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Author(s) :Toshinori Matsui, Tohru Moriyama and Ryuichi Kato

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Burrow Plasticity in the Deep-Sea Isopod *Bathynomus doederleini* (Crustacea: Isopoda: Cirolanidae)

Toshinori Matsui¹, Tohru Moriyama^{2*} and Ryuichi Kato³

¹Faculty of Textile Science and Technology, Shinshu University,
3-15-1 Tokida, Ueda, Nagano 386-8567, Japan

²Young Researchers Empowerment Center, Shinshu University,
3-15-1 Tokida, Ueda, Nagano 386-8567, Japan

³Graduate School of Science and Technology, Shinshu University,
3-15-1 Tokida, Ueda, Nagano 386-8567, Japan

We investigated whether the deep-sea isopod *Bathynomus doederleini* has the capacity to change burrow length in response to changes in environmental conditions. We observed burrowing behavior in individuals that were placed on substrates with either simple (ST) or complex (CT) surface topographies. Individuals in the ST group (N = 10) constructed seven burrows. The mean ratio of the burrow length to body length was 1.8. The individuals in the CT group (N = 10) constructed eight burrows with a mean ratio of burrow length to body length of 2.5. Thus the burrows were significantly longer in the CT group. In addition, the isopods in the CT group often incorporated a chamber in the mid-section of the burrow. Our results may be used to infer the determinants of burrow morphology and speculate about the lifestyle of this species in the deep sea.

Key words: burrow, plasticity, deep sea, isopod, Crustacea, *Bathynomus doederleini*

INTRODUCTION

The mesopelagic zone (200–1,000 m below sea level) contains the greatest biomass and diversity of animal life in the ocean (Warrant and Locket, 2004). The isopod *Bathynomus* is distributed primarily within this zone, and is classified as part of the littoral-bathyal benthos (Wolf, 1970). This isopod is a highly mobile, voracious scavenger that dominates the fauna associated with large dead animals (Sekiguchi et al., 1981).

There has been an increasing awareness that highly mobile epibenthic invertebrates play a significant role in the dynamics of deep-sea benthic communities (Hessler et al., 1978). Thus, it is important to understand the biology of *Bathynomus* and its role in the deep benthic environment (Tsuo and Mok, 1991). Researchers have studied the classification, geographical distribution, and development of *Bathynomus* (Holthuis and Mikulka, 1972; Sekiguchi et al., 1982; Tsuo and Mok, 1991), but little is known about the ecology and behavior of this species because of the difficulty observing animals in situ at such great depths. However, *Bathynomus* is able to survive for several months in aquaria at atmospheric pressure, affording researchers the opportunity to study its behavior. For example, Sekiguchi (1985) reported burrowing behavior in a captive *Bathynomus doederleini* individual. Because the burrow was equal in length to the isopod, the author concluded that the burrow

was a shelter, not a nest. More recently, Iwasaki et al. (2001) reported that burrow construction was initiated whenever an individual made contact with a vertical acrylic wall, which was placed away from the lateral side of the aquarium on a gelatin substrate. In the absence of this wall, the individual dug along the side of the aquarium. These observations suggest that the burrowing behavior of *B. doederleini* is induced by mechanical stimulation of the head. Furthermore, these two studies suggest that the length of the burrow is equal to that of the body in both natural and artificial substrates.

In contrast, Matsuoka and Koike (1980) reported that the burrow length of a Miocene period *Bathynomus* sp. was approximately six times longer than that of the occupant's body length. In addition, the burrow had an expanded region, approximately twice as wide as the occupant's body width, in the mid-section of the burrow. Thus, it has remained unclear whether there are differences in burrow length among captive and wild *B. doederleini*.

To address this, we attempted to duplicate features of the *B. doederleini* natural habitat in the aquarium and evaluate whether the morphology of burrows dug by extant *B. doederleini* resembled those dug in the Miocene. The surface topography of the sea floor is highly complex, in part due to the presence of carcasses, e.g., whale skeletons (Gage & Tyler, 1991). Thus, we hypothesized that *B. doederleini* construct longer burrows in topographically complex substrates when compared with simple substrates, which are typically used in experiments with captive *B. doederleini*. To test this, we documented burrowing behavior in *B. doederleini* that were placed on substrates with simple or complex surface topography.

* Corresponding author. Phone: +81-(0)268-21-5589;
Fax : +81-(0)268-21-5884;
E-mail: toru@shinshu-u.ac.jp

MATERIALS AND METHODS

Animals

We collected specimens of *B. doederleini* using baited traps in Sagami Bay, Japan. The animals were then transferred to tanks containing recirculated sea water ($10 \pm 0.2^\circ\text{C}$; $\text{pH } 8 \pm 0.2$; $30 \pm 1\text{‰S}$) and held in the dark for six months. Each individual was fed slices of raw squid (5 g) once every two weeks. We placed the individuals in separate buckets while feeding.

Experimental aquaria

We used a transparent cylindrical aquarium (60 cm in diameter, 40 cm in height) that was placed in the laboratory (room temperature, 15°C). We created two types of substrate having differing surface topography, simple (ST) and complex (CT). For both groups, the aquaria were filled with 0.3% agar to a depth of 25 cm. The concentration of agar was determined during preliminary tests in which *B. doederleini* individuals were placed in aquaria filled with various concentrations agar substrata. We observed the behavior of the isopods to ensure they were able to crawl and burrow in the agar. After the agar set, sea water was poured into the aquarium to a depth of 10 cm above the surface of the agar substrate. The experimental setup was left until the temperature at the center of the substrate reached $16 \pm 1^\circ\text{C}$.

In half of the aquaria, we placed five plastic, transparent T-shaped tubes (6 cm diameter, 12 cm trunk length, 9 cm branch length) on the surface of the substrate (Fig. 1). The tubes were connected to the base of the aquarium using thin plastic poles to prevent movement. The distance between each tube and the aquarium wall or a neighboring tube was sufficient to allow passage of the isopods. This more complex, maze-like substrate surface was intended to duplicate the surface topography of the animals' natural habitat. Individuals were able to move freely and were expected to occasionally enter the T-tubes, resulting in mechanical stimulation of their body surface. The animals are also forced to select a direction at the junction of the T. We believe this behavioral pattern simulates activity in their natural habitat, as they are likely to encounter carcasses and animal skeletons that resemble a maze-like structure.

Experiments

We installed a CCD camera with built-in infrared LEDs (Corona-Dengyo CZ-100, Japan) above the aquarium at a distance



Fig. 1. Experimental aquarium illustrating the setup of the complex substrate topography (CT). The tubes were absent in the simple surface topography (ST) setup. Seawater was added before the animals were introduced.

of 100 cm from the surface of the substrate. The camera was connected to a digital high-resolution recorder (Sharp DV-ACW72). The LEDs were turned on during the experiments to allow recording while the aquaria were in the dark.

We randomly selected 20 isopod individuals from the holding tanks and divided them into two groups: ST ($N = 10$) and CT ($N = 10$). We measured the body length and width of each individual and determined their sex (Tsuo and Mok, 1991). Each isopod was individually placed on the center of the aquarium on the surface of the substrate (ST group) or in one of the tubes (CT group). We recorded the behavior of animals in both groups during a 6 h period.

At the end of the experiment, we measured the burrow length. If an individual was found in the burrow, it was gently removed by hand to avoid damage to the burrow. We injected green fluid into each empty burrow to create a cast. The burrow morphology was photographed using a digital camera (Nikon Coolpix P5100).

Each individual was used only once. The agar substrate and seawater were changed between individuals. The plastic tubes were also washed with water between individuals.

Statistical analyses

We evaluated the differences in mean body length, mean body width, mean time from the initial movement on the substrate to the completion of a burrow, and the mean time spent in a burrow between the two groups using an unpaired Student's *t*-test. This test was also used to evaluate differences in the mean ratio of the burrow length to the occupant's body length between burrows with and without chambers in the CT group. We evaluated the difference in the mean ratio of burrow length to the occupant's body length between the treatment groups using Welch's *t*-test. We tested for normality of the data using a Shapiro-Wilk test. If the data were normally distributed, we used an *F*-test to evaluate differences in the standard deviation between two samples. We used Fisher's exact probability test to evaluate differences in the sex ratio and in the incidence of specimens that constructed burrows between the treatment groups. We used Spearman's rank correlation test to evaluate the direction and strength of the relationship between total tube-passing time and the ratio of burrow length to the occupant's body length. We used the Mann-Whitney *U* test to evaluate differences in the mean time spent in the tubes between specimens that constructed burrows and those that did not in the CT group.

Differences with a *P* value of < 0.05 were considered significant. The Shapiro-Wilk test was performed using Origin 8.5 (OriginLab Corporation, Northampton, MA, USA). All other tests were conducted using Ekuseru-toukei 2006 (Social Survey Research Information Co., Ltd., Tokyo, Japan). The data are presented as the mean \pm S.E.

RESULTS

Body length, body width, and sex ratio

The mean body length, mean body width, and the sex ratio (male:female) were 9.6 ± 0.4 cm, 4.1 ± 0.2 cm, and 5:5, respectively (ST, $N = 10$) and 10.0 ± 0.7 cm, 4.3 ± 0.3 cm, and 6:4 (CT, $N = 10$). There was no difference among the treatment groups (body length: $F_{9,9} = 2.33$, $P = 0.223$; $t = 0.983$, $df = 18$, $P = 0.1692$; body width: $F_{9,9} = 2.53$, $P = 0.184$; $t = 1.175$, $df = 18$, $P = 0.128$; sex ratio: $P = 0.500$). All individuals were maturing (Soong and Mok, 1994), but none of the females had eggs.

Burrow construction behavior

The position of each individual was plotted each second (Fig. 2) to document the steps involved in burrow construction. Based on our observations, the process was divided into three stages:

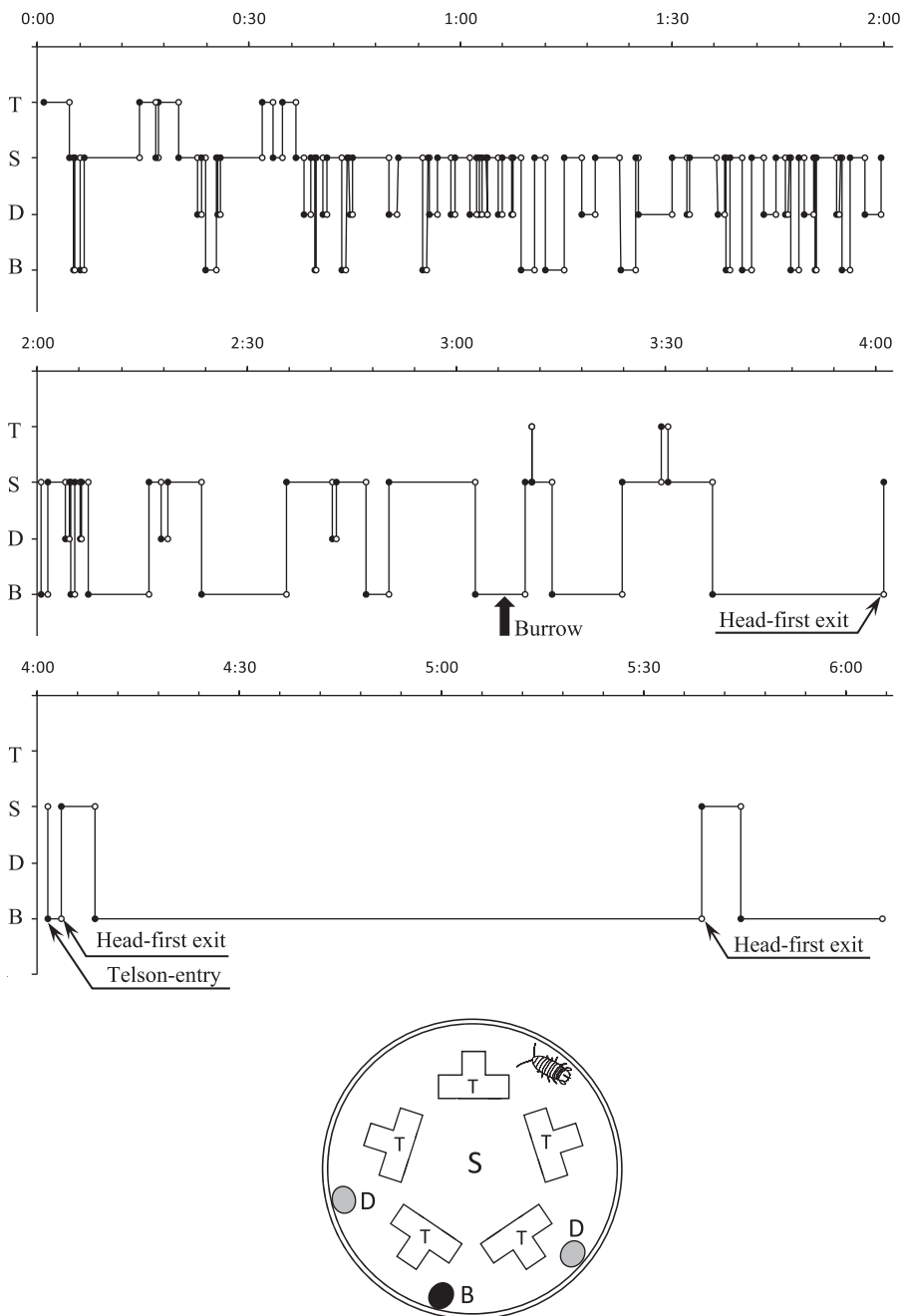


Fig. 2. A typical time sequence showing changes in the behavior of a specimen in the CT group. The horizontal axis represents time (30 min units). The vertical axis represents positions in the aquarium. T, S, D and B are illustrated in the inset figure. T: tubes; S: surface of substrate; D: depressions; B: a burrow. Each black horizontal line with a closed circle at the left end and open circle at the right end represents continuous occupation at a specific position. The closed circle denotes the initial time and the open circle represent the ending time. A thick black arrow denotes the time when a depression became a burrow (3:09:15). The specimen crept out of the burrow headfirst (head-first exit) at 4:01:15, 4:02:30, and 5:38:50. The individual entered the burrow 'telson-first' (telson-entry) at 4:02:23.

(a) Surface excavation

The individuals in the ST group conglobated and remained balled up for a short period (mean: 35.5 ± 11.2 s, $N = 10$) when first placed on the agar substrate. Conversely, the isopods in the CT group remained conglobated for sev-

eral minutes (mean: 4.4 ± 1.7 min, $N = 10$) when first placed into the aquarium. After this initial period, all the animals uncurled and began moving (walking or swimming) and excavating depressions in the agar along the wall of the aquarium (Fig. 3A). We did not observe any depressions being excavated away from the wall. The isopods dug into the agar using their thoracic legs and removed the debris using water currents produced by beating their swimmerets.

The depressions were mortar-shaped structures each approximately a quarter of the body length of the individual (Fig. 3A). Several individuals excavated multiple depressions, forming a groove along the wall (Fig. 3B). The isopods in the CT group were often observed moving through the tubes, entering head-first in most cases, but backwards in some. We also observed animals somersaulting in the tubes in a limited number of instances.

(b) Burrow construction

Following surface excavation, several individuals spent time repeatedly digging in one or two specific depressions located along the wall. As they dug, their body was positioned at around a 30° inclination, head down (Fig. 3C). All individuals exited the depression by moving backwards. We defined a depression as a 'burrow' when its length was approximately equal to the body length of the individual digging the burrow (Fig. 3C, D). The mean time from the initial motion on the substrate to the completion of a burrow (or the first burrow in the case of a specimen that constructed two burrows) was 126.8 ± 89.4 min ($N = 6$) and 96.0 ± 66.9 min ($N = 7$) in the ST and CT groups, respectively ($F_{5,6} = 1.39$, $P = 0.694$; $t = 0.706$, $df = 11$, $P = 0.247$).

We observed seven burrows in the ST group. Six individuals dug a single burrow, and one individual dug two. The four remaining individuals only dug depressions. Similarly, we observed eight burrows in the CT group. Seven individuals dug a single burrow and one individual dug two. The remaining three individuals only dug shallow depressions.

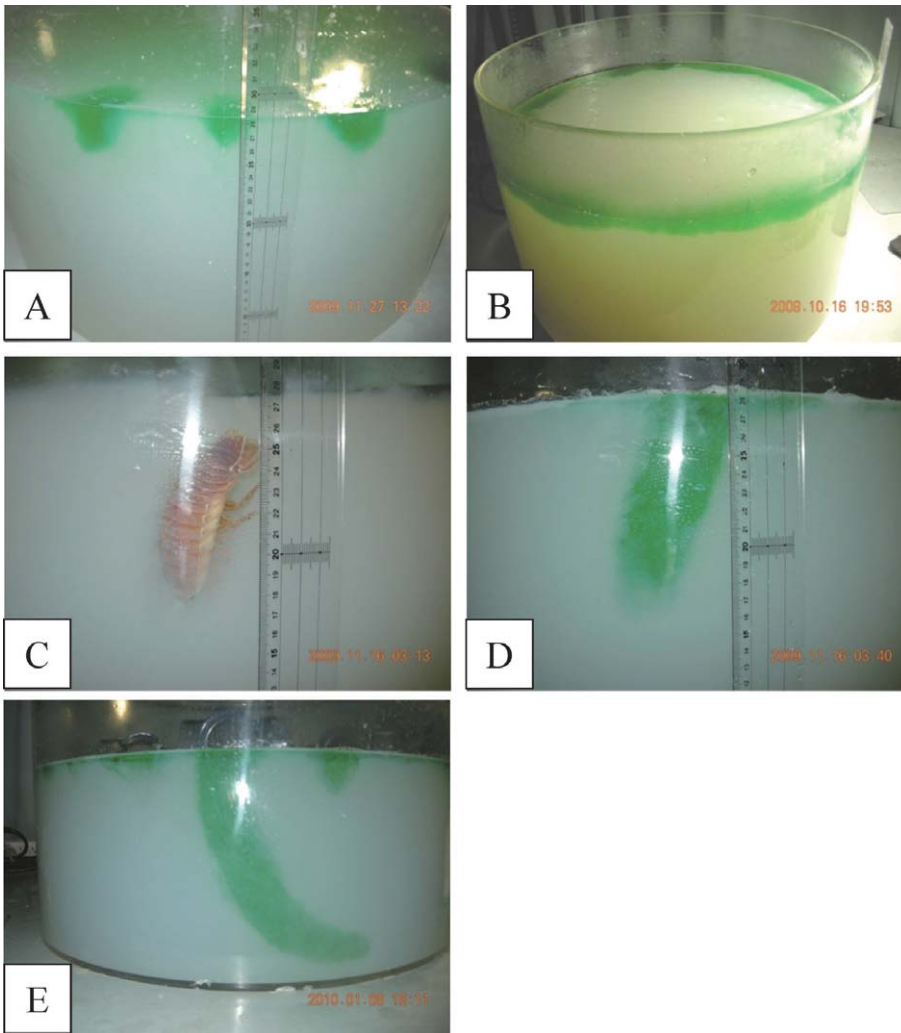


Fig. 3. Depressions and burrows. Typical depressions (A). Multiple depressions formed a groove (B). A typical burrow whose length was almost equal to that of the specimen (C) and into which green fluid agar was casted (D). A typical burrow whose length was almost twice that of the specimen and into which green fluid agar was casted (E).

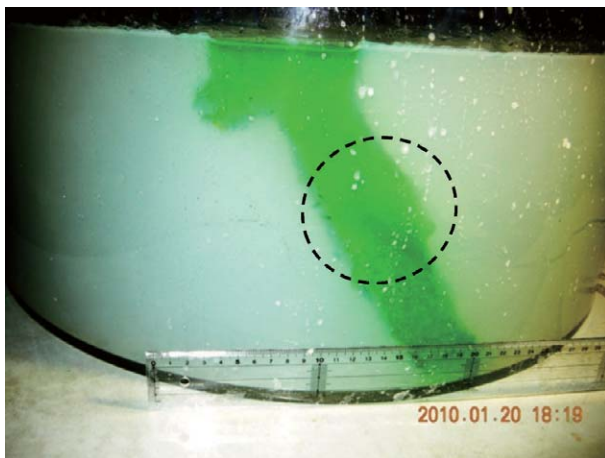


Fig. 4. Profile view of a chamber in the mid-section (surrounded by dashed circle) of a burrow in the CT group.

Specimens that constructed burrows were termed ‘burrowers’. Those that continued to move about the substrate without constructing a burrow were termed ‘wanderers’. There was no significant difference in the incidence of burrowers between the treatment groups ($P = 0.500$).

(c) Burrow modification phase

After completion of the burrow, the occupants spent the majority of time in their burrow, either digging or resting. Four of seven burrows were not elongated any further in the ST group (Fig. 3D). These four burrows were only slightly longer than the occupying individuals’ body length. In contrast, all eight burrows were elongated to almost twice the occupants’ body length in the CT group (Fig. 3E). Four burrows were even elongated to nearly three times the occupants’ body length and curved at the base of the aquarium. In these long burrows, the occupants sometimes somersaulted in the mid-section of the burrow, moved upward, then paused at the entrance before crawling out head-first. The somersaulting motion compacted the wall of the burrow, resulting in the formation of a chamber (Fig. 4).

Burrow length

We used the ratio of the burrow length to the occupant’s body length as an index for the length of a burrow ($R_{b/o}$). The mean $R_{b/o}$ was significantly higher in CT ($N = 8$) than ST ($N = 7$) ($F_{6,7} = 5.66, P = 0.039; t$ (Welch) = 2.22, $df = 7.84, P = 0.029$, Fig. 5). Within CT, the mean $R_{b/o}$ for burrows with chambers ($N =$

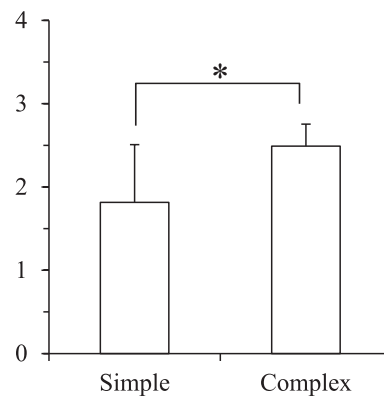


Fig. 5. Mean $R_{b/o}$ for the CT and ST groups (* $P < 0.05$).

4) was significantly higher than for those without them ($N = 4$) ($F_{3,3} = 1.26$, $P = 0.855$; $t = 5.04$, $df = 6$, $P = 0.0023$, Fig. 6).

Time in burrow

We calculated the total time spent in a burrow for each burrower in the ST and CT groups. The mean time for the CT group ($N = 8$) was significantly longer than for the ST group ($N = 7$) ($F_{6,7} = 1.02$, $P = 0.994$; $t = 1.89$, $df = 6$, $P = 0.040$) (Fig. 7).

Time in tubes

We calculated the time spent in the plastic tubes for

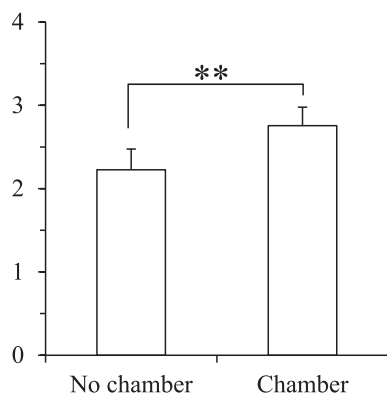


Fig. 6. Mean $R_{b/o}$ for 'no chamber' and 'chamber' groups (** $P < 0.01$).

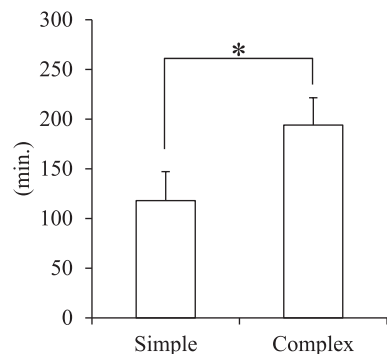


Fig. 7. Mean time spent in a burrow for the CT and ST groups (* $P < 0.05$).

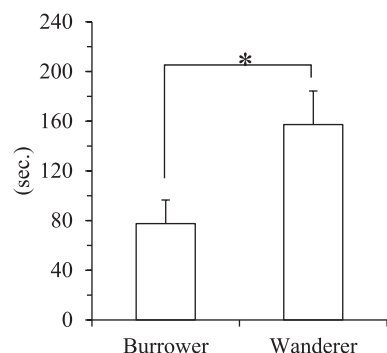


Fig. 8. Mean time to transit through the tubes for burrowers and wanderers (* $P < 0.05$).

each individual in the CT group. Among the burrowers, there was no significant correlation between the time to transit through the tubes and $R_{b/o}$ ($N = 7$, $r_s = 0.429$, $P = 0.337$). In one instance, a single individual constructed two burrows. Thus, the two $R_{b/o}$ values were summed and the total value was used for analysis. The mean time for wanderers ($N = 50$) was significantly longer than for burrowers ($N = 47$) ($U = 825.5$, $z = 2.52$, $P = 0.012$) (Fig. 8).

DISCUSSION

We demonstrated that substrate surface topography is correlated with the length of burrows constructed by *B. doederleini*. More complex substrate surface topography was associated with construction of longer burrows (Fig. 5). In addition, half of these longer burrows (4 of 8) had chambers in the mid-section (Fig. 6), suggesting they were used as a nest. The presence of these two features is consistent with observations of the fossilized burrows of Miocene period *Bathynomus* sp. These fossilized burrows were approximately six times longer than the constructing individual's body length, and contained an expanded region that was approximately twice as wide as the occupying individual (Matsuoka and Koike, 1980).

Our results suggest that extant *B. doederleini* construct a burrow that is approximately 2.5 times its body length and incorporates a chamber in the mid-section of the burrow. The chamber is constructed by initiating a vigorous somersaulting motion. Once construction was complete, the occupants were sometimes observed somersaulting, moving upward, pausing at the opening for a few minutes, then crawling out of the burrow head-first. The pause at the burrow entrance may be indicative of a 'sit and wait' foraging strategy, such as that observed in the deep-sea isopod, *Natanolana borealis* (Johansen and Brattegard, 1998). *Natanolana borealis* is also a voracious scavenger that inhabits soft substrates offshore (Wong and Moore, 1995). This species (body length: 2 cm) also constructs a permanent U-shaped burrow that extends 7–10 cm into the substrate (Taylor and Moore, 1995). *Natanolana borealis* enters one of the openings head-first then moves through the burrow to the opposite entrance/exit. Taylor and Moore (1995) observed individuals lying stationary near the entrance with only the anterior section visible and the second antennae pointing upwards above the sediment. These individuals emerged intermittently to feed when carcass odors were detected in the water.

Only one of the seven burrows constructed on the simple substrate incorporated a chamber. The length of the remaining burrows was slightly longer than the length of the occupants (Mean $R_{b/o} = 1.45 \pm 0.22$). These individuals were never observed somersaulting in the burrows, and exited by crawling backwards.

Given that this animal is a highly mobile, voracious scavenger, we hypothesize that it digs two types of burrows. The first is a short burrow that functions as a temporary shelter during foraging and the second is a deep burrow that the animal uses as a nest. Burrowing reduces predation risk by decreasing accessibility to predators (Zwarts et al., 1996) and deeper burrows may provide a better refuge against predators (Zwarts and Wanink, 1993). The depth of a burrow represents a tradeoff between energy expenditure and

benefit. Thus, *B. doederleini* occupied deeper burrows for longer periods than a shallow burrow (Fig. 7).

Sekiguchi (1985) observed burrow construction in *B. doederleini* and noted that the burrows were approximately equal in length to the body of the occupant. We also noted that the individuals moved rapidly, head-first into the burrows when disturbed, then later exited backwards, and concluded that the burrow most likely represents a temporary shelter, not a nest. Taken together, these observations suggest that *B. doederleini* individuals perceive a greater risk of predation in substrates with simple topography, so are compelled to dig a burrow that functions as a temporary shelter. Although the individuals on more complex substrates were clearly motivated to burrow deeply, the factors for this motivation remain unclear. The ability of a predator to locate and access subsurface prey is likely related to the substrate surface complexity. More complex substrates likely increase the difficulty of locating prey and/or accessing burrows. There is a need for further experiments to evaluate whether this feature of complex substrates motivates *B. doederleini* individuals to burrow more deeply.

We found no difference in the time from initial movement on the substrate to the completion of a burrow among the treatment groups. Similarly, there was no difference in the number of burrows constructed between the two groups. Taken together, these observations suggest that both spontaneous and passive tube-passing have no effect on an individual's motivation for burrowing. However, other environmental cues (e.g., seafloor topography) likely have an effect on the motivation to burrow.

We observed "wandering" individuals in both treatment groups. These individuals dug several shallow depressions in the agar, but never completed a burrow. In the simple substrate, these individuals repeatedly moved about the surface and excavated depressions on the substrate. However, on the more complex surface, these individuals often passed through the tubes, entering headfirst in most cases but backwards in others. The mean time to pass through the tubes was almost twice as long in the wanderers as in the burrowers (Fig. 8), suggesting that the wanderers used the tubes for temporary shelter.

In summary, we demonstrated phenotypic plasticity in the burrows of the deep-sea isopod *B. doederleini* in response to sea floor topography complexity. The capacity to alter burrow morphology in response to environmental differences suggests they have a highly organized central nervous system that is able to assess their environment. To identify the neurophysiological pathways involved in making this decision, we intend to investigate which stimuli the animals are responsive to.

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