0.33\pm 0.04\text{ BL s}^{-1}$  (an increase of 74%). When the threat is more urgent ( $<80\text{ mm}$  away), the isopod can jump

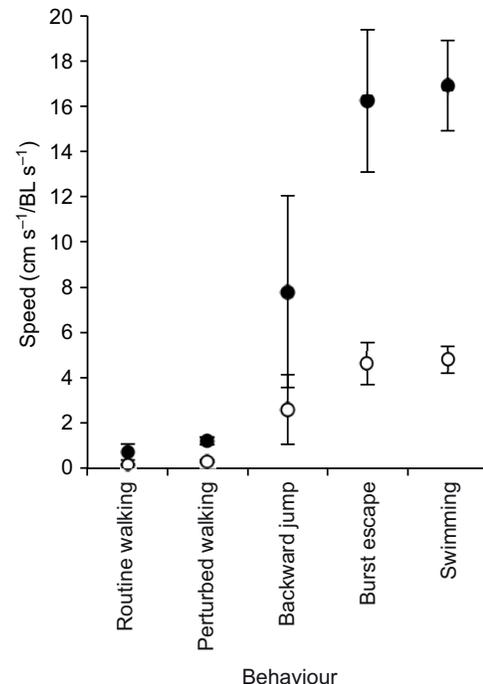


Fig. 9. Summary of absolute speeds (closed circles) and specific speeds (open circles) for routine walking, perturbed walking, backward jump, burst escape and swimming behaviours.

backwards, propelling itself with pereopods V–VII at  $2.6\pm 1.5\text{ BL s}^{-1}$  to a distance of  $1.9\pm 0.8\text{ BL}$  away. When the threat is imminent ( $<50\text{ mm}$ ), a burst swimming escape response is initiated whereby the isopod retracts pereopods I–IV and swims backwards in a spiralling motion using pereopods V–VII, either vertically or horizontally across the seafloor at  $4.63\pm 0.9\text{ BL s}^{-1}$ . After a  $<0.6\text{ s}$  burst of acceleration, they continue swimming at a mean velocity of  $4.8\pm 0.6\text{ BL s}^{-1}$  for at least 2 s until reaching an estimated 30–40 cm away from the threat. During vertical burst escapes, the descent back to the seafloor is dampened by fully extending pereopods I–IV and increasing projected body area (and thus drag) by descending (gliding) ventral side down to the seafloor. This ‘burst and coast’ behaviour is common among shallow-water decapods [e.g. lobsters (Newland et al., 1988; Spanier et al., 1991)]. The oxygen concentration in seawater at hadal depths is  $\sim 3.43\text{ ml l}^{-1}$  (Jamieson et al., 2010), which is sufficient to sustain aerobic metabolism for routine activity, but we presume that oxygen debt is incurred during escape responses and burst swimming.

The video system used in the present study has previously been used to compare the swimming activity of two hadal snailfish (Family Liparidae): *P. amblystomopsis* and *Notoliparis kermadecensis* from 6945 m in the Japan Trench and 6890 m in the Kermadec Trench, respectively (Jamieson et al., 2009c; Fujii et al., 2010). Measurements of tail-beat frequency and caudal–pectoral fin synchrony suggest no obvious relaxation of locomotive capability compared to other shallower-living liparids (Jamieson et al., 2009c). Likewise, the same lander system observed the natantian decapod *B. crenatus* between 6007 and 7703 m in the same trenches and the caridean prawn *Acantheephyra* sp. from 6007 to 6890 m in the Kermadec Trench (Jamieson et al., 2009d). These decapod data are also consistent or comparable to other measurements of malacostracan crustaceans at much shallower depths (Neil and Ansell, 1995). More recently, swimming speeds and burst swimming

speeds were obtained for two species of princaxelid amphipods (*Princaxelia abyssalis* and *Princaxelia jamiesoni*; Family Pardaliscidae) from depths ranging between 7703 and 9316 m in the Japan, Izu-Ogasawara, Kermadec and Tonga Trench (Jamieson et al., 2012). The results showed that these organisms were capable of rapid burst predatory attacks on smaller lysianassoid amphipods, and their routine swimming speeds were comparable to shallow-water analogues (Laver et al., 1985). The present data on isopods add to the weight of evidence from other orders of Crustacea (amphipods, decapods) and teleost fishes to show that the mobility of hadal demersal megafauna is not significantly impaired compared with shallow-water representatives of these taxa.

#### Future studies

The data presented here show that the non-sighted munnopsids are capable of rapid escape responses from perceived threats in close proximity and suggest no obvious relaxation in locomotor ability, although there is little comparative data. However, to test the visual interaction hypothesis, complementary studies such as *in situ* oxygen respirometry are required to evaluate the energetic costs of such behaviour to examine the links between locomotion and metabolic rate. Likewise, the recovery of specimens is required to establish body and muscle mass. Specimens would also permit an accurate species identification, and analysis of stomach contents would unequivocally determine whether these isopods use opportunistic necrophagy as a feeding strategy.

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#### REFERENCES

- Albertelli, G., Amaud, P. M., Della Croce, N., Drago, N. and Eleferiuri, A. (1992). The deep Mediterranean macrofauna caught by traps and its trophic significance. *C.R. Acad. Sci.* **315**, 139-144.
- Alexander, D. E. (1988). Kinematics of swimming in two species of *Idotea* (Isopoda: Valvifera). *J. Exp. Biol.* **138**, 37-49.
- Bailey, D. M. and Priede, I. G. (2002). Predicting fish behaviour in response to abyssal food-falls. *Mar. Biol.* **141**, 831-840.
- Barradas-Ortiz, C., Briones-Fourzán, P. and Lozano-Álvarez, E. (2003). Seasonal reproduction and feeding ecology of giant isopods *Bathynomus giganteus* from the continental slope of the Yucatán peninsula. *Deep Sea Res. I Oceanogr. Res. Pap.* **50**, 495-513.
- Belyaev, G. M. (1989). *Deep-Sea Ocean Trenches and Their Fauna*. Moscow, Russia: Naika Publishing House.
- Birstein, J. A. (1957). Certain peculiarities of the ultra-abyssal fauna at the example of the genus *Storhyngura* (Crustacea Isopoda Asellota). *Zool. Zh.* **36**, 961-985.
- Blankenship, L. E. and Levin, L. A. (2007). Extreme food webs: Foraging strategies and diets of scavenging amphipods from the ocean's deepest 5 kilometres. *Limnol. Oceanogr.* **52**, 1685-1697.
- Brandt, A., Maljutina, M., Borowski, C., Schriever, G. and Thiel, H. (2004). Munnopsid isopod attracted to bait in the DISCOL area. *Mitt. Hamb. Zool. Mus. Inst.* **101**, 275-279.
- Chamberlain, S. C., Meyer-Rochow, V. B. and Dossert, W. P. (1986). Morphology of the compound eye of the giant deep-sea isopod *Bathynomus giganteus*. *J. Morphol.* **189**, 145-156.
- Childress, J. J. (1995). Are there physiological and biochemical adaptations of metabolism in deep-sea animals? *Trends Ecol. Evol.* **10**, 30-36.
- Fujii, T., Jamieson, A. J., Solan, M., Bagley, P. M. and Priede, I. G. (2010). A large aggregation of liparids at 7703 m depth and a reappraisal of the abundance and diversity of hadal fish. *Bioscience* **60**, 506-515.
- Hazel, J. R. and Williams, E. E. (1990). The role of alterations in membrane lipid composition in enabling physiological adaptation of organisms to their physical environment. *Prog. Lipid Res.* **29**, 167-227.
- Hessler, R. R. (1981). Evolution of arthropod loco-motion: a crustacean model. In *Locomotion and Energetics in Arthropods* (ed. C. F. Herreid II and C. R. Fourtner), pp. 9-30. New York, NY: Plenum Publishing Corporation.
- Hessler, R. R. (1993). Morphology in *Eurycope cornuta* (Isopoda: Asellota). *J. Crustac. Biol.* **13**, 667-674.
- Hessler, R. R. and Sanders, H. L. (1967). Faunal diversity in the deep-sea. *Deep Sea Res.* **14**, 65-70.
- Hessler, R. R. and Strömberg, J.-O. (1989). Behavior of Janiroidean isopods (Asellota), with special reference to deep-sea genre *Sarsia* **74**, 145-159.
- Jamieson, A. J., Solan, M. and Fujii, T. (2009a). Imaging deep-sea life beyond the abyssal zone. *Sea Technol.* **50**, 41-46.
- Jamieson, A. J., Fujii, T., Solan, M. and Priede, I. G. (2009b). HADEEP: Free-falling landers to the deepest places on Earth. *Mar. Technol. Soc. J.* **43**, 151-160.
- Jamieson, A. J., Fujii, T., Solan, M., Matsumoto, A. K., Bagley, P. M. and Priede, I. G. (2009c). Liparid and macrourid fishes of the hadal zone: in situ observations of activity and feeding behaviour. *Proc. Biol. Sci.* **276**, 1037-1045.
- Jamieson, A. J., Fujii, T., Solan, M., Matsumoto, A. K., Bagley, P. M. and Priede, I. G. (2009d). First findings of decapod crustacea in the hadal-zone. *Deep Sea Res. I Oceanogr. Res. Pap.* **56**, 641-647.
- Jamieson, A. J., Fujii, T., Mayor, D. J., Solan, M. and Priede, I. G. (2010). Hadal trenches: the ecology of the deepest places on Earth. *Trends Ecol. Evol.* **25**, 190-197.
- Jamieson, A. J., Kilgallen, N. M., Rowden, A. A., Fujii, T., Horton, T., Lörz, A.-N., Kitazawa, K. and Priede, I. G. (2011). Bait-attending fauna of the Kermadec Trench, SW Pacific Ocean: evidence for an ecotone across the abyssal-hadal transition zone. *Deep Sea Res. I Oceanogr. Res. Pap.* **58**, 49-62.
- Jamieson, A. J., Lörz, A.-N., Fujii, T. and Priede, I. G. (2012). *In situ* observations of trophic behaviour and locomotion of *Princaxelia* amphipods (Crustacea, Pardaliscidae) at hadal depths in four West Pacific Trenches. *J. Mar. Biol. Assoc. U. K.* **92**, 143-150.
- Kaim-Malaka, R. A. (1997). Biology and life cycle of *Nutatoluna borealis* Lillj. 1851, a scavenging isopod from the continental slope of the Mediterranean. *Deep Sea Res. Part I Oceanogr. Res. Pap.* **44**, 2045-2067.
- Kaiser, M. J. and Moore, P. G. (1999). Obligate marine scavengers: do they exist? *J. Nat. Hist.* **33**, 475-481.
- Laver, M. B., Olsson, M. S., Edelman, J. L. and Smith, K. L., Jr (1985). Swimming rates of scavenging deep-sea amphipods recorded with a free-vehicle video camera. *Deep Sea Res.* **32**, 1135-1142.
- Neil, D. M. and Ansell, A. D. (1995). The orientation of tail-flip escape swimming in decapod and mysid crustaceans. *J. Mar. Biol. Assoc. U. K.* **75**, 55-70.
- Newland, P. L., Chapman, C. J. and Neil, D. M. (1988). Swimming performance and endurance of the Norway lobster *Nephrops norvegicus*. *Mar. Biol.* **98**, 345-350.
- Pearcy, W. G. and Ambler, W. (1974). Food habits of deep-sea macrourid fishes off the Oregon coast. *Deep Sea Res.* **21**, 745-759.
- Perry, H., Waller, R., Trigg, C., McBee, J., Erdman, R. and Blake, N. (1995). A note on by-catch associated with deepwater trapping of Chaceon in the North Central Gulf of Mexico. *Gulf Res. Rep.* **9**, 139-142.
- Pradillon, F. and Gaill, F. (2007). Pressure and life: some biological strategies. *Rev. Environ. Sci. Biotechnol.* **6**, 181-195.
- Samerotte, A. L., Drazen, J. C., Brand, G. L., Seibel, B. A. and Yancey, P. H. (2007). Correlation of trimethylamine oxide and habitat depth within and among species of teleost fish: an analysis of causation. *Physiol. Biochem. Zool.* **80**, 197-208.
- Saunders, P. M. (1981). Practical conversion of pressure to depth. *J. Phys. Oceanogr.* **11**, 573-574.
- Seibel, B. A. and Drazen, J. C. (2007). The rate of metabolism in marine animals: environmental constraints, ecological demands and energetic opportunities. *Philos. Trans. R. Soc. Lond. B* **362**, 2061-2078.
- Somero, G. N. (1992). Adaptations to high hydrostatic pressure. *Annu. Rev. Physiol.* **54**, 557-577.
- Soong, K. and Mok, H. K. (1994). Size and maturity stage observations of the deep-sea isopod *Bathynomus doederleini* Ortmann, 1894 (Flabellifera: Cirolanidae), in Eastern Taiwan. *J. Crustac. Biol.* **14**, 72-79.
- Spanier, E., Weihs, D. and Almog-Shtayer, G. (1991). Swimming of the Mediterranean slipper lobster. *J. Exp. Mar. Biol. Ecol.* **145**, 15-31.
- Svane, I. and Barnett, J. (2008). The occurrence of benthic scavengers and their consumption at tuna farms off Port Lincoln, South Australia. *J. Exp. Mar. Biol. Ecol.* **363**, 110-117.
- Svavarsson, J., Strömberg, J.-O. and Brattegard, T. (1993). The deep-sea asellote (Isopoda, Crustacea) fauna of the Northern Seas: species composition, distributional patterns and origin. *J. Biogeogr.* **20**, 537-555.
- UNESCO (2009). *Global Open Oceans and Deep Seabed (GOODS) – Biogeographic Classification*. IOC Technical Series 84. Paris, France: UNESCO-IOC.
- Wilson, G. D. F. and Thistle, D. (1985). *Amuleta*, a new genus for *Ilyarachna abyssorum* Richardson, 1911 (Isopoda: Asellota: Eurycopidae). *J. Crustac. Biol.* **5**, 350-360.
- Wolff, T. (1960). The hadal community, an introduction. *Deep Sea Res.* **6**, 95-124.
- Wolff, T. (1962). The systematics and biology of bathyal and abyssal Isopoda Asellota. *Galathea Rep.* **6**, 1-320.
- Wolff, T. (1970). The concept of the hadal or ultra-abyssal fauna. *Deep Sea Res.* **17**, 983-1003.
- Wolff, T. (1976). Utilization of seagrass in the deep sea. *Aquat. Bot.* **2**, 161-174.
- Wong, Y. M. and Moore, P. G. (1995). Biology of feeding in the scavenging isopod *Natatolana borealis* (Isopoda: Cirolanidae). *Ophelia* **43**, 181-196.