

Mass deposition event of *Pyrosoma atlanticum* carcasses off Ivory Coast (West Africa)

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Abstract

Thousands of moribund thaliacean carcasses (*Pyrosoma atlanticum*) were deposited between February and March 2006 at the seafloor in the Ivory Coast area (West Africa). Remotely operated vehicle surveys were conducted in a continuous depth gradient between 20 and 1275 m along an oil pipeline. Video and still photography were used to estimate the carcass distribution, density, and size on the seabed, as well as recording the local megafauna interactions with the gelatinous material. Large patches of dead pyrosomids covered extensive areas on the continental slope, whereas minor aggregations were found on the shelf. The carcasses were in many instances trapped along the pipelines, accumulating extensively in troughs and furrows in the slope, and especially in soft sediment channels. *Pyrosoma atlanticum* dried samples were used to calculate the carbon content, enabling the extrapolation to the densities and sizes recorded in the video surveys. The average standing stock of organic carbon associated with the carcasses was $>5 \text{ g C m}^{-2}$ in the whole slope and canyon, with values as high as 22 g C m^{-2} in certain areas. Eight megafaunal species from three different phyla were observed 63 times directly feeding on the decomposing carcasses. The gelatinous carbon may have contributed substantially to the detrital food web including microbes at the seabed, and certainly to the diet of larger benthic organisms. The organism-level carbon measurements and documented fate of pyrosomid organic carbon is new evidence of the importance of gelatinous material in large-scale processes and elemental cycling.

Carbon inputs to the deep sea—The deep sea can experience rapid inputs of organic carbon from the overlying surface waters with rapid responses by micro- and macrofaunal taxa (Goody 2002). Deep-sea benthic ecosystems rely mainly on primary production from the surface waters and material originating from primary consumers (fecal pellets, dead bodies, discards; Robison et al. 2005). Other less-studied sources of organic carbon include gelatinous zooplankton carcasses (Billett et al. 2006), detrital particles (Beaulieu 2002), episodic deliveries of large organic parcels (Smith and Baco 2003), and macrophyte detritus (Vetter 1996). The significance of these organic carbon pathways to biogeochemical processes and benthic communities vary between habitat and distance from neritic waters, although reliable estimations remain still in their infancy (Pilskaln et al. 1996).

Continental shelves and slopes effectively comprise less than 20% of the oceans' area, but are net sinks of inorganic and especially organic carbon (Walsh et al. 1981). Carbon not buried or accumulated in the continental shelf is exported to the open ocean and either redeposited, or potentially converted to dissolved organic carbon (DOC), entering the water column (Bauer and Druffel 1998). For understanding of biogeochemical cycles it is necessary to analyze the collective contributions of all possible active carbon inputs, particularly those that are poorly enumerated. A major problem in this respect is that the settling flux of organic carbon and the active accumulation in sediments is assumed to be correlated directly with primary

production (Lallier-Verges et al. 1993). The important vertical transport of larger carbon parcels, such as gelatinous zooplankton carcasses, has been widely overlooked (Billett et al. 2006).

Gelatinous zooplankton carbon export—Gelatinous zooplankton populations do not only affect pelagic ecosystem functioning (Mills 1995), but may also alter the ultimate organic matter flux to the seafloor in both coastal and deep-sea areas (Billett et al. 2006). Data on episodic export of carbon from the carcasses of gelatinous zooplankton populations are sparse. The majority of the literature has focused on “discarded organogenic” inputs, such as mucous sheets (Robison et al. 2005) and fecal pellets (Perissinotto and Pakhomov 1998). Gelatinous animals have been considered not the preferred prey item for other species (Moline et al. 2004). However, there is evidence that they form part of the diet of many fish (Harbison 1998), and probably are important diet items in benthic communities (Roe et al. 1990; Yamamoto et al. 2008). There is also evidence that their carbon may be channeled by bacteria in the water column and in the benthos, contributing greatly to the microbial detrital food web (Riemann et al. 2006; Titelman et al. 2006). Since the biomass of gelatinous organisms has been reported to increase in past decades (Mills 2001), and new studies have appeared considering the importance of organism-level measurements at the ecosystem and carbon cycling levels, their role in biogeochemical cycles needs to be reconsidered. Billett et al. (2006) stated that even if a major input and deposition of material derived from dead gelatinous zooplankton has been suggested, no direct quantification has been made. Cacchione et al. (1978) observed salp carcasses rolling in the Hudson Canyon at more than 3000-m depth, whereas jellyfish bodies have been recorded on continental slopes

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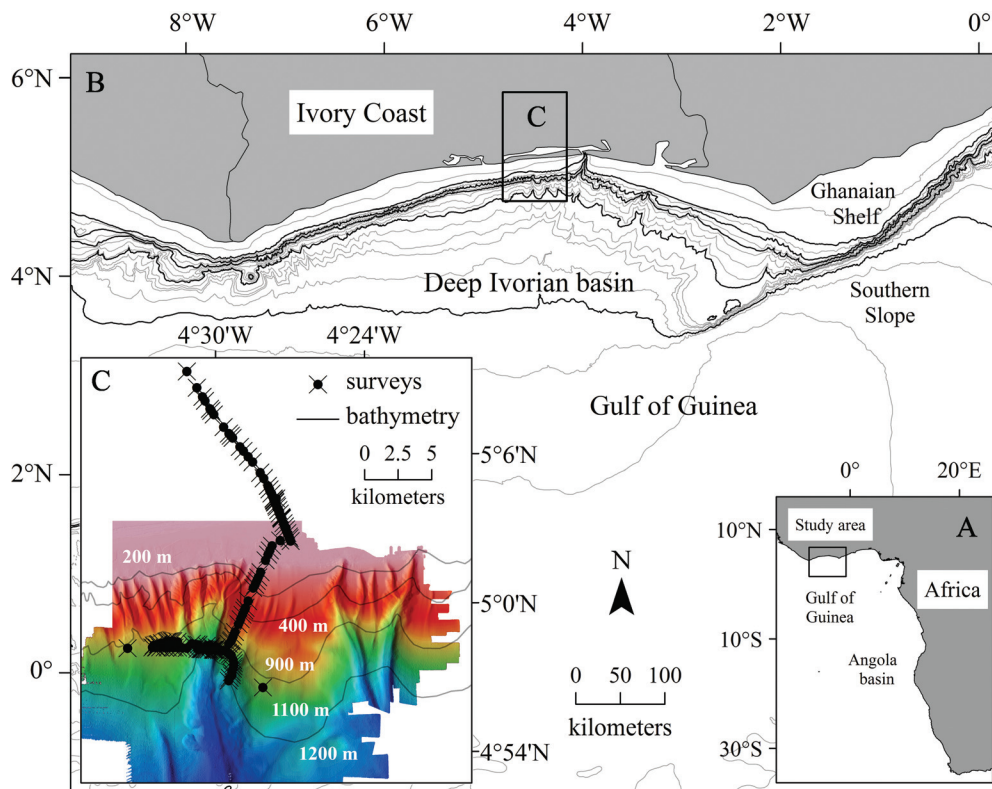


Fig. 1. (A) The Gulf of Guinea in the equatorial Atlantic and the location of the study area. (B) Detailed bathymetric chart of the Ivory Coast and the adjacent areas (Sierra Leone and Ghana). The black box indicates the study area represented in C. Bold bathymetric lines indicate the 100-, 500-, 1000-, 2000-, and 4000-m zones. (C) Detailed bathymetric chart of the surveys in the continental shelf and slope areas. Gridded data taken from the general bathymetric chart of the oceans (GEBCO) Digital Atlas (Centenary Edition).

(Miyake et al. 2005). One of first records of pyrosomids at the seabed was a patch recorded by Monniot and Monniot (1966) off the Cape Verde Islands. *Pyrosoma atlanticum* carcasses have been observed on the Madeira Abyssal Plain (Roe et al. 1990) and *Crambionella orsini* bodies were recorded in canyon systems on the continental slope and rise off Oman in the Arabian Sea (Billett et al. 2006). Yamamoto et al. (2008) provided the most recent evidence of the deposition of jellyfish carcasses (*Nemopilema nomurai*) in the Japan Sea.

The observation of large patches of dead pyrosomids on the seabed off Ivory Coast (West Africa) motivated a detailed quantification of this *P. atlanticum* mass deposition event. This study aims to (1) quantify in detail carcass densities and sizes from a remotely operated vehicle (ROV) video, with relation to depth and topography on the continental shelf and slope, (2) calculate the associated carbon standing stock on the basis of video data and organism-level carbon measurements, and (3) assess the fate of the pyrosomid carcasses at the seabed, and their contribution to the food web. This study highlights the limited understanding of major processes associated with gelatinous zooplankton blooms and the carbon cycle, especially when mass deposition events seem to be a major feature of the world oceans. The work stresses the

importance of organism-level measurements in carbon budget calculations regionally and globally.

Methods

Study site—The Ivory Coast occupies a critical position for the Atlantic Equatorial Current system (Hardman-Mountford 2000) (Fig. 1A). The Guinea Current and the Guinea Undercurrent dominate the physical environment, mediating coastal upwelling and the development of warm and saline waters. Sea surface temperature is reduced during these periods, as well as oxygen, whereas nutrients increase, triggering primary productivity in the area (Mensah and Koranteng 1988). There is no continuous oxygen minimum zone development, such as found in the Arabian Sea (Billett et al. 2006), but oxygen levels approach suboxic values at around 300 m.

The continental shelf off Ivory Coast is characterized by its narrowness, covering some 10,000 km², with the slope normally starting at about 120 m, gaining depth relatively fast (Fig. 1B). From the coast down to 2000 m, in the area between Sassandra and Grand Bassam (near Abidjan), there is a predominantly gently sloped seafloor, with few irregularities except for a marine canyon, known as “le Trou-sans-fond” (the bottomless hole). In the vicinity, a

Table 1. ROV transect data in the depth zones referred to in the text.

Depth zone (m)	Date	<i>n</i> ^a	Depth (m)		Position		Area sampled (m ²)
			Min.	Max.	Start–end (°N)	Start–end (°W)	
0–200	Feb–Mar 06	55	26.3	139.5	5.155–5.028	4.519–4.466	5500
200–400	01 Mar 06	5	200.6	385.5	4.942–5.009	4.468–4.474	500
400–900	Feb–Mar 06	11	510.8	899.6	5.000–4.973	4.478–4.532	1100
900–1100	Feb–Mar 06	30	901.3	1095.7	4.973–4.968	4.533–4.497	3000
1100+	Feb–Mar 06	29	1133.1	1275.7	4.969–4.947	4.499–4.491	2900

^a Each *n* represents one ROV transect (100 m²).

series of submarine canyons and structures dissect the underwater landscape from the outer edge of the shelf and slope down to 2000 m (Fig. 1B,C).

Thaliaceans only represent a minor part of the zooplankton biomass in the Gulf of Guinea. However, they bloom periodically, increasing the living zooplankton biomass significantly and dominating the standing stock. Roger (1982) reported on the high densities of *P. atlanticum*, accounting for 34% of the total zooplankton biomass in the water column, whereas Goy (1977) recorded *P. atlanticum* populations around the shallow thermocline dominating in the Guinea Dome. Le-Borge (1983) estimated that salp blooms off Ivory Coast may occasionally occupy more than 100 km².

ROV video surveys—Data collection: The Baobab oil field (discovered 2001) lies in 1484 m of water off Ivory Coast. ROV surveys conducted between 18 February and 19 March 2006 were used for this quantitative investigation (Table 1). The surveys made several traverses of the continental shelf and slope along seabed oil pipelines, from 26- to 1276-m water depth (Table 1; Fig. 1C). Data were collected by a Sonsub work-class ROV operated from the vessel *DP Reel*. The original data had a geodetic datum of Port Bouet (Abidjan, Ivory Coast 1987 data). Data were recorded from the videos as universal transverse Mercator northings and eastings; these were transformed to latitude and longitude (WGS84) with FRANSON CoordTrans.

ROV video analyses: A total of 309 videos with a mean duration of 20 min were analyzed. Of these, 130 were used in subsequent analysis. The survey videos were visualized and analyzed with VisualReview 6.5 (VisualSoft Limited). Transects were divided into segments representing 100 m² of seafloor area (precision ± 1 m²) using ROV position data; this represented an average of 7 min of video. Size estimations were made by comparison with known dimensions of the pipeline. The field of view was oblique, so size estimations were always performed at the base of the screen, ensuring the highest possible resolution. Biological and pyrosomid carcass data (megafaunal densities, carcass densities, carcass size, carcass condition, and observations of feeding on carcasses) were recorded from videos within each 100-m² sampling unit (Table 1).

All megafaunal organisms that could be identified visually and repeatedly (>50 mm) (Jones et al. 2007) were recorded per 100-m² sampling unit. Taxonomic uncertainties were resolved by taking a still frame of the animal and

comparing it with taxonomic guides (e.g., Koranteng 2001). Expert advice (see Acknowledgments) was also used in the case of a few echinoderms and crustaceans. For quantitative analyses, data were averaged from every 100-m depth interval (*n* in Table 1). Owing to the nature of the survey there were different total areas sampled and hence different numbers of sample units at each 100-m depth interval (Table 1).

Data analyses: Statistical analyses of the carcass density and size and carbon standing stocks at different depth intervals were performed. Data processing was carried out with Minitab 14.0 and graphs were plotted with SigmaPlot 10.0. *Pyrosoma atlanticum* average carcass size and density were recorded for each sampling unit. These were subsequently averaged at each depth interval. Statistical analyses of depth interval medians were performed using the nonparametric Kruskal–Wallis test. The Miller (1981) post hoc nonparametric Tukey-type test (Zar 1999) was used for further comparisons.

Pyrosoma atlanticum carbon analyses—*Pyrosoma atlanticum* carcasses were obtained from the Catalan Sea (northwest Mediterranean) because no samples were available from the Ivory Coast. The carcasses were collected from 650- to 1000-m depth in trawling surveys (OTSB-14 and commercial) during the spring of 2007 (J. Cartes pers. comm.). Carcasses were already at the seabed when collected (freshly deposited), which maximizes the extrapolation potential with the Ivory Coast carcasses observed in video. *Pyrosoma atlanticum* samples were stored at -20°C after capture, and subsequently dried at 80°C for 24 h, and then dried again upon arrival for another 24 h. Samples were disintegrated to powder with a metal blade before analysis. Carbon analyses were performed for inorganic carbon (IC) in an IC CO₂ coulometer and for total carbon (TC) using model 5012 UIC coulometers in triplicate (Johnson et al. 1998). The amount of pyrosomid homogenized material used in the subsample measurements was 12.31 ± 1.51 mg ($n = 5$) for IC, and 11.43 ± 2.31 mg ($n = 12$) for TC. Calibration of the coulometers was verified with pure, dry CaCO₃ standards. IC was determined to be $11.99\% \pm 0.33\%$ (cf. 12.00%), equivalent to $99.90\% \pm 2.80\%$ CaCO₃ ($n = 8$) for IC. TC content of the standard was determined to be $11.98\% \pm 0.01\%$ (cf. 12.00%), equivalent to $99.85\% \pm 0.81\%$ of CaCO₃ ($n = 8$). Organic carbon (OC) was estimated as the difference between TC and IC.

Table 2. *Pyrosoma atlanticum* sample morphometrics and carbon component estimations. TC is total carbon, IC is inorganic carbon, and OC is organic carbon. SD is the standard deviation on the basis of triplicate measurements.

Sample cruise	Date	Depth (m)	Weight (wt, g)		Dry wt: wet wt (%)	Length (mm)	Carbon %		
			Wet	Dry			TC (SD)	IC ^a	OC (SD)
BIOMARE BOU5	28 Dec 07	800	1.801	0.206	11.43	45.9	41.05 (0.71)	0.17	40.88 (0.71)
BIOMARE3B BOU10	17 Sep 07	650	1.046	0.087	8.31	27.8	31.14 (5.71)	0.16	30.98 (5.71)
BIOMARE3 OTSB6	01 Jul 07	650	0.362	0.041	11.32	17.8	29.60 (0.55)	0.18	29.42 (0.55)
BIOMARE2 OTSB2	28 Apr 07	650	1.007	0.135	13.40	35.9	40.15 (0.68)	0.19	39.96 (0.68)

^a No triplicate measurements for IC due to lack of sample material.

An average of the sample carbon components ($n = 4$) was used to estimate the carbon standing stock from the carcasses in the ROV videos: IC = 0.17%, TC = 35.10%, OC = 34.93%. The calibration against four individuals is limiting, but literature data from Davenport and Balazs (1991) revealed OC% data comparable with our results (a dry weight of 39.2%). An equation was used to translate the total length (TL) of the carcasses recorded in the videos to the dry weight: “log dry weight = $-1.804 + 1.692 \log TL$ ” (Mayzaud et al. 2007). Subsequently, the dry weights were converted to carbon per 100 m². The values were converted to standing stocks per square meter in each depth interval, to be comparable with other literature data. An underestimation of the *P. atlanticum* standing stock is possible because when they accumulated in the sediment they formed piles, sometimes to 1 m in height, with potentially greater numbers in channels and troughs. Density counts from video were carried in the two visible dimensions; the actual standing stock is potentially higher than calculated. Densities and the estimated carbon standing stocks were influenced by the presence of the pipelines in all ROV videos. The pipelines act as an artificial trap for drifting carcasses, and they also may attract a higher number of scavengers as a result of accumulation of organic matter and an artificial reef effect.

Results

Sample morphometrics and carbon estimations—*Pyrosoma atlanticum* wet weight ranged from 1.007 to 1.801 g, with dry weights of 0.041 to 0.206 g (Table 2). The dry weight as a percentage of wet weight varied between 8.31% and 13.40% (an average of 11.21%). The length varied from a small specimen of 18 mm to a larger one of 46 mm (Table 2). TC ranged from 29.60% and 41.05% of the dry weight, IC from 0.16% and 0.19% of the dry weight, and OC from 29.42% and 40.88% of the dry weight (Table 2). The dry weight, on average, had 35.10% TC, 34.93% OC, and 0.17% IC.

Pyrosoma atlanticum carcass observations at the sea floor—Continental shelf: Few carcasses were observed rolling or accumulating at shelf depths from 26 to 200 m. Some of the carcasses between 60 and 100 m appeared to have been deposited recently, owing to their smooth appearance. Detritus and macrophyte detritus occurred

on the seafloor (Fig. 2A). The average bottom current speed on the continental shelf was $<0.5 \text{ m s}^{-1}$, as determined by video observations of current flow. Some areas had current speeds up to 2 m s^{-1} . Near-bed currents resuspended *Pyrosoma* carcasses in the water column and actively rolled them along the bottom. No carcasses were trapped along the pipelines on the shelf. The seabed was characterized by a mixture of fine and coarse sediment with biogenic material accumulating along the pipelines (Fig. 2A).

Upper continental slope and canyon: Many *P. atlanticum* carcasses were recorded at the shelf break and the upper slope between 300 and 400 m (>2000 carcasses per 100 m² in some cases) (Fig. 2B). The carcasses appeared to be degrading on both sides of the pipeline or in the vicinity. The seafloor environment was characterized by fine and coarse sediments. In many areas the pipeline was buried, and numerous channels and troughs were observed, with substantial quantities of carcasses accumulating there. The average current speed was $<0.5 \text{ m s}^{-1}$, varying between 0 and 1 m s^{-1} in the majority of cases. At mid-slope depths and along the walls of the canyon (ca. 400–800 m) there was high variability in the number of carcasses, with <100 to >2000 carcasses per 100 m² recorded (Fig. 2C). The pyrosomids were in some cases degrading, forming gelatinous aggregates (coalescence). The current was less than 1 m s^{-1} . The bottom topography was characterized by fine sediment with the sporadic presence of channels and troughs. Toward the bottom of the steep continental slope (ca. 900 m) the number of rolling carcasses decreased. Where the pipeline was buried, many carcasses were observed accumulating in piles and in the troughs, and in much of the video the carcasses were transported across the field of view by a strong current between 1 and 2 m s^{-1} (Fig. 2D,E).

Lower continental slope: A relatively tranquil seabed environment with a very patchy distribution of the pyrosomid bodies was recorded at the lower continental slope (ca. 1000 m). The density varied between <20 to >2000 carcasses per 100 m² in some cases, and the carcasses were in advanced degradation, starting decomposition, with an increase in the number of coalescent gelatinous aggregates rolling along the bottom. In the majority of cases current speeds were very low. Carcasses were not moving and formed patches close to the pipelines or rolled very slowly along the seabed in small groups

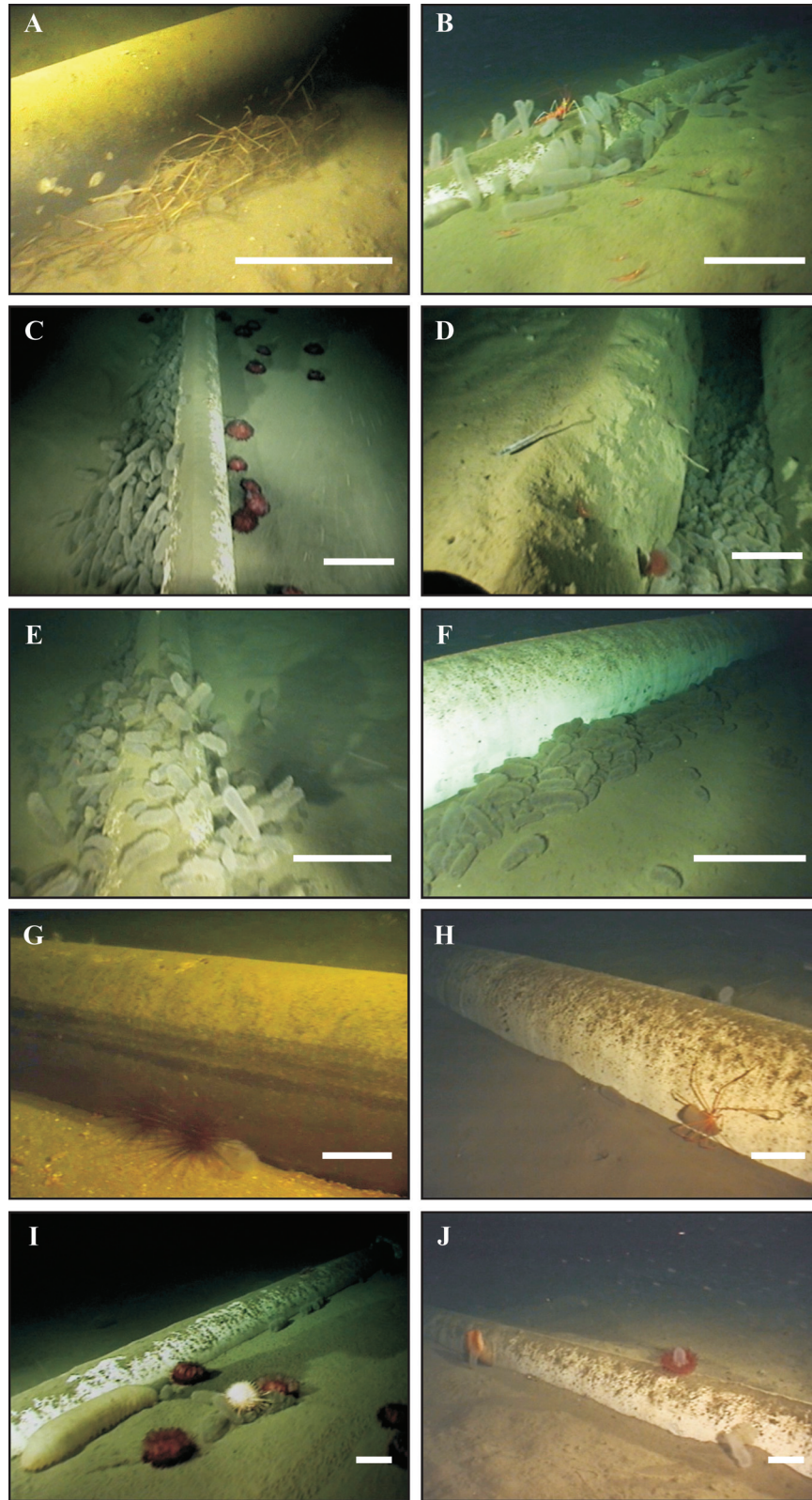


Fig. 2. *Pyrosoma atlanticum* observations in the continental shelf and slope areas in the surveys at (A) 105 m, (B) 379 m, (C) 744 m, (D) 952 m, (E) 954 m, and (F) 1244 m. The carcasses were observed accumulating in patches along the pipelines, and in troughs and mounds in the sediment. Megafaunal taxa were observed feeding on *P. atlanticum* carcasses: (G) *Diadema* sp. at 107 m, (H) *Colossendeis* sp. at 1198 m, (I) *Phormosoma* sp. and a regular echinoid at 827 m, and (J) *Actinostola* sp. and *A. aurelia* at 889 m. Scale bars refer to 25 cm from (A) to (F) and to 10 cm from (G) to (J).

Table 3. *Pyrosoma atlanticum* carcass density and size, along with the estimated carbon standing stock per unit area in the depth zones referred to in the text. TC, total carbon; IC, inorganic carbon; OC, organic carbon.

Depth zone (m)	Mean carcasses (100 m ⁻²)		Mean carbon standing stock (g C m ⁻²)		
	Density (min–max)	Size (cm) (min–max)	TC (min–max)	IC (min–max)	OC (min–max)
0–200	1.87 (0–19)	7.9 (4–14)	0.01 (8×10 ⁻⁴ –0.70)	6.5×10 ⁻⁵ (4.5×10 ⁻⁶ –3.7×10 ⁻⁴)	0.01 (8.4×10 ⁻⁴ –0.07)
200–400	1077 (25–4198)	14.4 (13–16)	5.40 (0.10–20.35)	2.9×10 ⁻² (5.7×10 ⁻⁴ –0.10)	5.37 (0.10–20.24)
400–900	908.18 (80–3011)	14.72 (12–18)	5.29 (0.38–22.24)	2.8×10 ⁻² (2×10 ⁻³ –0.11)	5.26 (0.38–22.12)
900–1100	836.66 (80–3020)	15.1 (11–19)	5.08 (0.43–22.74)	2.7×10 ⁻² (2.3×10 ⁻⁴ –0.12)	5.05 (0.43–22.63)
1100+	707.41 (11–2800)	14.37 (11–18)	4.23 (0.04–20.75)	2.3×10 ⁻² (2×10 ⁻⁴ –0.11)	4.21 (0.04–20.65)

(Fig. 2F). A fine sediment environment with many small seabed ripples (wavelength <200 mm) composed the landscape. Occasional terrigenous and neritic plant material was seen.

Pyrosoma atlanticum carcasses—Density and size: Density of pyrosomid carcasses was found to be significantly different between the five depth zones (Table 3; Kruskal–Wallis, $H = 92.64$, $df = 4$, $p < 0.01$). The density of the moribund pyrosomids was significantly lower between 26 and 200 m than the deeper zones (post hoc analysis $p < 0.05$). Carcass density increased significantly from 200 to 400 m, coinciding with the shelf break (Table 3). The maximum density was recorded at 385 m, with 4200 carcasses per 100 m² (note the clear contrast between the shelf and the start of the slope in Fig. 3). At midslope and toward the bottom of the upper slope (400–900 m) the

pyrosomid density decreased slightly (Table 3), but patchiness of the carcass distribution increased (Fig. 3). Beyond these depths, at the bottom of the steep upper slope and on the lower slope (>900 m), the density decreased further with increasing depth (Table 3). In the canyon wall regions *Pyrosoma* density was low and immediately outside the canyon no carcasses were found (Fig. 3).

Carcass size, as with density, was significantly different between depth zones (Kruskal–Wallis, $H = 42.62$, $df = 4$, $p < 0.01$). *Pyrosoma* were significantly smaller (post hoc analysis $p < 0.05$) shallower than 200 m (Table 3). The average size of the carcasses almost doubled at deeper than 200 m and increased slightly, but not significantly, with depth to 1100 m (Table 3).

Carbon standing stock: The associated OC was significantly different between depth bands (OC: Kruskal–

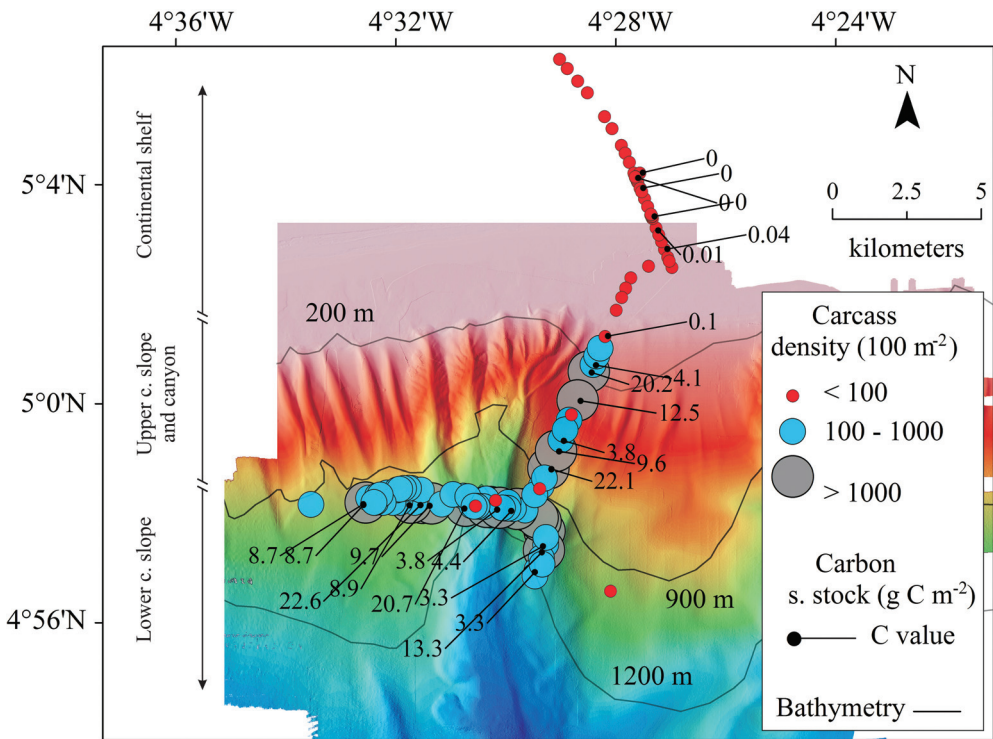


Fig. 3. *Pyrosoma atlanticum* carcass density (per 100 m²) distribution, and the estimated carbon standing stock in grams of organic carbon per 1 m² (g C m⁻²) in the seabed surveys of the continental shelf and slope.

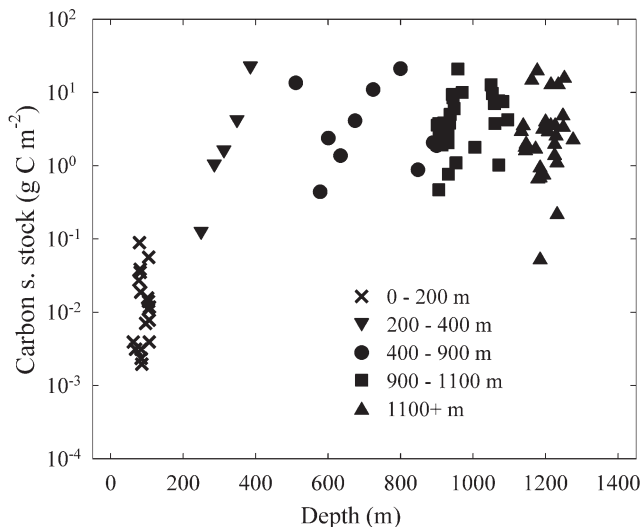


Fig. 4. The trend in the calculated carcass carbon standing stock (g C m^{-2}) against depth for the five depth zones in the surveys (y-axis in log scale).

Wallis, $H = 48.53$, $df = 4$, $p < 0.01$). The OC standing stock estimations over the month of the survey were very small, from 26 to 200 m (Table 3). A significant difference was observed between 200 m and the deeper depth bands (post hoc analysis $p < 0.05$). In the 200–400-m depth band the average OC standing stock significantly increased (Table 3), with a maximum at 385 m (Table 3; Fig. 3 for location and Fig. 4 for trend). From 400 to 900 m the OC decreased slightly, but the maximum was greater than in the previous depth band (Table 3; Figs. 3, 4). There was a decrease in the average OC standing stock in the 900–1100-m depth band, but the greatest localized calculation occurred between these depths (Table 3; Figs. 3, 4). The deepest parts of the survey (1100+ m) showed a further decrease in the average OC standing stock, although dense patches were still seen (Table 3; Figs. 3, 4).

Pyrosoma atlanticum carcasses in the benthic system—Associated megafaunal community: A total of 57 species from 8 phyla were recorded on and around hard (pipelines) and soft substrata (Table 4). In the 26- to 200-m depth zone the Echinodermata had the highest density, with the echinoid *Diadema* sp. found commonly on the pipeline (Table 4). Comatulid crinoids were also abundant in vast aggregations on the pipeline. Fish were present in high numbers from 26- to 200-m depth; unfortunately the most abundant fish could not be identified from the video. *Trachurus trachurus* was highly abundant (Table 4). In the Cnidaria, *Pennatulula* sp. was common on sediment and a red alcyonacean was observed regularly attached to the pipeline. Within the Crustacea only the shrimp *Parapenaeus* sp. occurred at this shallow depth. Polychaetes were also present, observed as mounds in the sediment (Table 4).

In the 200–400-m depth zone fish had reduced richness, with Scorpaeniformes most abundant (Table 4). The crustaceans *Galathea* sp. and *Parapenaeus* sp. dominated the benthic community. Crinoids were also particularly abundant (Table 4). From 400 to 900 m only three fish

species were present. *Phormosoma* sp. (Echinoid) was abundant (Table 4). The Ophiopodidae (ophiuroidea) occurred on the soft sediment (Table 4). The 900–1000-m zone was populated by a similar suite of species as in the previous zone but at lower densities. The Cnidarian *Actinostola* sp. attached to the pipeline and sediment and was found at notably higher densities in this depth band (Table 4). *Parapenaeus* sp. were again common. In the deepest transect (1100+ m) no species were particularly abundant, but almost every phylum was represented. *Actinostola* sp. had the greatest density (Table 4).

Direct feeding on Pyrosoma atlanticum carcasses—Four echinoderms (*Cidaris* sp., *Diadema* sp., “white Echinoid,” and *Phormosoma* sp.; Fig. 2G,I), three cnidarians (“white Actinaria,” *Actinoscyphia aurelia*, and *Actinostola* sp.; Fig. 2J), and one arthropod (*Colossendeis* sp.; Fig. 2H) were observed directly consuming carcasses 63 times. Scorpaeniformes and a few elasmobranchs were always observed in the vicinity of carcasses. Within the echinodermata, echinoids used their spines to trap carcasses (Fig. 2G,I). The asteroid *Solaster* sp. was not seen scavenging directly, but there was an instance where an individual appeared to be engulfing a *P. atlanticum* corpse. Actinaria (cnidarians) were regularly observed feeding or attempting to feed on carcasses (engulfing whole pyrosomids) wherever they were found (Fig. 2J). *Colossendeis* sp. intercepted and manipulated the carcasses with its legs (Fig. 2H). No microbial assemblages were directly quantified, but in many instances carcasses seemed to have a white matlike covering on their surface. This was particularly observed in the deeper carcasses, which have been decomposing for a longer time.

Discussion

Gelatinous detritus at the seafloor—Spatiotemporal patterns in carcasses: Jellyfish and thaliaceans are reported to be distributed patchily in their environment (Graham 2001), but may rapidly increase in many oceanic areas, altering ecosystem balances (Mills 1995). Here, mass blooming of pyrosomids has led to significant transport of corpses from the coastal margins to the deep sea. This finding indicates that gelatinous zooplankton populations have a major effect on large-scale processes, adding new evidence into the fate of their biomass once dead and their importance in the carbon cycle. Future changes in abundance, and biomass linked to the projected global anthropogenic and climatic influence, may change their role and importance in nutrient and element cycling. Coastal margins tend to accumulate gelatinous zooplankton owing to physical barriers being compressed along the shoreline. For example, the widely distributed *Salpa democratica* has occurred in dense aggregations in Australia, New Zealand, Japan, and South Africa (Gibbons 1996). Populations of the same species and *Salpa fusiformis* have been reported in the Mediterranean Sea, and *Salpa aspera* in the Carolina Slope (Madin et al. 2006). Dense populations of *Pegea confoederata* have been widely recorded in the Arabian Sea (Ramaswamy et al. 2005).

Table. 4. Megafaunal taxa observed off Ivory Coast at each depth zone, along with the substratum type and the density per unit area. Also included are the observed feeding events of megafauna on *Pyrosoma atlanticum* carcasses.

Depth zone (m)	0–200	200–400	400–900	900–1100	1100+
Substratum type	Pipeline fine + coarse sediment	Pipeline fine sediment	Pipeline fine sediment + deep channels	Pipeline fine sediment + deep channels	Pipeline fine sediment
Density (per 100 m ²)					
Chordata					
<i>Balistes</i> sp.	1.72	0	0	0	0
<i>Bathyraja</i> sp.	0.01	0	0.09	0.03	0
<i>Bathysolea</i> sp.	0.01	0	0	0	0
<i>Branchiostegus semifasciatus</i>	0.03	0	0	0	0
<i>Cephalopholis taeniops</i>	0.01	0	0	0	0
Chimaera	0.01	0	0	0	0
<i>Dentex</i> sp.	2.36	0.40	0	0	0
<i>Epinephelus</i> sp.	0.12	2.20	0	0	0
<i>Hoplostethus atlanticus</i>	0	2.20	0	0	0
<i>Muraena</i> sp.	0.14	0	0	0	0
<i>Mycteroperca</i> sp.	0.49	0.20	0	0	0
<i>Oxynotus centrina</i> ^b	0	0.20	0	0	0
<i>Pagrus</i> sp.	0.07	0	0	0	0
<i>Pseudupeneus prayensis</i>	0.69	0	0	0	0
<i>Psychrolutes</i> sp.	0	0	0.18	0	0
<i>Sargocentron</i> sp.	0.56	0	0	0	0
Sciaenidae	3.49	0.20	0	0	0
Scorpaeniformes ^b	11.50	7.40	1.00	0	0
<i>Serranus cabrilla</i>	1.38	0	0	0	0
<i>Sparus</i> sp.	0.20	0	0	0	0
<i>Trachurus trachurus</i>	25.45	0	0	0	0
<i>Zeus faber</i>	0.03	0	0	0	0
Indet. fish 1	86.69	0	0	0	0
Indet. fish 2	0	0	0	0.03	0.10
Indet. fish 3	0	0	0	0	0.24
Indet. fish 4	0	0	0	0.10	0.10
Echinodermata					
<i>Marthasterias glacialis</i>	0.02	0	0	0	0
Indet. red asteroid	0.33	0.20	0	0	0
<i>Henricia</i> sp.	0	0	0.64	0	0
Crinoidea	16.11	58.40	0	0	0
<i>Cidaris</i> sp. ^a	2.31	0	0.09	0	0
<i>Diadema</i> sp. ^a	106.40	2.00	0	0	0
Indet. white echinoid ^a	0	0	0.82	0.53	0.83
<i>Phormosoma</i> sp. ^a	0	0	193.64	20.77	2.69
<i>Mesothuria</i> sp.	0	0	0.36	0.47	0.41
Ophiopodidae	0	0	14.82	11.10	0
Indet. red ophiuroid	0.15	0	0	0	0
<i>Solaster</i> sp. ^b	0	0	0.09	0.17	0.03
Cnidaria					
Indet. white Actinaria ^a					
Indet. red Actinaria	1.04	0.60	0.09	0	0
<i>Actinoscyphia aurelia</i> ^a	0	0	0.36	1.47	2.66
<i>Actinostola</i> sp. ^a	0	0	1.91	4.37	3.28
<i>Pennatula</i> sp.	13.15	0	0	0.03	1.38
Indet. red soft coral	11.55	0	0	0	0
Crustacea					
<i>Galathea</i> sp. ^b	0.04	71.20	0	0	0
Majidae	0.18	0	0	0	0
<i>Neolithodes grimaldi</i> ^b	0	0.20	0.09	0	0
<i>Neolithodes</i> sp. ^b	0	0	0	0	0.03
<i>Pagurus</i> sp.	0	0	0	0	0
<i>Paralomis</i> sp.	0	0	0	0.03	0.07
<i>Parapenaeus</i> sp. ^b	14.76	160	2.18	33.70	3.66
Polychaeta					
Indet. annelid	10.13	0.6	0.73	0	0

Table. 4. Continued.

Depth zone (m)	0–200	200–400	400–900	900–1100	1100+
Substratum type	Pipeline fine + coarse sediment	Pipeline fine sediment	Pipeline fine sediment + deep channels	Pipeline fine sediment + deep channels	Pipeline fine sediment
Mollusca					
Gastropods	0.09	0	0	0	0
<i>Octopus</i> sp.	0.20	0.04	0.27	0.03	0
<i>Sepia</i> sp.	1.02	0	0	0	0
Arthropoda					
<i>Colossendeis</i> sp. ^a	0	0	0.09	0.13	0.86
Urochordata					
Ascidians	0.07	0	0	0	0

^a Observed directly feeding on *Pyrosoma atlanticum* carcasses.

^b Potential feeders on the carcasses.

As seen here and in Le-Borgne (1983), pyrosomatidae may accumulate in dense numbers in African waters. At present, when these extensive blooms collapse and sink, they transfer large amounts of organic carbon to both coastal and deep-sea environments. The observation of vast quantities of *Pyrosoma atlanticum* moribund bodies at the seabed adds new evidence toward a major “gelatinous pathway” of carbon to the ocean’s interior (Billett et al. 2006).

Off Ivory Coast, few pyrosomid carcasses were recorded on the continental shelf (26–200 m). The shelf environment is highly dynamic, especially shallower than 50 m. The few carcasses observed were not transported laterally along the shelf, but downward. They were directed toward the shelf break, in some cases along the pipelines (acting as an artificial trapping structure), being rolled along the bottom or suspended in the water column close to the seafloor. The slope area represented a major change in topographic complexity. As a consequence, large accumulations of carcasses occurred. The greater decomposition of the pyrosomids with increasing depth led to the formation of elongated gelatinous aggregates. The coalescence of several carcasses and formation of gelatinous patches were similar to the jelly lakes observed on the seabed of the Arabian Sea and caused by the decomposition of the scyphomedusan *C. orsini* (Billett et al. 2006). The pipeline was present above the seabed in many instances along the slope. Structures such as pipelines were observed to intercept and accumulate pyrosomids, translating to elevated carbon standing stocks. However, in areas recorded without pipelines, vast numbers of pyrosomids were observed on the seafloor or in depressions. There were no data from adjacent canyons without any seabed features, but it is highly possible that they trap vast numbers of carcasses at sites of high topographic complexity along the whole slope.

The maximum density of *Pyrosoma* carcasses occurred in canyon settings and on the open slope (especially in deep channels with no pipeline laid). This was in contrast to *C. orsini*, where the greatest amounts of jelly detritus occurred on the continental rise in the Arabian Sea (Billett et al. 2006). This may be related to spatiotemporal variation (carcasses may eventually have accumulated on the

continental rise after a time period), or to differences in the topographic complexity of the Ivory Coast and Oman slope areas. There is also the possibility that the pipelines retard the transport to the continental rise at depths where currents are slow, and the carcasses just stay at the seabed. It is likely that greater quantities of *Pyrosoma* would be transported deeper than observed here because many individuals were seen being transported downslope below 950 m. The video data only cover a limited area. The results support the hypothesis that canyon systems are important in the transfer of organic matter to the deep ocean (Harrold et al. 1998). The patchy distribution of the gelatinous detritus on the Ivory Coast margin was a consequence of the bottom complexity at fine and broad scales, which includes the presence of pipelines and channels. Cacchione et al. (1978) commented on the accumulation of *S. aspera* carcasses and salp-like material in hollows and furrows in the slope area off New England (NW Atlantic). They also observed “string-like aggregations of mucous material,” which could well resemble the coalescent material off Ivory Coast.

Carbon export: The estimated organic carbon standing stocks during the month of the survey were highly dependent on the density and size of the pyrosomid aggregations recorded. They were very patchy and in <100-m distance, the carbon stocks changed from about 1 g C m⁻² to >20 g C m⁻². The greatest amounts occurred on the upper and lower continental slope within channels and areas of high topographic complexity (also associated with the pipelines). The carbon standing stock in carcasses of gelatinous zooplankton is an important feature of ocean biogeochemical cycles that has generally been overlooked. Compared with sediment trap flux data in the area (1.09 g C m⁻² yr⁻¹ at 696 m) (Wefer and Fischer 1993) (Table 5), the average gelatinous carbon standing stock estimated in this study, most likely from one single deposition event, was always higher (>4 g C m⁻² in the upper and lower slope as a whole). At the same depth of the sediment trap data, carcass standing stocks were above 20 g C m⁻² in less than 2 months. Gelatinous zooplankton also release DOC, contributing to the pool of total OC. Hansson and

Table 5. A selection of organism-level (gelatinous zooplankton) organic carbon (OC) standing stocks, fluxes, and sediment trap fluxes in the world oceans.

Organism level	Depth (m)	Carbon origin	OC standing stock flux	Reference
Arabian Sea	3196	<i>Crambionella orsini</i> carcasses	1.5 g C m ⁻²	Billett et al. 2006
Arabian Sea	3188	"	31.3 g C m ⁻²	"
Arabian Sea	3314	"	78.0 g C m ⁻²	"
Monterey Bay	200–2979	<i>Bathochordaeus charon</i> houses	7.6 g C m ⁻² yr ⁻¹	Robison et al. 2005
Sargasso Sea	>1500	<i>Salpa aspera</i> carcasses	909 mg C m ⁻²	Wiebe et al. (1979)
Shetland Islands	-	<i>Salpa thompsoni</i> carcasses	560 mg C m ⁻²	Nishikawa et al. (1995)
Sediment trap				
Cape Blanc	730	Open ocean	3.76 g C m ⁻² yr ⁻¹	Fischer et al. 2000
Guinea Basin	859	"	2.94 g C m ⁻² yr ⁻¹	"
Guinea Basin	3965	"	2.18 g C m ⁻² yr ⁻¹	"
Guinea Basin	696	"	1.09 g C m ⁻² yr ⁻¹	Wefer and Fischer 1993
Guinea Basin	3921	"	2.19 g C m ⁻² yr ⁻¹	"
Arabian Sea	828	Coastal	13.5 g C m ⁻² yr ⁻¹	Honjo et al. 1999
Arabian Sea	903	"	17.2 g C m ⁻² yr ⁻¹	"
Arabian Sea	1974	"	17.4 g C m ⁻² yr ⁻¹	"
Arabian Sea	800	Open ocean	5.7 g C m ⁻² yr ⁻¹	"
Walvis Ridge	1648	"	3.83 g C m ⁻² yr ⁻¹	Wefer and Fischer 1993
Walvis Ridge	599	"	5.07 g C m ⁻² yr ⁻¹	"

Norrman (1995) calculated 0.012 mg C g wet wt⁻¹ d⁻¹ release in the jellyfish *Aurelia aurita* decomposing carcasses. These DOC data, coupled with major OC inputs from the decomposing carcasses as well as fecal pellets (Wiebe et al. 1979), will have contributed significant quantities to the carbon pool and to export from continental shelves and slopes globally.

Pyrosoma atlanticum has one of the highest carbon contents (see Table 6) recorded in gelatinous animals studied to date (Davenport and Balazs 1991). This has major implications in the role of pyrosomatidae as vectors of carbon transport in the global oceans because they have the potential to export more carbon per unit area than other bloom-forming species. In the study of the elemental composition of gelatinous animals, inter- and intraspecific variation is a common feature (e.g., owing to feeding preferences, environment, and life history). This may add uncertainties about the carbon flux at any time and space. The available literature used conversions from published standard observations (Billett et al. 2006), which should be avoided if it is possible to measure carbon directly from the species under investigation.

Organism-level carbon measurements importance: Rapidly sinking, carbon-enriched vectors such as pyrosomids, larvacean houses, and jellyfish carcasses (Robison et al. 2005; Billett et al. 2006) are not detected and measured by traditional sampling methods in the water column (sediment traps). Yet, they are important contributors to regional and global carbon inventories, and may have been ignored in vertical nutrient fluxes and budgets calculations. West et al. (2009) presented data on the influence of decomposing jellyfish on nutrients in the water column, with increases in dissolved organic nitrogen and phosphorus between 8 and 25 times greater than in controls. There were significant differences when comparing the Ivory Coast *Pyrosoma* carbon measurements over a period of 2 months and the sediment trap data in the area (Table 5). Average standing stocks above 5 g C m⁻² over 2 months seen here were similar to that estimated by Robison et al. (2005) of 7.6 g C m⁻² yr⁻¹ from larvacean houses off Monterey Bay, which matched Pilskaln et al. (1996) 7.2 g C m⁻² yr⁻¹ sediment trap benthic flux at the midslope (Table 5). Billett et al. (2006) in the Arabian Sea reported jellyfish standing stocks of carbon between 1.5 and

Table 6. *Pyrosoma atlanticum* percentage of dry weight to wet weight (dry wt : wet wt %), inorganic carbon percentage (IC), and organic carbon percentage (OC) composition along with other thaliacean and jellyfish species values from the literature.

Species	Dry wt : wet wt (%)	IC (%)	OC (%)	Reference
<i>Pyrosoma atlanticum</i>	11.21	0.17	34.9	This study
"	6.31	-	39.2	Davenport and Balazs 1991
<i>Thalia democratica</i>	8.04	-	18	Heron et al. 1988
<i>Salpa fusiformis</i>	4.7	-	11.9	Clarke et al. 1992
"	3.8	-	17–22	Dusbischar et al. 2006
<i>Cyclosalpa bakeri</i>	-	-	3.2	Madin and Purcell 1992

78.0 g m⁻², which in some places were substantially higher than Honjo et al. (1999) sediment trap flux estimations (between 3.3 g C m⁻² yr⁻¹ and 17.4 g C m⁻² yr⁻¹) (Table 5). The evidence that dead carcasses of animals effectively provide major carbon pathways to the seabed has been gathered very slowly (Billett et al. 2006). In addition, direct quantification of the fluxes and the origins are difficult and may rely on advanced technology and effective spatiotemporal sampling. Particulate carbon fluxes from the photic zone (understanding by “particulate” any vertically directed flux of particles, organism discards, or organisms themselves) effectively sink while being remineralized on their way down, releasing nutrients and elemental components in the water column.

Gelatinous carcasses in the food web—Off Ivory Coast several species belonging to different phyla were recorded directly feeding on *P. atlanticum* carcasses. However, it is difficult to assess if animals are attracted to the pipeline as a hard substratum or by a substantial source of food from carcasses. It is most likely a combination of the two. An artificial structure, combined with a large input of organic matter (in this case from carcasses), will attract scavengers and detritivores that dominate at times the benthic community (see Fig. 2C).

Rapidly sinking pyrosomid bodies off the Ivory Coast will have made a substantial contribution to benthic energy supply. Pyrosomids appeared to be actively fed on by crustaceans, echinoderms, cnidarians, and arthropods. Fish, mainly Scorpaeniformes, were always close to the carcasses, but they were not observed feeding directly on the *Pyrosoma*. The limited literature suggests that feeding opportunities are created by carcasses in other areas. A crustacean (*Munidopsis* sp.) and an echinoderm (*Hyphalaster inermis*) were observed close to a moribund pyrosomid in the Madeira Abyssal Plain at 5440 m (Roe et al. 1990). Duggins (1981) also recorded a sea urchin feeding on salp carcasses in Alaska. Fish have also been recorded feeding on pyrosomids (see Harbison 1998 and references therein).

The notion of gelatinous carcasses as rare items in trophic webs (Moline et al. 2004) is not supported by the observations in the benthic system off Ivory Coast. Gelatinous zooplankton corpses are food parcels to benthic communities, with many animals observed feeding on this resource (Harbison 1998). Yamamoto et al. (2008) observed dense beds of ophiuroids (*Ophiura sarsii*), anemones, shrimps (*Pandalopsis japonica*), and molluscs (*Chionoecetes opilio*) close to the carcasses of *N. nomurai* in the Sea of Japan. Billett et al. (2006) saw no evidence that the jelly detritus was a direct food source for benthic invertebrates. In the Arabian Sea, and probably in all systems, the high organic carbon standing stocks are eventually channeled through bacteria. Protozoans may also channel part of the organic carbon, since they are known to enter thaliacean fecal pellets, reducing the bacterial populations (Pomeroy et al. 1984). If the same applies for carcasses, then both bacteria and protozoa will consume and metabolize the available carbon (Yoon et al. 1996). Off Ivory Coast, *Pyrosoma atlanticum* carcasses were observed covered at times by a mat-like substance of a white color, which may

indicate that their carbon is channeled through bacteria to benthic communities. Titelman et al. (2006) have shown experimentally that gelatinous detritus originating in jellyfish can be decomposed within a week by bacterial activity. If this short time frame applied to pyrosomids is uncertain, but based on the state of the carcasses at the bottom, it will seem that their footprint will last much longer than the jellyfish. Over large areas, the ultimate fate of gelatinous carbon will certainly be its incorporation to the detrital food web and the sediments through microbial pathways.

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