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Swimming deep-sea holothurians (Echinodermata: Holothuroidea) on the northern Mid-Atlantic Ridge*

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Abstract

The ability to swim was recorded in 17 of 32 species of deep-sea holothurians during the RRS *James Cook* ECOMAR cruise in 2010 to the Mid-Atlantic Ridge. Holothurians were observed, photographed, and video recorded using the ROV *Isis* at four sites around the Charlie-Gibbs Fracture Zone at approximate depths of 2,200–2,800 m. For eleven species swimming is reported for the first time. A number of swimming species were observed on rocks, cliffs and steep slopes with taluses. These habitats are unusual for deep-sea holothurians, which are traditionally common on flat areas with soft sediment rich in detritus. Three species were found exclusively on cliffs. Swimming may provide an advantage in cliff habitats that are inaccessible to most epibenthic deposit-feeders.

Key words: sea cucumbers, benthopelagic species, diversity, Northern Atlantic Ocean

Introduction

Mid-ocean ridges remain one of the least studied environments in the ocean. They are characterised by remoteness, high relief, very complicated topography and complex current regimes. In the North Atlantic, the bathyal benthic ridge fauna has been less studied than those of open ocean seamounts (review in Mironov *et al.* 2006). In recent years, the bathyal fauna of the Mid-Atlantic Ridge was targeted by several expeditions onboard the RV *Akademik Mstislav Keldysh* (2003), *G.O. Sars* (2004) and the RRS *James Cook* (2007, 2009 and 2010) as part of two projects: MAR-ECO (a field project of the Census of Marine Life programme) (Bergstad & Godø 2003; Bergstad *et al.* 2008; www.mar-eco.no) and the UK-consortium project ECOMAR (www.oceanlab.abdn.ac.uk/ecomar). Among the goals of these projects was a better understanding of biodiversity and distribution patterns of benthic fauna on the Mid-Atlantic Ridge.

The most diverse component of megafauna on the ridge appears to be holothurians or sea-cucumbers (Echinodermata, Holothuroidea) (Gebruk 2008; Gebruk *et al.* 2010). Holothurians dominated the invertebrate biomass in the samples taken by ECOMAR in 2007 and 2009 (original data). In 2010 the ECOMAR cruise investigated four sites around the Charlie-Gibbs Fracture Zone (from 48 to 54°N) with the ROV *Isis*. Numerous observations documented by video and photo records were made

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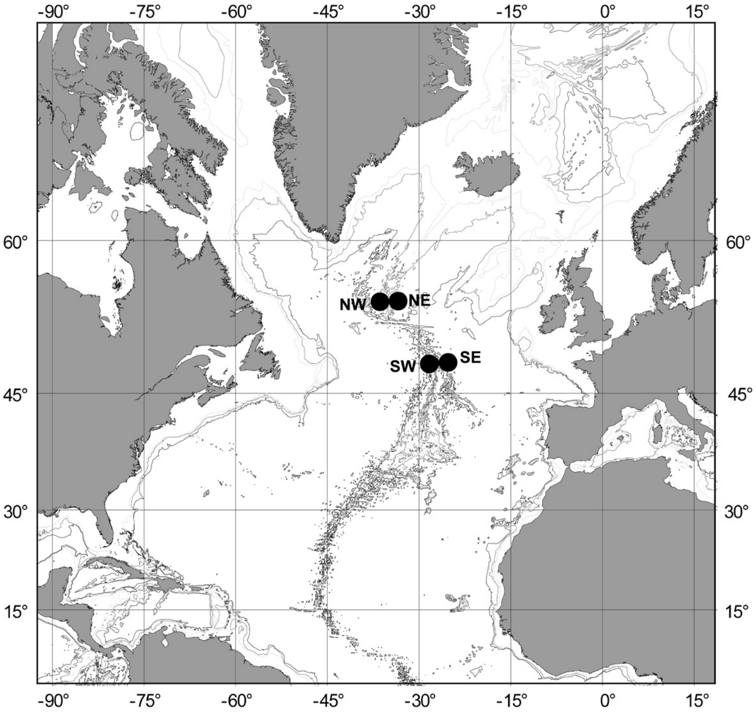

FIGURE 1. Location of study areas. Map source: PanMap, GEBCO

on holothurians *in situ* and many species were found to be able to swim. The ROV data gave unique information on species diversity in the ECOMAR area and species behaviour. Further, the ROV data added valuable information on steep slope and cliff habitats inaccessible to trawling. In the present paper we analyse and discuss data on swimming holothurians on the Mid-Atlantic Ridge.

Material and Methods

Material was collected from the Mid-Atlantic Ridge in the Charlie-Gibbs Fracture Zone (CGFZ) area onboard the RRS *James Cook* on several ECOMAR expeditions: JC011 (2007), JC037 (2009) and JC048 (2010). Stations were located at four pre-selected sites, at depths ranging from 2,100 m to 2,800 m to the west and east of the ridge axis, north 54°N and south 49°N of the Charlie-Gibbs Fracture Zone (CGFZ) respectively. We refer to these stations as the Southwest (SW), Southeast (SE), Northwest (NW), and Northeast (NE) (Fig. 1, Table 1). On the cruises JC011 and JC037, holothurians were sampled using a semi-balloon otter trawl (OTSB). On the JC048 cruise holothurians were observed *in situ*, video recorded, photographed, and sampled with the ROV *Isis*. On JC048, an additional ROV *Isis* station was made inside the CGFZ.

A High Definition Video pilot camera equipped with two laser pairs (red and green) and four HMI (hydrargyrum medium-arc iodide) lights were used for observations on the ROV *Isis* dives. Photographs were taken with the Scorpio digital still camera, with flash unit. Observations on benthic fauna were conducted during video transecting (T) and on dedicated specimen collection (C) dives (Table 1). Results of the video transecting will be presented separately. On collection dives, prior to sampling, each specimen was video recorded and photographed. Sampling was conducted using a suction sampler (slurp-gun) equipped with a carousel of six transparent chambers with video control. Larger specimens were sampled using two ROV manipulators. After retrieval of the ROV, samples were sorted and processed in a temperature controlled room at 4–6°C. Holothurians were identified

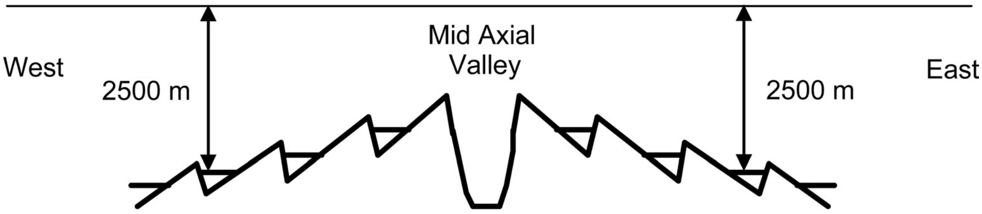

FIGURE 2. Schematic latitudinal profile of the Mid-Atlantic Ridge (Priede *et al.* in press).

TABLE 1. Station data. C, collection dive; T, video transecting dive; OTSB, semi-balloon otter trawl; ROV, remotely operated vehicle (for explanation see "Materials and methods")

Site	**Cruise Nr.**	**Station Nr.**	**ROV Dive**			**Gear**	**Latitude, N, Start–End**	**Longitude, W, Start–End**	**Depth, m**	**Date**
			Nr.	**Category**	**Time on the bottom, hrs**					
SE	JC037	JC037/19	–	–	–	OTSB	48°58.05'–49°14.36'	27°51.6'–27°49.29'	2750	10–11.08.2009
NW	JC048	JC048/6	159	C	7.81	ROV	53°58.78'–53°59.41'	36°11.49'–36°12.17'	2538	01–02.06.2010
NW	JC048	JC048/11	160	T	6.15	ROV	53°56.47'–53°57.60'	36°12.38'–36°12.10'	2500	02–03.06.2010
NW	JC048	JC048/16	162	C	15.63	ROV	53°59.42'–53°59.35'	36°11.67'–36°12.34'	2450–2272	06–07.06.2010
NW	JC048	JC048/17	163	C	4.78	ROV	53°59.44'–53°59.48'	36°11.65'–36°11.58'	2450	07.06.2010
NE	JC048	JC048/24	165	C	10.75	ROV	54°01.03'–54°00.92'	34°09.46'–34°08.99'	2501–2398	09–10.06.2010
NE	JC048	JC048/26	167	T	28.2	ROV	54°02.41'–53°59.72'	34°08.45'–34°11.51'	2364–2404	10–11.06.2010
NE	JC048	JC048/28	168	C	6.42	ROV	54°01.48'–54°01.49'	34°10.64'–34°10.77'	2445–2435	12–13.06.2010
CGFZ	JC048	JC048/29	169	T	3.33	ROV	52°40.86'–52°41.30'	35°04.20'–35°04.82'	3599–3670	14.06.2010
SW	JC048	JC048/33	170	T	4.95	ROV	48°43.63'–48°43.97'	28°38.87'–28°39.35'	2500–2641	16.06.2010
SW	JC048	JC048/36	171	T	28.65	ROV	48°43.86'–48°45.33'	28°39.70'–28°36.63'	2600–2480	18–19.06.2010
SW	JC048	JC048/38	172	C	2.85	ROV	48°43.68'–48°43.64'	28°38.81'–28°38.78'	2630	19–20.06.2010
SW	JC048	JC048/40	173	C	10.58	ROV	48°44.08'–48°44.25'	28°39.32'–28°39.47'	2619–2600	20–21.06.2010
SW	JC048	JC048/43	174	C	9.0	ROV	48°43.87'–48°44.23'	28°39.01'–28°39.57'	2620–2547	22.06.2010
SE	JC49	JC048/48	176	C	13.17	ROV	49°07.47'–49°05.03'	27°49.89'–27°50.41'	2741	23–24.06.2010
SE	JC048	JC048/51	177	C	21.33	ROV	49°00.82'–49°02.95'	27°40.49'–27°44.47'	2951–2227	26–27.06.2010
SE	JC048	JC048/53	178	C	11.12	ROV	49°00.82'–49°01.27'	27°40.49'–27°42.28'	2442–2630	27–28.06.2010
SE	JC048	JC048/54	179	C	5.92	ROV	49°05.91'–49°06.27'	27°50.33'–27°50.20'	2760–2767	28.06.2010
SE	JC048	JC048/56	180	C	4.5	ROV	49°01.18'–49°01.05'	27°42.37'–27°42.47'	2630–2658	29.06.2010

after the cruise in a laboratory by examining external and internal taxonomic characteristics with a light dissecting microscope. The morphology of calcareous ossicles in the skin and internal organs, and of the calcareous ring, was studied with a compound microscope on temporary and permanent slides made from pieces of tissue dissolved in chlorinated bleach solution.

Topography of the study area

The ridge in the ECOMAR area has a terraced structure, with flat, sediment-covered areas (plains), approximately two km wide (Priede *et al.* in press). These structures stretch along the ridge axis and increase their depth with distance from the axis (Fig. 2). On one side these terraces border on cliffs and steep slopes with taluses, and on the other side on gentle slopes (5–10°) covered with fine sediment. This type of topography forms a complex habitat, where rough terrains with rocky outcrops and cliffs create strong hydrodynamics. These are combined with flat areas covered with soft sediment suitable for deposit-feeders.

Ecological classification of swimming holothurians

In the present analysis we accept the following classification.

Categories of lifestyle (after Gebruk 1990):

1) Pelagic: live and feed in the water column. Only one representative—*Pelagothuria natatrix* Ludwig, 1894 (Miller & Pawson 1990).

2) Benthopelagic: spend some time in the water column, but always feed on the seafloor. By frequency of swimming can be subdivided into three groups:

Preferential swimmers (P): spend most of time in the water column *e.g.*, *Enypniastes eximia* Théel, 1882 (Miller & Pawson 1990), and *Peniagone diaphana* (Théel, 1882) (Barnes *et al.* 1976);

Frequent swimmers (F): often swim, but spend most of time on the seafloor: many elpidiid holothurians such as species of *Peniagone*, *Ellipinion* and *Amperima*;

Occasional swimmers (O): swim rarely, usually in response to disturbance or when changing location at the seafloor: large forms including some Psychropotidae and Synallactidae and shallow-water swimming holothurians (Miller & Pawson 1990).

Species composition of the benthopelagic holothurians

A total of 32 species of holothurians were identified in the material collected by the three ECOMAR cruises. Among those species five are infaunal. Others are epifaunal (six species) and benthopelagic (17 species), another four species are suggested as benthopelagic. The ability to swim was observed for the first time in the following eleven species: *Benthodytes gosarsi* Gebruk, 2008, *B. lingua* Perrier, 1896, *Amperima furcata* (Hérouard, 1899), *Ellipinion delagei* (Hérouard, 1896), *Ellipinion* sp. nov. “alani” (Rogacheva *et al.*, in press), *Peniagone longipapillata* Gebruk, 2008, *P. azorica* von Marenzeller, 1893, *P. islandica* Deichmann, 1930, *Peniagone* sp. nov. “coccinea” (Rogacheva *et al.* in press), *Peniagone* sp. “transparent” and *Kolga nana* (Théel, 1879). Details on the benthopelagic

TABLE 2. Information on benthopelagic holothurians found during the cruise JC048 * For abbreviations see 'Classification of swimming holothurians'

Species	Material	Regu-larlity of swim-ming*	Swimming observed		References on swimming repre-sentatives	Comments
			in situ	in collection chamber		
Order Aspidochirotida; Family Synallactidae						
Paelopatides grisea Perrier, 1899	Dives 159 and 179	O	–	–	Billett *et al.* 1985	Observed several times motionless at the seabed
Bathyplotes natans Sars, 1867	St. JC37/19	O	N/O**	N/O	Sars 1867; Ohta 1983	Not observed in situ on Isis dives
Synallactidae, sp. indet.	Dives 173, 174, 178	O	–	+	Original data	
Hansenothuria sp.	Dives 160, 173	O	–	+	Original data	
Order Elasipodida; Family Psychropotidae						
Benthodytes gosarsi Gebruk, 2008	Dives 168, 169, 173 and 177	O	+	N/C	Original data	A specimen about 20 cm in length was observed taking off for swimming after defecating (Fig. 3J–L)
Benthodytes lingua Perrier, 1896	Dives 174 and 177	O	–	+	Original data	A specimen about 20 cm in length was recorded swimming in the suction sampler chamber. Another specimen reaching 40 cm in length has been sampled with the ROV manipulator and later was observed actively swimming trying to escape from collection box mounted on platform in front of the ROV
Psychropotes depressa (Théel, 1882)	Dives 163, 165, 174, 177, 179 and 180	O	–	–	Arrhenius 1963; Pawson 1978; Billett *et al.* 1985	
Family Elpidiidae						
Amperima furcata (Hérouard, 1899)	Dives 174, 177, 179 and 180	F	+	+	Original data	
Ellipinion delagei (Hérouard, 1896)	Dives 162 and 165	F	–	+	Original data	
Ellipinion sp. nov "alani"	Dives 162, 165, 174 and 177	F	+	+	Original data	

TABLE 2.(continued)

Species	Material	Regularlity of swimming*	Swimming observed		References on swimming representatives	Comments
			in situ	in collection chamber		
Kolga nana (Théel, 1879)	Dives 165 and 169	F	+	+	Original data	This species forms extensive aggregations on the seafloor, with abundances reaching several tens of specimens per 1 m^2. Many specimens in these aggregations were observed swimming close to seafloor. Several tens of specimens have been sampled with suction sampler and were observed swimming in the suction sampler chamber
Peniagone longipapillata Gebruk, 2008	Dives 162, 165, 173 and 177	F	+	+	Original data	
Peniagone azorica von Marenzeller, 1893	Dive 165 and 167	F	+	+	Original data	
Peniagone islandica Deichmann, 1930	Dives 174, 176, 178, 179 and 180	F	+	+	Original data	Figure 3F–I
Peniagone sp. nov.“coccinea”	Dives 170, 171, 172, 174 and 179	F	+	+	Original data	Figure 3A–C
Peniagone sp. “transparent”	Dives 172 and 174	F	+	+	Original data	Frequent swimmer (Figure 3D–E). The species is characterised by the absence of spicules in the body skin and transparent skin with no pigmentation. This species several times was observed swimming and also taking off from the seabed for swimming
Family Pelagothuriidae						
Enypniastes eximia Théel, 1882	Dive 174	P	+	N/C	Hansen and Madsen 1956; Pawson 1978; Ohta 1983; Billett *et al.* 1985; Miller and Pawson 1990 (full list of references on swimming activity)	

species in our material are listed in the Table 2.

Additionally, for some species with no recorded swimming activity, a benthopelagic lifestyle is suggested. These species include:

Benthothuria funebris Perrier, 1902. Observed on Dives 169, 176, 177 and 179. This species has gelatinous skin and a row of ventrolateral papillae forming a brim. The external morphology resembles the benthopelagic *Paelopatides*.

Synallactes crucifera Perrier, 1898 (Dives 162 and 177) and *Laetmogone* sp. nov. "billetti" (Rogacheva *et al.* in press) (Dives 159, 162, 165, 173 and 180). Both species were repeatedly observed on cliffs and steep slopes (on rocks covered with sediment). It is likely that such habitats can be accessed only by means of swimming. Both species have soft skin allowing body undulation.

Penilpidia midatlantica Gebruk, 2008. St. JC037/19. This species was only found in our trawl catches. The external morphology of *P. midatlantica* is similar to that in other elpidiid genera, such as *Peniagone*, *Amperima* and *Kolga* with swimming representatives. On its anterior end *Penilpidia* has a lobe composed of tentacles on the ventral side, and a velum on the dorsal side. The posterior end shows a swimming lobe comprising of crowded tubefeet. This type of morphology in Elpidiidae is typical for swimming forms.

Topographical distribution

Benthopelagic holothurians were found in various types of habitat common to the Mid-Atlantic Ridge, such as flat sediment-covered plains, gentle sediment-covered slopes, steep slopes with taluses, rough terrains with rocky outcrops and cliffs. We analysed the species distribution in the following habitats: sedimentary plains/gentle slopes and cliffs/steep slopes with taluses (Table 3). Among the 18 species of benthopelagic holothurians observed *in situ* (including supposed swimmers), 15 species occurred on flat areas and gentle sedimented slopes, and nine species on taluses and cliffs. Half of the species (50%) occurred only on the plains and on gentle slopes; 33.3% of the species were observed both on planes/gentle slopes and cliffs/taluses; 16.7% of the species were found exclusively on cliffs and taluses (Table 4).

Discussion

All records of swimming holothurians discussed in this paper refer to adult forms. Most holothurians, regardless of whether they are epibenthic, infaunal, or benthopelagic have pelagic larvae. After metamorphosis juvenile specimens turn into benthic forms when settling. Pelagic juveniles are known in a number of deep-sea holothurians: *Enypniastes eximia*, *Peniagone diaphana*, *Benthodytes typica* Théel, 1882, *B. lingua*, *Psychropotes semperiana* Théel, 1882 and *P. longicauda* Théel, 1882 (Billett *et al.* 1985). A large juvenile of *P. longicauda*, 35 mm long, recorded at a depth of 4,940–5,930 m, 2,000–3,000 m above the seafloor, in the Kurile-Kamchatka Trench, was described as a new genus and species *Nectothuria translucida* because of its unusual habitat and transparent skin (Belyaev & Vinogradov 1969). Later Hansen (1975) regarded *N. translucida* as a juvenile of *Psychropotes longicauda*.

Published data on benthopelagic holothurians summarised by Gebruk (1989, 1990) and Miller &

Pawson (1990) consider approximately 25 species. In the present paper we report eleven more swimming species and suggest a potential ability for swimming in another four species. The list of species of benthopelagic holothurians will most likely increase. Many video records of swimming holothurians have been obtained from different locations. However, most of the recorded specimens could not be identified down to species level. Many species that have not been reported swimming yet, appear to have morphological characteristics suitable for such behaviour (see below). New potential swimmers can be expected among elpidiid genera *Peniagone*, *Amperima*, *Ellipinion*, *Kolga*, *Achlyonice*, *Psychroplanes* and *Penilpidia* also among psychropotids and synallactids. Pawson (1978) suggested that at least half of the Elasipodida species are benthopelagic.

All swimming holothurians are planktonic animals, *i.e.*, they are not able to swim against the current. Swimming in holothurians is used to maintain buoyancy in the water column for drifting. The truly pelagic *Pelagothuria natatrix* swims with its mouth directed upwards using lobe which surrounds the anterior part of the body (Miller & Pawson 1990). It resembles a funnel that can act like a sediment trap. Intestine content of this holothurian showed pelagic diatoms, radiolarians, foraminiferans and copepod pellets (Gebruk 1990). It has been suggested that *Pelagothuria* traps marine snow with its tentacles in the funnel formed by the swimming lobe (Gebruk 1990).

Different phases of swimming in various species, with vertical or horizontal positioning have been described (Barnes *et al.* 1976; Pawson & Foel 1986; Gebruk 1990; Miller & Pawson 1990). Our new observations show that orientation (vertical, horizontal *etc.*) in the water column can change rapidly depending on phase of swimming and water current.

The important phases of swimming are taking off after feeding and landing for feeding. Sometimes

TABLE 3. Benthopelagic holothurians recorded in two types of habitat (includes species that are suggested to be benthopelagic).

Species (taxon)	Sedimentary plain and slope	Cliff-tallus
Benthothuria funebris	+	
Paelopatides grisea	+	
Synallactes crucifera	+	+
Synallactidae, sp. indet.		+
Hansenothuria sp.		+
Laetmogone sp. nov. “billetti”	+	+
Benthodytes gosarsi	+	
Benthodytes lingua	+	
Psychropotes depressa	+	
Amperima furcata	+	
Ellipinion delagei	+	+
Ellipinion sp. nov. “alani”	+	+
Peniagone longipapillata	+	+
Peniagone azorica	+	
Peniagone islandica	+	
Peniagone sp. nov. “coccinea”	+	+
Peniagone sp. “transparent”		+
Kolga nana	+	
TOTAL	15 species	9 species

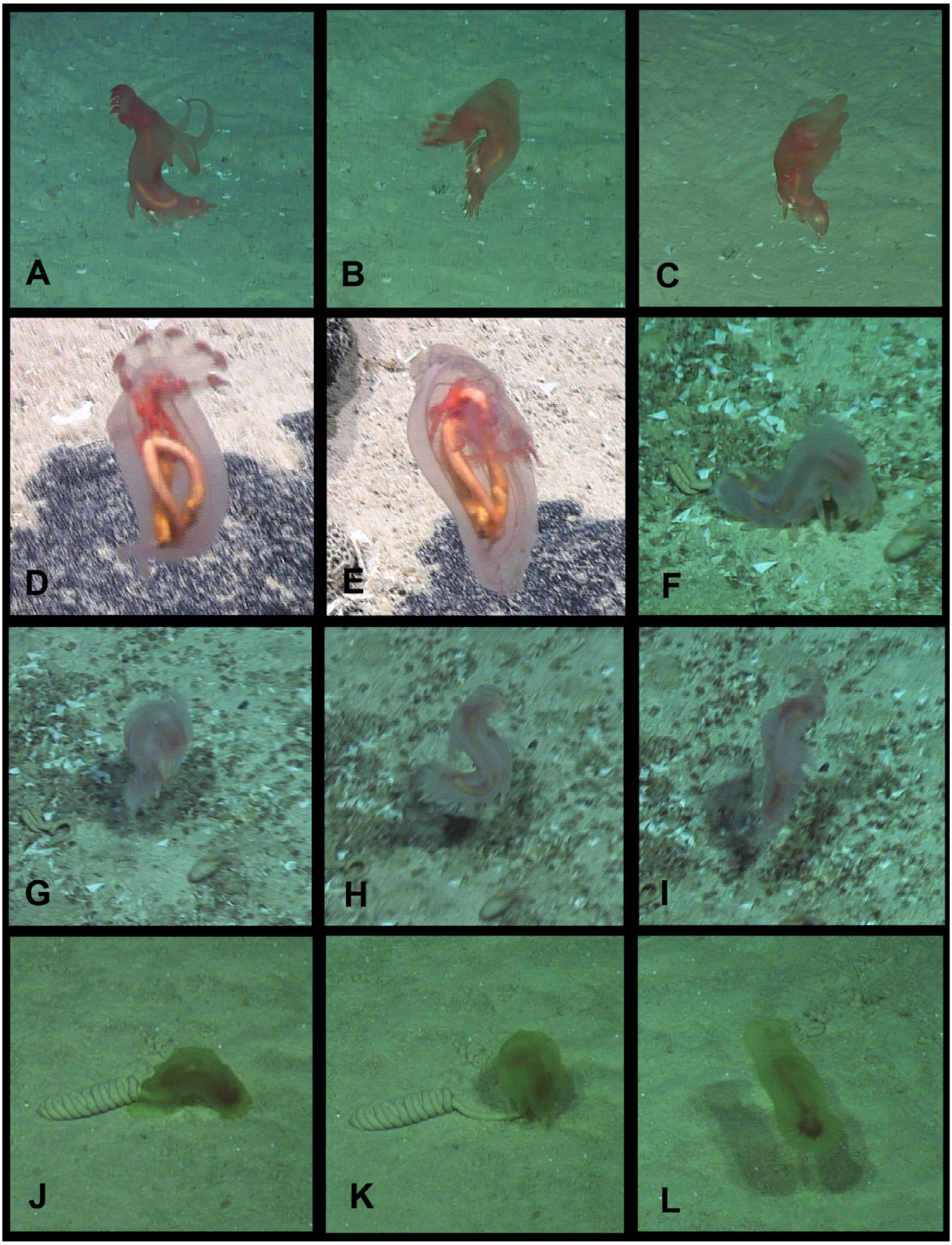

FIGURE 3. Phases of swimming in: *Peniagone* sp. nov. "coccinea" (A–C); *Peniagone* sp. "transparent" (D–E); *Peniagone islandica* (F–I); *Benthodytes gosarsi* (J–L).

feeding takes place by wiping the sediment with tentacles while drifting very close to the seabed, without actual landing. Between these two phases it is not important to orientate, but to maintain buoyancy in the water column. This is achieved by various morphological adaptations such as flattening of the body (to form a brim), development of various swimming lobes and gelatinous consistency of the skin. Many Elpidiidae use the anterior dorsal lobe (velum) and expanded mouth tentacles (Fig. 3A–I) for swimming. The development of the dorsal velum in elpidiids is evolutionary correlated with displacement of tubefeet to the posterior half of the body (Gebruk 1994). The ultimate stage in this trend is the posterior lobe that is formed by a few pairs of closely placed tubefeet, as can be seen in *Peniagone diaphana*. Holothurians with similar morphology can be expected to be able to swim rather than being truly epibenthic. In contrast, when tubefeet are evenly spaced along both sides of the body and there is no dorsal velum (as in *Scotoplanes*, *Protelpidia* and *Elpidia*) these indicate a truly epibenthic lifestyle and suggest that locomotion is achieved by "walking"—lifting the body on extended large tubefeet (Hansen 1972).

According to our new observations, before taking off from the seafloor, benthopelagic holothurians usually empty their intestines (defecate). It is likely that this is a common mechanism to achieve buoyancy. The intestines in holothurians can occupy a large part of the body volume. According to Sokolova (1986) average index of fullness (ratio of gut content weight/total body weight) can reach 20 % in Elpidiidae, 38.5 % in Psychropotidae (*Psychropotes*) and 44.5 % in Synallactidae (*Paelopatides*).When the intestine is full with sediment and detritus, it can hinder the ability to swim. Based on our observations, holothurians have a little negative buoyancy in the water column even with empty guts.

A variety of swimming movements in benthopelagic holothurians described in the literature (Barnes *et al.* 1976; Pawson 1986; Miller & Pawson 1990) is a combination of body flexing movements, using or not using swimming lobes. The only known exception is *Pelagothuria natatrix* that swims exclusively by undulating its large swimming lobe.

During the JC048 cruise with the ROV *Isis*, deep-sea holothurians were observed in habitats untypical for this group, such as cliffs and steep slopes with taluses. Most species occurred on soft sediment on plains and gentle slopes. However, some forms were found exclusively on cliffs and they may be restricted to this habitat. Latter forms include *Peniagone* sp. "transparent", *Hansenothuria* sp. and an unidentified synallactid species. ROV observations on cliffs and taluses showed that the sediment is accumulated in numerous sediment pockets and cracks in rocks, thus making this type of habitat suitable for deposit-feeding holothurians. Apparently swimming provides an advantage to benthopelagic holothurians in the ridge environment characterised by increased hydrodynamics and rough and changing topography. Using benthic currents for locomotion, swimming holothurians gain access to habitats such as cliffs and steep slopes with rocks, that are inaccessible to most epibenthic deposit-feeders.

As planktonic animals, benthopelagic holothurians are not advanced swimmers. The deep-sea environment is characterised by a low supply of organic matter input, its intermittent arrival, a comparatively low energy, and a patchy distribution. These conditions force deposit-feeders to a more mobile strategy of foraging, although increasing mobility needs to save energy at the same time. Benthopelagic holothurians use currents for drifting thus saving energy. Passive drifting with a current in vertical position with mouth directed downwards has been observed in *Peniagone diaphana*

TABLE 4. Occurrence of benthopelagic holothurians in different habitats on the Mid-Atlantic Ridge.

	Plain/gentle slope	**Plain/gentle slope and cliffs/talluses**	**Cliffs /talluses**
Number of recorded species	9	6	3
Percent from total number of species, %	50.0	33.3	16.7

by Barnes *et al.* (1976) and was considered by Lipps & Hickman (1982) as a ‘big bag construction’—an adaptation for retaining energy. By using currents, drifting benthopelagic holothurians save energy required for locomotion and this in turn increases the area that can be used for foraging. Expanding the foraging area can be advantageous in the deep-sea environment, for example in responding to seasonal flows of fresh organic matter, the most valuable source of energy for deposit-feeders in the deep sea. We suggest that a benthopelagic life style developed as an adaptation to vast abyssal plains, also appears advantageous in the mid-ocean ridge environment, characterised by changing topography and increased and highly variable near-bottom current regimes.

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