

High occurrence of the elasipodid holothurian *Penilpidia ludwigi* (von Marenzeller, 1893) in bathyal sediment traps moored in a western Mediterranean submarine canyon

F. Pagès, J. Martín*, A. Palanques, P. Puig, J.-M. Gili

Institut de Ciències del Mar (CSIC), Passeig Marítim de la Barceloneta 37-49, 08003 Barcelona, Catalonia, Spain

Received 29 December 2006; received in revised form 2 September 2007; accepted 11 September 2007

Available online 18 September 2007

Abstract

One hundred and fifty specimens of the elasipod holothurian *Penilpidia ludwigi* (von Marenzeller, 1893) were collected in sediment traps moored near the seabed in the La Fonera Canyon (Catalan Sea, north-western Mediterranean) and on the adjacent continental slope. These provide the third record of this apparently endemic Mediterranean species and the first record from the western Mediterranean. This was the only holothurian species trapped and the most abundant macroscopic organism found in the traps between 1200 and 1700 m depth over the whole sampling period (March–November 2001). It was particularly abundant in spring during the main flux of organic particles in the canyon. This coupling suggests that *Penilpidia* may aggregate at the seafloor during these events, making food availability a plausible explanation of the seasonal occurrence. Lateral transport of material re-suspended locally or up-canyon by near bottom currents appear to be the mechanism behind this uncommon occurrence, although *in situ* observations have recently been made on the swimming capability of this holothurian. The occurrence of benthic organisms in sediment traps set close to the seabed can provide information on bathyal benthic and benthopelagic populations.

© 2007 Elsevier Ltd. All rights reserved.

Keywords: Elasipodida; *Penilpidia*; Swimmer; Submarine canyons; Mediterranean

1. Introduction

Knowledge of the bathyal and abyssal fauna of the Mediterranean Sea is as sparse as the exploration conducted in its basins (Sardà et al., 2004). New information on species composition, community structure and ecology sometimes comes to light by serendipity. For instance, significant advances in

the study of benthopelagic populations in the northwestern Mediterranean have been obtained from the study of swimmers collected in sediment traps moored by geologists in submarine canyons. Swimmers are considered organisms that were apparently alive at the time of collection (Harbison and Gilmer, 1986) and were poisoned and preserved by the formalin solution in the trap sample cups. Among trapped swimmers, several new species, genera and families of medusae and polychaetes have been described (Gili et al., 1998, 1999, 2000; Sardà et al., submitted for publication). Yet only a few canyons have been explored and the potential

*Corresponding author. Present address: Marine Environment Laboratories (IAEA-MEL), 4 Quai Antoine Premier 98000, Monaco. Tel.: +377 97 97 72 60; fax: +377 97 97 72 73.

E-mail address: J.Martin@iaea.org (J. Martín).

for new discoveries is considerable. Swimmers are usually considered a nuisance that interferes with the particle flux in a sediment trap. The list of problems and biases attributed to them can be long (Silver et al., 1991), but in complex bathyal environmental settings they collect novel organisms that have never been sampled by conventional and even sophisticated sampling devices (such as ROVs). However, the by-catch of sediment traps is rarely examined by marine zoologists, although sometimes it is composed of new or poorly described plankton species.

Over the last two decades, submarine canyons have received increasing attention because of their particular geobiological and environmental characteristics (e.g. Palanques et al., 2005) and as key habitats of commercially exploited species (Cartes et al., 2004). La Fonera Canyon, also known as Palamós Canyon (Serra, 1981), is one of the largest submarine canyons in the Catalan Sea (Fig. 1). As part of the CANYONS project (see Palanques et al., 2005, for details), several moorings equipped with

sediment traps and current meters were deployed within and around this submarine canyon. The examination of the swimmers collected by these traps has resulted in the present study, which reports the taxa captured with emphasis on the extraordinarily high occurrence of the rarely reported elasipodid holothurian *Penilpidia ludwigi* (von Marenzeller, 1893) (Fig. 2). This tiny species (5–21 mm in length) was described originally from a few specimens



Fig. 2. Photograph of a preserved specimen of *Penilpidia ludwigi* 16 mm in length.

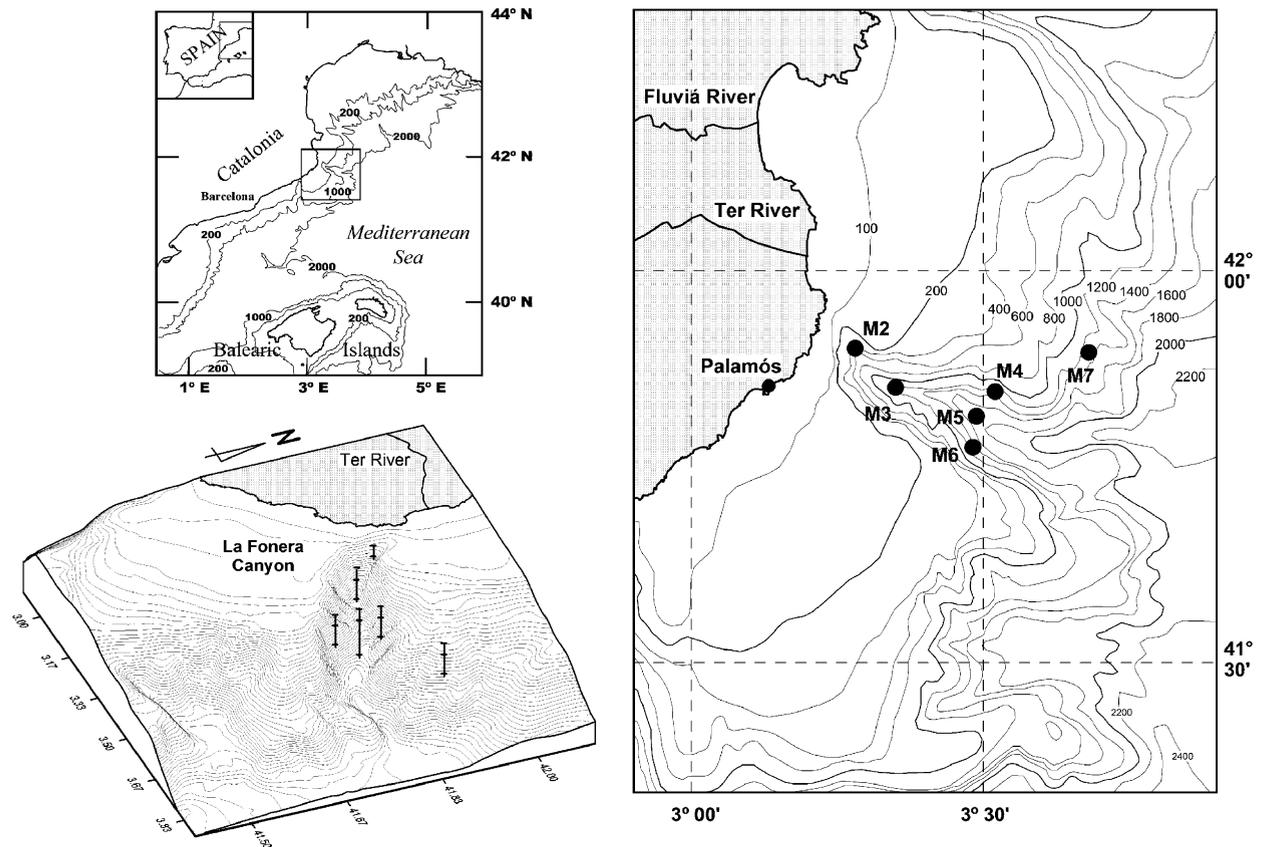


Fig. 1. General map of the area investigated. The block diagram and location map show the distribution of mooring arrays in La Fonera Canyon.

collected in the eastern Mediterranean by the *Pola* Expedition in 1890–1892. Fiege and Liao (1996) re-discovered this holothurian over 100 years later in the same basin during a *Meteor* cruise that collected 37 specimens in nine sediment cores collected between 1006 and 4766 m depth. These authors suggested that the two sporadic records only in the Mediterranean Sea, and the apparent absence in the western basin, could be the result of inadequate sampling. It was also suggested that mass aggregations may occur owing to the high abundances found (up to 14 holothurians per 0.25 m^{-2}). High densities of elpidiid holothurians are characteristic of canyon systems (Rowe, 1970; Belyaev, 1989), but no examples have been reported from Mediterranean canyons before the present study.

2. Materials and methods

Six mooring lines (Fig. 1) were deployed to collect time series data on currents, particulate fluxes, temperature, conductivity and turbidity along and across La Fonera Canyon in 2001. Three moorings (M2, M3 and M5) were deployed along the canyon axis at depths of about 470, 1200 and 1700 m, respectively. Another two moorings (M4 and M6) were placed near the canyon walls at 1300 m depth. One mooring (M7) was deployed at a distance of 15 km north of the canyon axis in order to monitor flow rates and fluxes on the slope upstream from the canyon.

Each mooring was equipped with a sediment trap 22 meters above the bottom (mab), coupled with a current meter placed 12 mab to record hydrodynamic data and to measure particle fluxes near the bottom. Mooring M3 was equipped with an additional sediment trap in midwater (400 m depth, 800 mab). Six of the sediment traps used in this study were cylindrical Technicap PPS3/3 traps, with an un baffled collecting area of 0.125 m^2 . A set of 12 sampling cups was attached to a mechanical system that rotated the collecting cup at programmed time intervals. The sediment trap installed on the open slope (M7) was an earlier Technicap model PPS3 equipped with only six cups. This unit was programmed with half the resolution of the rest of the traps to cover the same time period. Sediment traps hereafter will be referred to using the same designations (M2, M3, etc.) as the moorings to which they were attached. Mooring M3 had two sediment traps, namely M3B (bottom trap) and M3I (intermediate or mid-water trap).

All sediment traps worked successfully throughout the deployment period, which was divided into two parts for maintenance operations (from late March to early July 2001 and from mid-July to late November 2001). Both the geographical location of the moorings and the vertical position of each instrument before and after the maintenance break were very similar. Differences between the bottom depths of the moorings after re-deployment were always less than 50 m. Inside the canyon, sampling intervals of cups were set to 9 and 11 days (18 and 22 days in the open slope trap) for the first and second deployment, respectively. The sediment trap samples were treated and subsampled following the protocols applied by Heussner et al. (1990). Swimmers were collected in all the sediment traps deployed. They were sorted by wet-sieving the sample with filtered seawater through a 1-mm nylon mesh, picked with forceps and preserved in 5% formalin solution. They were examined under a binocular microscope and identified to specific level when possible. After sorting of the swimmers from the particulate material, the organic carbon, carbonate and biogenic silica concentration in the particulate sample were determined as described in Martín et al. (2006).

3. Results

The high abundance of the holothurian *P. ludwigi* (Fig. 2) was the most outstanding feature of the deep sediment trap samples. This was the only holothurian species trapped and the most abundant metazoan at depths between 1200 and 1700 m (Tables 1 and 2). The size range of the *Penilpidia* specimens preserved in formalin was 5–21 mm length and 2–9 mm width.

During the first deployment (late March–early July), the holothurian was found in all near-bottom sediment traps placed about 1200, 1300 and 1700 m depth (Fig. 3). The greatest number of specimens was recorded in the deepest trap in the canyon axis (M5, 1700 m, 57 specimens) and in the sediment trap set near the southern canyon wall (M6, 1300 m, 49 specimens). The other near-bottom traps, moored at 1200–1300 m depth (i.e. M3B-canyon axis, M4-northern wall and M7-slope), had fewer specimens (Table 1). It is important to highlight the fact that *P. ludwigi* was not collected in the upper canyon, shallowest near-bottom trap (M2, 470 m) nor in the mid-canyon midwater trap (M3I, 400 m). In M3B, the highest numbers of *P. ludwigi* were

Table 1
Number of individuals and taxa collected in each sediment trap during the first mooring deployment period (March–July 2001)

Trap	M2	M3I	M3B	M4	M5	M6	M7	Total
Depth (m)	470	400	1200	1300	1700	1300	1300	
mab	22	800	22	22	22	22	22	
Copepods	98	28	19	6	8	17	2	178
Salps	93	44	3	–	–	15	–	155
<i>Penilpidia ludwigi</i>	–	–	23	8	56	49	3	139
Polychaetes	42	52	11	4	11	2	6	128
Hyperid amphipods	6	27	4	–	1	–	–	38
Pteropods	–	8	2	10	1	1	16	38
Siphonophores	5	30	1	–	–	–	1	37
Hydromedusae	9	17	–	–	1	1	–	28
Ostracods	4	1	3	4	2	4	1	19
Decapod larvae	1	–	4	–	–	1	–	6
Cumaceans	2	–	–	1	1	2	–	6
Gammarian amphipods	2	2	–	1	1	–	–	6
Ctenophores	3	2	–	–	–	–	–	5
Pyrosomids	3	1	–	–	–	–	–	4
Hydropolyps	4	–	–	–	–	–	–	4
Chaetognaths	2	–	2	–	–	–	–	4
Bryozoans	–	–	4	–	–	–	–	4
Mysids	3	–	–	–	–	–	–	3
Bivalves	2	–	1	–	–	–	–	3
Fish larvae	2	–	–	–	–	–	–	2
Euphausiids	–	1	–	–	–	–	–	1
Crab larvae	–	1	–	–	–	–	–	1
Anemone larvae	–	–	1	–	–	–	–	1
Scyphomedusae	–	–	–	–	–	1	–	1
Total specimens	281	214	78	34	82	93	29	811
Total taxa	17	13	13	7	9	10	6	24

found in late March (up to 11 specimens in 9 days, Fig. 3), but it was found frequently until late June. In M4, it was collected from mid-April to early May in very low numbers (1–2 specimens). In M5, it had high abundances from late March to early May (Fig. 3). In M6, it was continuously captured from late March to early May (3–12 specimens) but less frequently in late June (1–4 specimens). In M7, single occurrences were found in April, May and June. In the shallowest near-bottom (M2) and midwater (M3I) traps, copepods, salps, polychaetes, hyperid amphipods, siphonophores and hydromedusae were the most numerous swimmers (Table 1).

During the second deployment (mid July–late November), only 11 specimens of *P. ludwigi* were collected in the sediment traps, and they were absent in M2, M3I and M5 (Fig. 3, Table 2). In M3B, single individuals were collected in early August and late October. In M4, a single specimen was captured in early November. In M6, seven specimens were collected from early August to early September. In M7, one specimen was caught by mid-August.

Pteropods, polychaetes and copepods were the most abundant swimmers in the near-bottom traps. Pteropods were also the most abundant in the mid-water trap (Table 2).

Fluxes of biogenic silica and organic carbon showed similar seasonal trends at all sites. Greater values were recorded in early spring and the lesser ones from late spring to early autumn (Figs. 3 and 4). The good relationship between biogenic silica and organic carbon during March–April indicates a significant down-canyon transport of particles rich in these components over this period.

It should be noted that the high fluxes at M3B during summer (Fig. 3) can be misleading. This shallower site received a much higher input of total particulate matter, but the material was composed mostly of terrigenous particles resuspended as a result of fishing activities along the canyon flanks (Palanques et al., 2006; Martín et al., 2006). These particles had a low organic content (Fig. 4), and were presumably depleted in labile compounds. On the other hand, although weaker organic fluxes

Table 2

Number of individuals and taxa collected in each sediment trap during the second mooring deployment period (July–November 2001)

Trap	M2	M3I	M3B	M4	M5	M6	M7	Total
Depth (m)	470	400	1200	1300	1700	1300	1300	
mab	22	800	22	22	22	22	22	
Pteropods	3	33	1	16	36	–	37	126
Polychaetes	61	15	17	5	1	16	6	121
Copepods	50	16	14	4	–	4	–	88
Ostracods	5	3	1	1	–	1	–	12
<i>Penilpidia ludwigi</i>	–	–	2	1	–	7	1	11
Decapod larvae	6	2	–	–	–	–	–	8
Gammarid amphipods	–	6	–	–	–	–	–	6
Hydromedusae	1	2	2	–	–	–	–	5
Siphonophores	1	–	–	3	–	1	–	5
Chaetognaths	3	–	2	–	–	–	–	5
Ophiuroids	2	–	2	–	–	–	–	4
Fish larvae	1	2	–	–	–	–	–	3
Hyperid amphipods	2	1	–	–	–	–	–	3
Salps	1	–	1	–	–	–	–	2
Bivalves	1	–	1	–	–	–	–	2
Ctenophores	1	–	1	–	–	–	–	2
Mysids	1	–	1	–	–	–	–	2
Heteropods	–	2	–	–	–	–	–	2
Euphausiids	–	2	–	–	–	–	–	2
Insects	–	1	–	–	–	–	–	1
Crab larvae	–	–	1	–	–	–	–	1
Radiolarians	–	–	–	1	–	–	–	1
Appendicularians	–	–	–	1	–	–	–	1
Pycnogonids	–	–	–	1	–	–	–	1
Total specimens	141	85	47	33	37	29	44	414
Total taxa	16	12	14	9	2	5	3	24

occurred in the offshore traps (as a consequence of lower total particle fluxes), a greater part of the particle input was composed of fresh material that had recently sunk from the upper water column (Martín et al., 2006).

Currents near the bottom (12 mab) were highly variable and apparently decoupled from currents in the overlying water column. In the canyon axis, currents were constrained to flow preferentially in an along-axis direction and they were stronger along the northern than along the southern wall (Palanques et al., 2005). There was not a clear relationship between the occurrence of the highest numbers of individuals and the periods of enhanced current speed near the seafloor (Fig. 5).

4. Discussion

Specimens of *P. ludwigi* were trapped mostly in spring. During this season, high fluxes of organic constituents were noted in La Fonera Canyon (Fig. 3; Martín et al., 2006). This coupling suggests that this

species may aggregate at the seafloor during these spring events, when primary production also blooms for short periods in surface waters (Estrada, 1999). The collected particles rich in biogenic silica and organic carbon were probably derived from diatoms that bloom seasonally (Estrada, 1999). Gili et al. (2000) have shown a link between the flux of particles and the occurrence of benthic-pelagic medusae in other canyons of the Catalan Sea.

The greatest numbers of *P. ludwigi* occurred in the deepest trap above the canyon axis (M5, 1700 m) and at the southern wall (M6, 1300 m). Previous observations have also recorded significant increase of holothurian densities (mostly elpidiids) at the bottom of some trenches, canyons and other seafloor depressions (Rowe, 1970; Belyaev, 1989). The other traps moored at 1200–1300 m depth (M3B-canyon axis, M4-northern wall and M7-slope) had lower numbers (Table 1) that correlated with variable and lesser organic-rich particle fluxes at these sites (Figs. 3 and 4). The results indicate that different environmental conditions have an

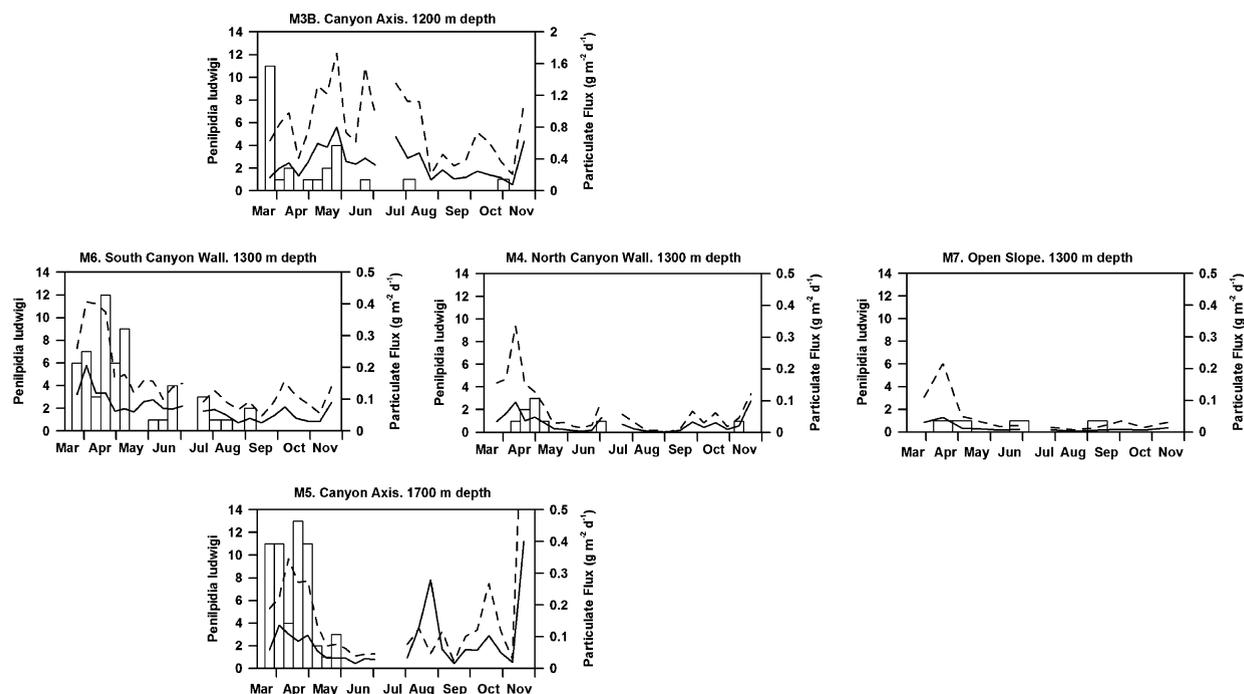


Fig. 3. Number of specimens of *Penipedia ludwigi* (bars), organic carbon flux (solid lines) and biogenic silica flux (dashed lines) collected by near-bottom sediment traps during the two mooring deployments.

effect on the number of holothurians collected by the sediment traps at similar depths across the canyon and on the adjacent open slope.

The general matching between the period of highest holothurian densities in the sediment traps and the highest flux and contents of organic particles (biogenic silica and carbon) makes food availability a plausible explanation of the seasonal occurrence, as first suggested by Billett and Hansen (1982), who linked the occurrence of large aggregations of the elaspodid *Kolga hyalina* in the Porcupine Seabight with the arrival of diatoms. In the same area, *Benthogone rosea* ingests phytodetritus from the seafloor (Billett et al., 1983), and the population structure and reproduction of *Amperima rosea* seems highly dependent on the organic matter flux to the seafloor (Wigham et al., 2003).

It is interesting to note that the ups and downs in the number of holothurians captured follow a pattern similar to that shown by the values of biogenic silica and organic carbon, both as flux and as percentage of dry weight (Figs. 3 and 4). Although the samples are not quantitative, the number of specimens collected could be indicative of their relative abundance on the canyon bottom

and re-suspension. An examination of Figs. 3 and 4 shows that holothurian numbers fit better with fluxes and percentages at sites in the canyon axis (M3B and M5) than at sites located on the canyon walls (M4 and M6), where a slight decoupling can be discerned. Thus, on the canyon walls, holothurians seem to react to the particle fall some days later. However, the sampling intervals of the cups (9 and 11 days) do not make it possible to determine how quickly the holothurians responded because the traps cannot record if animals entered into a particular sample cup at one time or over several days. Moreover, an explanation based on food availability may not be applicable to all Elpidiidae. Ruhl and Smith (2004) found a negative relationship between particulate organic carbon flux and *Elpidia minutissima* abundance in the North Atlantic that suggested a potential increase in abundance for this elpidiid during periods of lower food supply. Nevertheless, it is known from other deep-sea areas of the northeastern Atlantic that benthic animals feed upon re-suspended particles that were deposited previously in the so-called food banks (Duineveld et al., 2004).

One of the most intriguing questions raised by our study is how the specimens reached the mouth

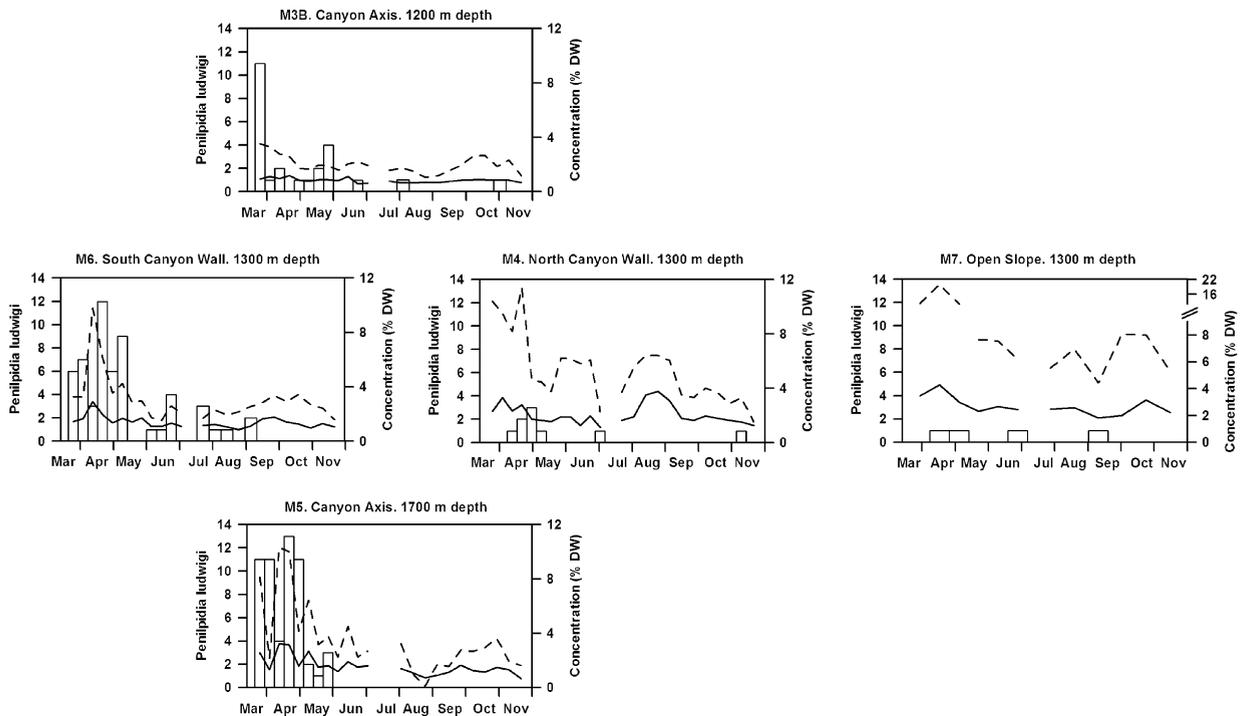


Fig. 4. Number of specimens of *Penilpidia ludwigi* (bars), organic carbon content (solid lines) and biogenic silica content (dashed lines) of samples collected by near-bottom sediment traps during the two mooring deployments. Particulate contents are expressed as percentage of the sample dry weight.

of the sediment trap placed 22 mab. Fiege and Liao (1996) found *P. ludwigi* living epibenthically and feeding upon sediment. The specimens collected in sediment traps also ingested sediment, as could be seen in their guts through the transparent body wall. Re-suspension or swimming of these organisms is the most likely mechanism to explain this benthopelagic distribution.

Although most of the swimmers found to co-occur with *P. ludwigi* were planktonic organisms or planktonic stages of benthic ones (Table 1), the presence of benthic polychaetes (Rafael Sardá, personal communication, May 2007) supports re-suspension as the mechanism that lifted holothurians into the water column. *Penilpidia* is gelatinous and its somatic water content may range between 85.3% and 93.9%, the percentage estimated for eight other elpidiid species (Billett, 1991). This high water content must provide almost neutral buoyancy. For instance, video cameras have recorded the neutral buoyancy and easy displacement of the tiny elpidiid *A. rosea* by the bow wave formed ahead of a towed sledge (Wigham et al., 2003). The current speeds measured 12 mab at the mooring

sites (Fig. 5) could cause enough shear stress on the seafloor to entrain these light holothurians and place them in suspension. Furthermore, periodic lateral (horizontal) transport of sediment particles resuspended up-canyon has been reported in La Fonera Canyon (Palanques et al., 2005). Once in the water column, the elapsipodids could drift with the current enhanced by the positive or almost neutral buoyancy characteristic of gelatinous organisms. We believe that this could be a highly efficient mechanism for transporting the holothurians as drifters with the main flow of particles and depositing them as aggregations in the sediment traps.

Vetter and Dayton (1999) found the benthic siphonophore *Dromalia alexandri* to be abundant in a canyon (at 300 and 500 m) and rare on the nearby slope. This rhodaliid can disperse as a member of the plankton and then attach itself to the seafloor using its tentacles. It is suspected that this animal remains in place when the food supply is sufficient and relocates when the flux of food is low. This could result in larger numbers occurring in canyons, if these environments experience higher current

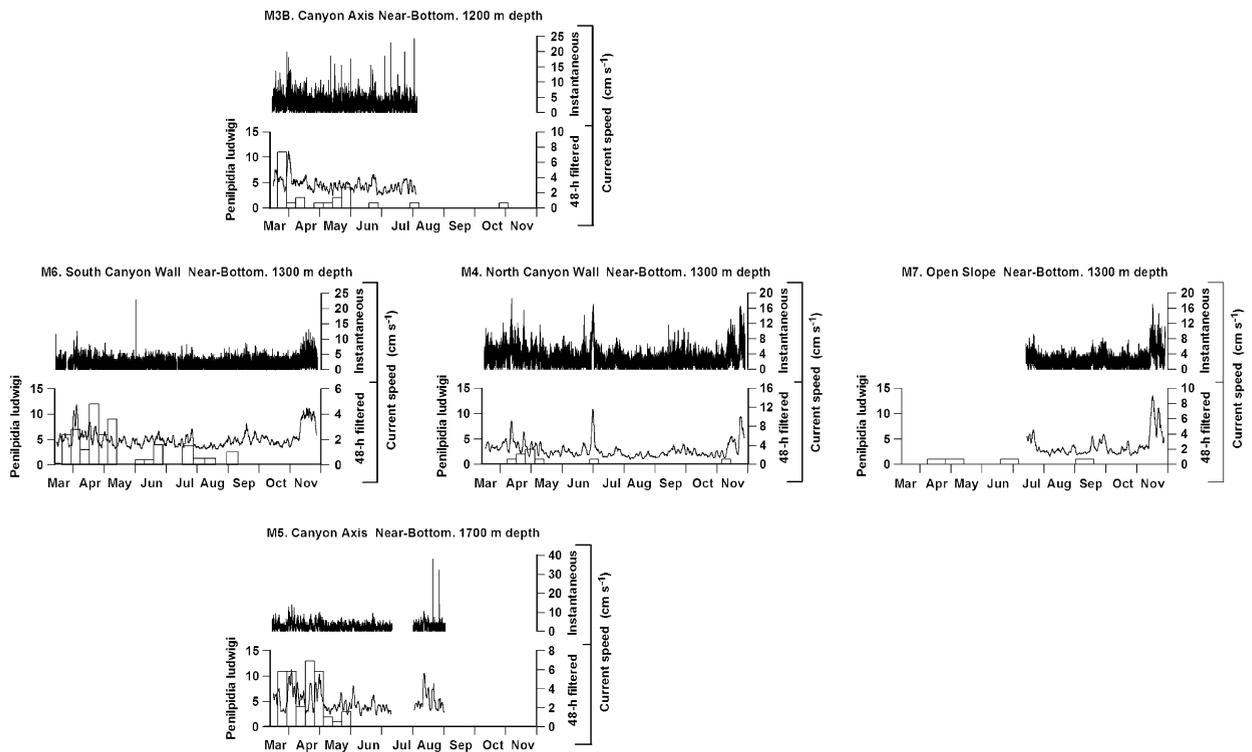


Fig. 5. Number of specimens of *Penilpidia ludwigi* (bars) collected in the sediment traps; lines: instantaneous current speed and low-pass filtered (48 h) current speed measured beneath the trap during the sampling period. A few time series of current data ended prematurely owing to technical malfunctions.

speeds than the adjoining slope. It may be that *Penilpidia* uses a similar foraging method.

An alternative explanation for the high occurrence of this elaspodid holothurian at 22mab is that they entered the sediment trap by their own mobility. This raises the question of whether *Penilpidia* can swim. Miller and Pawson (1990) listed 25 species of swimming sea-cucumbers. Most of them are benthic species that do not swim without first being stimulated and then can swim for only short periods before returning to the seafloor. The potential of a holothurian to swim is often difficult to determine, because many species are very fragile and fall apart during capture and preservation (Billett, 1991).

Other elaspod species form dense aggregations on the seafloor but have not yet been recorded in the water column. These include *K. hyalina* (Billett and Hansen, 1982), *Irpa abyssicola* (Gebruk et al., 2003), *Elpidia glacialis* (Dahl et al., 1976), *E. minutissima* (Ruhl and Smith, 2004) and *A. rosea* (Bett et al., 2001). All these species are smaller than those reported to be swimmers, which suggests that only

large elphidiids swim. Moreover, *P. ludwigi* lacks the antero-dorsal velum that allows for occasional swimming of other elpidiids such as *Peniagone* (Pawson and Foell, 1986) nor the frontal lobe of pelagothuriids such as *Eynpiates eximia* (Ohta, 1985). However, other species without a velum swim by flexing the posterior portion of the body with a rhythmic pulsation of the anterior brim (Miller and Pawson, 1990) possibly responding to an increase in bottom current velocity. This behavior was suggested by Shirayama et al. (1985) based on observations and photographs taken of *Pannychia moseleyi* from the submersible SHINKAI 2000. Gebruk (1995) did not list *Penilpidia* when he related the lifestyle of elaspodids to the type of locomotion and locomotive organs. However, this holothurian could be classified as a benthic form with walking as the main locomotion type, owing to the relatively hypertrophied tube-feet, as indicated by Gebruk (1995) for the close genus *Elpidia*.

The question of whether or not *Penilpidia* swims was discussed during the 11th Deep-Sea Biology Symposium, held in Southampton (UK) in July

2006, and where this study was presented. Just after the presentation, Peter Herring (National Oceanography Centre, Southampton, UK) vividly commented that many individuals of *P. ludwigi* (identified by Dave Pawson) were observed swimming just above the bottom during Dive 2952 of the Johnson Sealink submersible, April 1991 at 36°03.5N, 02°48.0W (Alborán Sea, southwestern Mediterranean). The observed *Penilpidia* clearly swam off the bottom by their own efforts, but they could be advected anywhere once in the water column (Peter Herring, personal communication, July 2006). It is interesting to note that these *in situ* observations were made in April and at approximately 700 m water depth (the shallowest depth record for this species). Herring (1995) published some observations on the bioluminescence of this species (as *Irpa ludwigi*), noting that the specimens were captured by a submersible but not mentioning where they were collected.

Based on our results, it is still soon to assess whether *P. ludwigi* is a rare species in the deep Mediterranean. Gebruk (1994) believed that the elasipodids were broadly distributed in the old Tethys basin before being split between at least three main sub-basins, namely the Mediterranean, the Indo-Malayan and the eastern Pacific (Panama). Thus, the endemic Mediterranean *P. ludwigi* is a relict species from the ancient Tethys. New species of medusae discovered in several western Mediterranean submarine canyons have also been interpreted as relicts from the Tethys (Gili et al., 1998, 1999, 2000). The gelatinous swimmers collected in the near-bottom sediment traps deployed in these submarine canyons were mainly new medusae and no holothurian species was reported, suggesting a degree of specificity in the relict fauna among canyons. The few previous studies reporting bathyal echinoderms in the Catalan Sea and adjacent waters (Reyss, 1971; Alvà, 1987; Gili et al., 1987) listed fragile holothurians, but they were large species such as *Pseudostichopus occultatus*. However, sampling equipment that might catch tiny soft-bodied organisms was not used. To our knowledge, holothurians have never been reported previously in sediment traps. Some ROVs seem to be very good vehicles for observing and collecting tiny elasipodids (Gebruk et al., 2003). Submersibles are excellent vehicles for this purpose (Barnes et al., 1976; Shirayama et al., 1985; Herring, 1995). In the northwestern Mediterranean, epibenthic sledges are the devices most frequently used for sampling benthopelagic fauna (e.g. Cartes et al., 2003), and

they could provide material suitable for assessing the occurrence and distribution of *P. ludwigi*.

In summary, the Mediterranean elasipodid holothurian *P. ludwigi* is reported for the first time in the western basin, where it seems to be relatively common near the seafloor in a large submarine canyon in spring between 1200 and at least 1700 m depth. The seasonal occurrence fits quite well with the highest downward fluxes of biogenic silica and organic particles, making food availability a plausible explanation for the reported high abundances. We suggest that the occurrence of this holothurian in sediment traps placed 22 mab was caused by resuspension, lateral transport with particulate matter, and swimming.

Acknowledgments

Michael Stachowitsch kindly provided a copy of the original description of *Penilpidia (Kolga) ludwigi*. Andrey Gebruk provided advice and helpful interpretations on elasipodid behavior. Dhugal J. Lindsay helped to improve the manuscript with comments and corrections. Special thanks to Peter Herring for bringing to light his *in situ* observations on *Penilpidia (Irpa) ludwigi* in the Alborán Sea, as well as for making available some unpublished results derived from this encounter. Edie Widder (HBOI) provided further comments on the swimming behavior of *Penilpidia ludwigi* derived from experiments conducted during the cruise that she led. We thank Andrew J. Gooday, Michael P. Bacon and three anonymous reviewers for their constructive comments on the manuscript, which have definitely helped to improve this work. This study has been supported by the HERMES project, funded by the European Commission's Six Framework Programme, under the priority Sustainable Development, Global Change and Ecosystems (Contract no. GOCE-CT-2005-511234-1).

References

- Alvà, V., 1987. Equinodermos batiales de la cubeta catalano-balear (Mediterráneo noroccidental). Miscel·lània Zoològica 11, 211–219.

- Barnes, A.T., Quetin, L.B., Childress, J.J., Pawson, D.L., 1976. Deep-sea macroplanktonic sea cucumbers: suspended sediment feeders captured from deep submergence vehicle. *Science* 194, 1083–1085.
- Belyaev, G.M., 1989. Glubokovodnye Okeanicheskie Zheloba i Ikh Fauna (Abyssal Oceanic Troughs and Their Fauna), Nauka, Moscow, 255pp.
- Bett, B.J., Malzone, G., Narayanaswamy, E.B., Wigham, B.D., 2001. Temporal variability in phytodetritus and megabenthic activity at the seabed in the deep Northeast Atlantic. *Progress in Oceanography* 50, 349–368.
- Billett, D.S.M., 1991. Deep-sea holothurians. *Oceanography and Marine Biology* 29, 259–317.
- Billett, D.S.M., Hansen, B., 1982. Abyssal aggregations of *Kolga hyalina* Danielsen and Koren (Echinodermata: Holothuroidea) in the northeast Atlantic Ocean, a preliminary report. *Deep-Sea Research* 29A, 799–818.
- Billett, D.S.M., Lampitt, R.S., Rice, A.L., Mantoura, R.F.C., 1983. Seasonal sedimentation of phytoplankton to the deep-sea benthos. *Nature* 302, 520–522.
- Cartes, J.E., Jaume, D., Madurell, T., 2003. Local changes in the composition and community structure of suprabenthic peracarid crustaceans on the bathyal Mediterranean: influence of environmental factors. *Marine Biology* 143, 745–758.
- Cartes, J.E., Maynou, F., Sardà, F., Company, J.B., Lloris, D., Tudela, S., 2004. The Mediterranean deep-sea ecosystems: an overview of their diversity, structure, functioning and anthropogenic impacts. In: *The Mediterranean Deep-sea Ecosystems an Overview of Their Diversity, Structure, Functioning and Anthropogenic Impacts, with a Proposal for Conservation*. IUCN, Málaga and WWF, Roma, pp. 9–38.
- Dahl, E., Laubier, L., Sibuet, M., Stromberg, J.-O., 1976. Some quantitative results on benthic communities of the Deep Norwegian Sea. *Astarte* 9, 61–79.
- Duineveld, G.C.A., Lavaleye, M.S.S., Berghuis, E.M., 2004. Particle flux and food supply to a seamount cold-water community (Galicia Bank, NW Spain). *Marine Ecology Progress Series* 277, 13–23.
- Estrada, M., 1999. Hidrodinàmica i fitoplàncton en el mar Català. *Memòries de la Real. Acadèmia de Ciències i Arts de Barcelona* 58, 3–61.
- Fiege, D., Liao, Y., 1996. *Penilpidia ludwigi* (Marenzeller, 1893) (Holothuroidea, Elpidiidae) rediscovered from the eastern Mediterranean Sea. In: Uiblein, F., Ott, J., Stachowitsch, M. (Eds.), *Deep-sea and Extreme Shallow-Water Habitats: Affinities And Adaptations*. Biosystematics and Ecology Series, vol. 11, pp. 61–66.
- Gebruk, A.V., 1994. Two main stages in the evolution of the deep-sea fauna of elapsidid holothurians. In: David, Guille, Féral, Roux (Eds.), *Echinoderm Through Time*. Balkema, Rotterdam, pp. 507–513.
- Gebruk, A.V., 1995. Locomotory organs in the elapsidid holothurians: functional-morphological and evolutionary approaches. In: Emson, R., Smith, A., Campbell, A. (Eds.), *Echinoderm Research 1995*. Balkema, Rotterdam, pp. 95–102.
- Gebruk, A.V., Bluhm, H., Soltwedel, T., Thiel, H., 2003. A re-description of the enigmatic deep-sea holothurian *Irpa abyssicola* (Elpidiidae, Elapsidida) with remotely operated vehicle observations on benthic organisms in the Norwegian-Greenland Basin. *Sarsia* 88, 49–54.
- Gili, J.-M., Ros, J.D., Pagès, F., 1987. Types of bottoms and benthic cnidaria from the trawling grounds (littoral and bathyal) off Catalonia (NE Spain). *Vie Milieu* 37, 85–98.
- Gili, J.-M., Bouillon, J., Pagès, F., Palanques, A., Puig, P., Heussner, S., 1998. Origin and biogeography of deep-water Mediterranean hydromedusae including the description of two new species collected in submarine canyons of north-western Mediterranean. *Scientia Marina* 62, 113–134.
- Gili, J.-M., Bouillon, J., Pagès, F., Palanques, A., Puig, P., 1999. Submarine canyons as habitat of singular plankton populations: three new deep-sea hydrodromedusae in the western Mediterranean. *Zoological Journal of the Linnean Society* 125, 313–329.
- Gili, J.-M., Bouillon, J., Pagès, F., Palanques, A., Puig, P., Heussner, S., 2000. A multidisciplinary approach to the knowledge of gelatinous zooplankton populations inhabiting Mediterranean submarine canyons. *Deep-Sea Research I* 47, 1513–1533.
- Harbison, G.R., Gilmer, R.W., 1986. Effects of animal behaviour on sediment trap collections: implications for the calculation of aragonite fluxes. *Deep-Sea Research I* 33, 1017–1024.
- Herring, P.J., 1995. Bioluminescent echinoderms: unity of function in diversity of expression? In: Emson, R., Smith, A., Campbell, A. (Eds.), *Echinoderm Research 1995*. Balkema, Rotterdam, pp. 9–17.
- Heussner, S., Ratti, C., Carbonne, J., 1990. The PPS 3 time-series sediment trap and the trap sample processing techniques used during the ECOMARGE experiment. *Continental Shelf Research* 10, 943–958.
- Martín, J., Palanques, A., Puig, P., 2006. Composition and variability of downward particulate matter fluxes in the Palamós Submarine Canyon (NW Mediterranean). *Journal of Marine Systems* 60, 75–97.
- Miller, J.E., Pawson, D.L., 1990. Swimming sea cucumbers (Echinodermata: Holothuroidea): a survey, with analysis of swimming behavior in four bathyal species. *Smithsonian Contributions to Marine Science* 35, 1–18.
- Ohta, S., 1985. Photographic observations of the swimming behavior of the deep-sea pelagothuriid holothurian *Enypniastes* (Elasipodida, Holothuroidea). *Journal of the Oceanographical Society of Japan* 41, 121–133.
- Palanques, A., García-Ladona, E., Gomis, D., Martín, J., Marcos, M., Pascual, A., Emelianov, M., Puig, P., Guillén, J., Gili, J.M., Tintoré, J., Jordi, A., Basterretxea, G., Font, J., Segura, M., Blasco, D., Montserrat, S., Ruiz, S., Pagès, F., 2005. A multidisciplinary program to study the dynamics and the ecology of a northwestern Mediterranean submarine canyon: the Palamós Canyon. *Progress in Oceanography* 66, 89–119.
- Palanques, A., Martín, J., Puig, P., Guillén, J., Company, J.B., Sardà, F., 2006. Evidence of sediment gravity flows induced by trawling in the Palamós (Fonera) submarine canyon (northwestern Mediterranean). *Deep-Sea Research I* 53, 201–214.
- Pawson, D.L., Foell, E.J., 1986. *Peniagone leander* new species, an abyssal benthopelagic sea cucumber (Echinodermata: Holothuroidea) from the Eastern Central Pacific Ocean. *Bulletin of Marine Science* 38, 293–299.
- Reyss, D., 1971. Les canyons sous-marines de la mer catalane: le rech du Cap et le rech Lacaze-Duthier. 3. les peuplements de macrofaune benthique. *Vie Milieu* 22, 529–613.

- Rowe, G.T., 1970. Observations on bottom currents and epibenthic populations in Hatteras Submarine Canyon. *Deep-Sea Research* 18, 569–581.
- Ruhl, H.A., Smith Jr., K.L., 2004. Shifts in the deep-sea community structure linked to climate and food supply. *Science* 305, 513–515.
- Sardà, F., Calafat, A., Flexas, M.M., Tselepidis, A., Canals, M., Espino, M., Tursi, A., 2004. An introduction to Mediterranean deep-sea biology. *Scientia Marina* 68 (Suppl. 3), 7–38.
- Sardà, R., Gil, J., Taboada, S., Gili, J.M., submitted for publication. Polychaete species captured in sediment traps located in Northwestern Mediterranean submarine canyons. *Zoological Journal of the Linnean Society*.
- Serra, J., 1981. Els canyons submarins del marge continental català. *Treballs de la Institució Catalana d'Història Natural* 9, 53–57.
- Shirayama, Y., Ohta, S., Horikoshi, M., 1985. Some results on the ecology of deep-sea benthos obtained using “SHINKAI 2000”. Technical Reports JAMSTEC Special Issue, pp. 119–121.
- Silver, M.W., Pilskaln, C.H., Steinberg, D., 1991. The biologist's view of sediment trap collections: problems of marine snow and living organisms. In: Wassmann, P., Heiskanen, A.-S., Lindahl, O. (Eds.), *Sediment Trap Studies in the Nordic Countries*, vol. 2. Nurmijärvi, Finland, pp. 76–93.
- Vetter, E.W., Dayton, P.K., 1999. Organic enrichment by macrophyte detritus, and abundance patterns of megafaunal populations in submarine canyons. *Marine Ecology Progress Series* 186, 137–148.
- von Marenzeller, E., 1893. *Zoologische Ergebnisse. I. Echinodermen, gesammelt 1890, 1891 und 1892. Berichte der Commission für Erforschung des Östlichen Mittelmeeres. V. Denkschriften der Mathematisch-Naturwissenschaftlichen Classe der Kaiserlichen Akademie der Wissenschaften*, vol. 60, pp. 1–24.
- Wigham, B.D., Tyler, P.A., Billett, D.S.M., 2003. Reproductive biology of the abyssal holothurian *Amperima rosea*: an opportunistic response to variable flux of surface derived organic matter? *Journal of the Marine Biological Association of the United Kingdom* 83, 175–188.