

Pyrosome consumption by benthic organisms during blooms in the northeast Pacific and Gulf of Mexico

In the fall of 2016 large populations of pyrosomes, preliminarily identified as *Pyrosoma atlanticum* (Péron, 1804), bloomed in the Gulf of Mexico (C. Du Preez, *personal observation*) and, in the spring and summer of 2017, a bloom occurred in the shelf and off-shore waters from Alaska, through British Columbia, and south to Oregon (I. Perry and M. Galbraith, *personal communications*). Pyrosomes are a member of the Thaliacean class of colonial pelagic tunicates that also includes salps and doliolids. Pyrosomes are historically rare in northern waters (Van Soest 1981) because they typically live in warm waters from 50° N to 50° S, such as in the Gulf of Mexico. The bloom that occurred in British Columbia during the summer of 2017 is the first recorded pyrosome bloom in these waters. Like other gelatinous zooplankton, these free-floating colonies sink rapidly when they die (Lebrato et al. 2013) and *P. atlanticum* undertake daily vertical migrations (Andersen et al. 1992). It is very likely, therefore, that these blooms affect benthic food webs.

In September 2016 and May and July of 2017, three research expeditions collecting benthic imagery sailed the areas of these pyrosome blooms. The first of these expeditions took place within the Northern Gulf of Mexico, in the Bureau of Ocean Energy Management (BOEM) lease block Vioska Knoll 906 (VK906; 29°04.191' N, 88°22.573' W). VK906 is typified by a known *Lophelia pertusa* reef. This survey was conducted on board the DSV *Ocean Inspector* using the *Global Explorer* remotely operated vehicle (ROV), between 17 September and 5 October 2016. The second survey aboard the CCGS *John P. Tully* and using the ROV *ROPOS* sailed within the Hecate Strait and Queen Charlotte Sound Glass Sponge Reefs Marine Protected Area (HSQCS-MPA) during 9–23 May 2017. The HSQCS-MPA is located on the continental shelf of British Columbia and has discontinuous glass sponge reefs between 53°24.084' and 51°14.565' N and 128°40.593' and 130°54.403' W. The third survey, also on board the CCGS *John P. Tully* using the “BOOTS” drop camera system (Bathyal Ocean Observation and Televideo System), sailed off-shore of Vancouver Island between 18 July and 1 August 2017 over the Dellwood (50°44.817' N,

130°54.322' W) and the Union (49°32.763' N, 132°42.150' W) seamounts within the Offshore Pacific Area of Interest (a potential future Marine Protected Area).

On and around the *L. pertusa* reefs in the Gulf of Mexico, we repeatedly observed a squat lobster, *Eumunida picta* (Smith, 1883) (Fig. 1a), a sea urchin, *Cidaroida* sp. (Fig. 1b), two species of anemones, an unidentified Actinaria sp. 1 (Fig. 1b, c) and *Ceriantheopsis americana* (Carlgren, 1912) (Fig. 1c), and the crab cf *Bathynectes longispina* (Stimpson, 1871) (Fig. 1d) feeding directly on pyrosomes between 395 and 412 m depth (Video S1). On the sponge reefs, we also observed a longhorn decorator crab, *Chorilia longipes* (Dana, 1851), feeding on a pyrosome at 172 m depth (Fig. 1e; Video S2). On the seamounts, two species of anemones, cf *Cribrinopsis fernaldi* (Siebert & Spaulding, 1976) (Fig. 1f, 573 m) and Actinaria sp. 2 (Fig. 1g, 1,429 m), tanner crabs, (*Chionoecetes* sp.: Fig. 1h, two observations at 572 and 1,821 m), brittle stars (Ophiuroidea sp.: Fig. 1i, 2,102 m), and a sea star (cf *Cheiraster dawsoni* (Verrill, 1880: Fig. 1j, 573 m) were directly feeding on pyrosomes (Video S3). These species, which were observed across a wide depth range (172–2,102 m), represent three phyla. These observations suggest that a wide variety of organisms in a large portion of the deep sea can directly consume pyrosomes. Our observations are, to the best of our knowledge, the first published reports of benthic organisms consuming pyrosomes in the Gulf of Mexico and northeast Pacific. These observations expand the work begun by Roe et al. (1990) and Lebrato and Jones (2009) and greatly increase the number of benthic species known to consume pyrosomes (from 22 to 33, Table 1). Despite the wide geographic distance between our observations and those of Lebrato and Jones (2009) (Table 1), there is a great deal of taxonomic similarity in the species observed consuming pyrosomes. This apparent global similarity may help guide research into the impacts of blooms on benthic systems where previous observations are lacking.

Benthic marine communities outside of the euphotic zone largely rely on the sinking of particulate organic carbon (predominantly plankton) from surface waters for food. Global climate change is predicted to change the composition of plankton assemblages from diatoms to microscopic picoplankton (Bopp et al. 2005). This shift will likely transfer less energy to the seafloor, raising questions about the consequences for deep-sea communities that are already food limited (Sweetman et al. 2017). However, in some regions, episodic blooms of gelatinous zooplankton and the resulting “jelly falls,” or the large depositions of gelatinous material to the benthos, may help balance the energy deficit in deep waters (Smith et al. 2014). Consequently, understanding how benthic

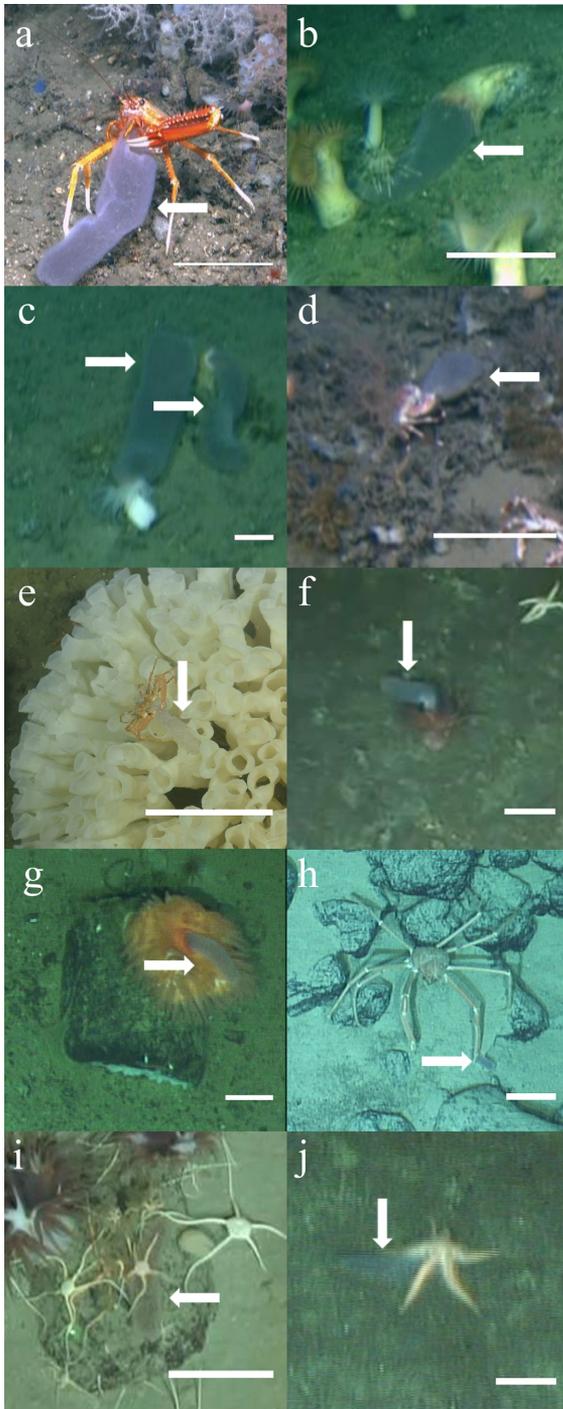


FIG. 1. Benthic organisms observed feeding on *Pyrosoma atlanticum* during (a–d) a mass bloom in the northern Gulf of Mexico in the fall of 2016 and (e–j) an anomalous bloom off of the coast of British Columbia, Canada in the spring and summer of 2017. *Eumunida picta* (a), an unidentified Actinaria (species 1, b, c), an unidentified Cidaroida sp. (b), *Ceriantheopsis americana* (c), and cf *Bathynectes longispina* (d) were observed feeding on pyrosomes on Vioska Knoll 906 in the Northern

organisms use the energy provided by sinking gelatinous zooplankton may help us predict how these systems will respond to a changing ocean.

There are two pathways through which jelly falls can enter the benthic food web. The first is through microbial decomposition and entrainment in the microbial loop (Lebrato et al. 2012). But microbial decomposition can also decrease oxygen levels (West et al. 2009) and potentially limit the organisms that can benefit from the episodic pulse of food. The second pathway is as a direct food source for some benthic organisms (Roe et al. 1990, Bulman et al. 2002, Lebrato and Jones 2009, Lebrato et al. 2012). The effect of gelatinous zooplankton detritus on benthic food webs was long thought to be minimal due to their relatively low energy content compared to other common allochthonous sources (e.g., fish, algae). However, *P. atlanticum* is among the most energy dense gelatinous zooplankton studied (~35% of dry mass is organic carbon) and has high sinking rates, which reduces the amount of remineralization during its descent through the water column. This rapid sinking rate maximizes the amount of energy and nutrients exported from pelagic zones to the benthic system (Lebrato and Jones 2009, Lebrato et al. 2013). Visual observations of jelly falls confirm that the amount of carbon delivered to the seafloor by these bloom events can approach, or even exceed, the estimated annual downward flux of non-gelatinous carbon in the system (Billett et al. 2006, Lebrato and Jones 2009). Accordingly, pyrosome blooms likely have significant implications for the structure and function of benthic communities. For example, food falls can stimulate reproduction and immigration in food-limited fauna, thereby increasing the populations of organisms capable of capitalizing on this episodic food source (Wigham et al. 2003). Although we present observations of direct consumption by organisms based on high-definition visual observations, these blooms certainly transferred energy to the benthos via microbial decomposition as well. In systems with filter-feeding foundation species, such as the glass sponge and *L. pertusa* reefs where many of our observations occurred, stimulation of the microbial community by this influx of energy may have interesting cascading consequences for the food web, such as an increase in dissolved organic carbon available for sponges and corals.

(Fig. 1. *Continued*)

Gulf of Mexico. *Chorilia longipes* (e) was observed in the Hecate Strait and Queen Charlotte Sound Glass Sponge Reef Marine Protected Area (MPA) while cf *Cribrinopsis fernaldi* (f), an unidentified Actinaria (species 2, g), *Chionoecetes* sp. (h), unidentified Ophiuroidea (i), and cf *Cheiraster dawsoni* (j) were observed feeding on pyrosomes on Dellwood and Union Seamounts in the Offshore Pacific Area of Interest (potential MPA). All scale bars represent 10 cm. In images a–d, scale bars are approximate and were estimated from known size ranges of benthic organisms present in the photos.

TABLE 1. Benthic feeding species known to directly consume *Pyrosoma atlanticum*.

Predator	Location	Source
Echinodermata		
<i>Cidaris</i> sp.	Eastern Atlantic	2
<i>Diadema</i> sp.	Eastern Atlantic	2
<i>Hyphalaster inermis</i>	Eastern Atlantic	3
<i>Phormosoma</i> sp.	Eastern Atlantic	2
cf <i>Cheiraster dawsoni</i>	Northeast Pacific	1
Unidentified Echinoidea sp. 1	Eastern Atlantic	2
Unidentified <i>Cidaroida</i> sp.	Gulf of Mexico	1
Unidentified <i>Ophiuroidea</i> species	Northeast Pacific	1
Arthropoda		
<i>Bathynectes longispina</i>	Gulf of Mexico	1
<i>Chionoecetes</i> sp.	Northeast Pacific	1
<i>Chorilia longipes</i>	Northeast Pacific	1
<i>Colossendeis</i> sp.	Eastern Atlantic	2
<i>Eumunida picta</i>	Gulf of Mexico	1
<i>Munidopsis</i> sp.	Eastern Atlantic	3
Cnidaria		
<i>Actinoscyphia aurelia</i>	Eastern Atlantic	2
<i>Actinostola</i> sp.	Eastern Atlantic	2
<i>Ceriantheopsis americana</i>	Gulf of Mexico	1
cf <i>Cribrinopsis fernaldi</i>	Northeast Pacific	1
Unidentified <i>Actinaria</i> sp. 1	Gulf of Mexico	1
Unidentified <i>Actinaria</i> sp. 2	Northeast Pacific	1
Unidentified <i>Actinaria</i> sp. 3	Eastern Atlantic	2
Chordata		
<i>Alepocephalus rostratus</i>	Mediterranean	4
<i>Alepocephalus</i> sp. 1	South Pacific	5
<i>Alepocephalus</i> sp. 2	South Pacific	5
<i>Galeus melastomus</i>	Mediterranean	4
<i>Hyperoglyphe antarctica</i> (previously <i>porosa</i>)	South Pacific	6
<i>Lepidion lepidion</i>	Mediterranean	4
<i>Neocyttus rhomboidalis</i>	South Pacific	5
<i>Nettastoma melanurum</i>	Mediterranean	4
<i>Pseudocyttus maculatus</i>	South Pacific	5
<i>Tetragonurus cuvieri</i>	South Pacific	5
<i>Trachyrhynchus trachyrhynchus</i>	Mediterranean	4
<i>Tubbia tasmanica</i>	South Pacific	5

Note: New observations presented in this study are presented in boldface type. *Sources:* 1, This study; 2, Lebrato and Jones (2009); 3, Roe et al. (1990); 4, Carrassón and Cartes (2002) (only predators reported to prefer *P. atlanticum* were included here as it was unclear if no consumption of pyrosomes would lead to a measurable negative value in the prey-selectivity index used); 5, Bulman et al. (2002); 6, Cowper (1960).

Targeted research is needed to determine if large rare events like the *P. atlanticum* blooms observed in the Gulf of Mexico in the fall of 2016 and in the Northeast Pacific in the spring and summer of 2017 stimulate benthic productivity and thus have cascading impacts on benthic food webs. However, our ability to direct such research is limited by our knowledge of which species directly consume gelatinous zooplankton and by logistical difficulties of working in the deep-sea combined with

the often unexpected nature of gelatinous zooplankton blooms. Consequently, reports of observations of deep-sea taxa directly feeding on gelatinous zooplankton increases our understanding of how benthic marine communities may respond to climate change and help direct future research into the consequences of “jelly falls” for benthic food webs.

ACKNOWLEDGMENTS

We would like to thank: the crews of the CCGS *J.P. Tully* and the DSV *Ocean Inspector* for their hard work, James Pegg, the CSSF ROPOS team, and the team of the Global Explorer for their technical expertise maintaining and operating the visual survey technology used in this study. We thank Ian Perry and Moira Galbraith (Fisheries and Oceans Canada) for their constructive comments on an earlier version of this manuscript. We also thank Christopher Mah for his help with species identification. Funding for this study was provided by Fisheries and Oceans Canada, NSERC Ship Time Grant 501173-2017 for ROPOS to S. P. Leys, and by a grant from the Gulf of Mexico Research Initiative. This is contribution no. 487 from the Ecosystem Impacts of Oil and Gas Inputs to the Gulf (ECOGIG) consortium.

LITERATURE CITED

- Andersen, V., J. Sardou, and P. Nival. 1992. The diel migrations and vertical distributions of zooplankton and micronekton in the Northwestern Mediterranean Sea. 2. Siphonophores, hydromedusae and pyrosomids. *Journal of Plankton Research* 14:1155–1169.
- Billett, D. S. M., B. J. Bett, C. L. Jacobs, I. P. Rouse, and B. D. Wigham. 2006. Mass deposition of jellyfish in the deep Arabian Sea. *Limnology and Oceanography* 51:2077–2083.
- Bopp, L., O. Aumont, P. Cadule, S. Alvain, and M. Gehlen. 2005. Response of diatoms distribution to global warming and potential implications: A global model study. *Geophysical Research Letters* 32.
- Bulman, C. M., X. He, and J. A. Koslow. 2002. Trophic ecology of the mid-slope demersal fish community off southern Tasmania, Australia. *Marine and Freshwater Research* 53: 59–72.
- Carrassón, M., and J. E. Cartes. 2002. Trophic relationships in a Mediterranean deep-sea fish community: partition of food resources, dietary overlap and connections within the benthic boundary layer. *Marine Ecology Progress Series* 241: 41–55.
- Cowper, T. R. 1960. Occurrence of *Pyrosoma* on the Continental Slope. *Nature* 187:878–879.
- Lebrato, M., and D. Jones. 2009. Mass deposition event of *Pyrosoma atlanticum* carcasses off Ivory Coast (West Africa). *Limnology and Oceanography* 54:1197–1209.
- Lebrato, M., P. D. J. Mendes, D. K. Steinberg, J. E. Cartes, B. M. Jones, L. M. Birsa, R. Benavides and A. Oschlies. 2013. Jelly biomass sinking speed reveals a fast carbon export mechanism. *Limnology and Oceanography* 58:1113–1122.
- Lebrato, M., K. A. Pitt, A. K. Sweetman, D. O. Jones, J. E. Cartes, A. Oschlies, R. H. Condon, J. C. Molinero, L. Adler, and C. Gaillard. 2012. Jelly-falls historic and recent observations: a review to drive future research directions. *Hydrobiologia* 690: 227–245.
- Roe, H., D. Billett, and R. Lampitt. 1990. Benthic/midwater interactions on the Madeira Abyssal Plain; evidence for

- biological transport pathways. *Progress in Oceanography* 24: 127–140.
- Smith, K. L., A. D. Sherman, C. L. Huffard, P. R. McGill, R. Henthorn, S. Von Thun, H. A. Ruhl, M. Kahru, and M. D. Ohman. 2014. Large salp bloom export from the upper ocean and benthic community response in the abyssal north-east Pacific: Day to week resolution. *Limnology and Oceanography* 59:745–757.
- Sweetman, A. K., A. R. Thurber, C. R. Smith, L. A. Levin, C. Mora, C.-L. Wei, A. J. Gooday, D. O. Jones, M. Rex, and M. Yasuhara. 2017. Major impacts of climate change on deep-sea benthic ecosystems. *Elementa Science of the Anthropocene*. <https://doi.org/10.1525/elementa.203>.
- Van Soest, R. 1981. A monograph of the order Pyrosomatida (Tunicata, Thaliacea). *Journal of Plankton Research* 3:603–631.
- West, E. J., D. T. Welsh, and K. A. Pitt. 2009. Influence of decomposing jellyfish on the sediment oxygen demand and nutrient dynamics. *Hydrobiologia* 616:151–160.
- Wigham, B. D., P. A. Tyler, and D. S. M. Billett. 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.
- STEPHANIE K. ARCHER,^{1,5} AMANDA S. KAHN,² SALLY P. LEYS,² TAMMY NORGARD,¹ FANNY GIRARD,³ CHERISSE DU PREEZ^{3,4}, AND ANYA DUNHAM¹
- Manuscript received 10 October 2017; revised 31 October 2017; accepted 8 November 2017. Corresponding Editor: John Pastor.
- ¹Fisheries and Oceans Canada, Pacific Biological Station, 3190 Hammond Bay Road, Nanaimo, British Columbia V9T 6N7 Canada.
- ²Department of Biological Sciences, University of Alberta, Edmonton, Alberta T6G 2E9 Canada.
- ³Department of Biology, Pennsylvania State University, University Park, Pennsylvania 16802 USA.
- ⁴Fisheries and Oceans Canada, Institute of Ocean Sciences, 9860 West Saanich Road, Sidney, British Columbia V8L 5T5 Canada.
- ⁵E-mail: stephanie.archer@dfo-mpo.gc.ca
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