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Title: Range expansion of tropical pyrosomes in the northeast Pacific Ocean

List of Authors: Kelly R. Sutherland[1*], Hilarie L. Sorensen[1], Olivia N. Blondheim[2], Richard D. Brodeur[3], Aaron W. E. Galloway[1]

1. Oregon Institute of Marine Biology, University of Oregon, Charleston, Oregon 97420 USA

2. Department of Biology, Drew University, Madison, New Jersey 07940 USA

3. Northwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Newport, Oregon, 97366, USA

* Corresponding Author: ksuth@uoregon.edu

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"I have just watched the moon set in all her glory, and looked at those lesser moons, the beautiful Pyrosoma, shining like white-hot cylinders in the water" (T.H. Huxley, 1849, *Diary of the Voyage of H.M.S. Rattlesnake*).

Pyrosomes are colonial pelagic tunicates that have fascinated marine biologists for over a century. Their name comes from the “fiery” bioluminescence that luminous organs produce at night time. Blooms of pyrosomes, identified as *Pyrosoma atlanticum* (Peron, 1804), have recently appeared in the North Pacific Ocean (Fig. 1), prompting questions about environmental factors that triggered their appearance and persistence over multiple seasons as well as potential ecosystem impacts.

Pelagic tunicates, which include salps, dolioloids and pyrosomes, are Urochordates that spend their whole life cycle in the plankton and feed using fine mucus meshes. Pyrosomes are colonies of zooids that are connected in a chitinous tunic and resemble colonial benthic ascidians (Class Ascidiacea). Genetically identical blastozooids are added to the colony via asexual budding. Pyrosome colonies can reach lengths of several meters, with pyrosomes in the Northeastern Pacific reaching up to 80 cm in length (Brodeur et al. 2018). Ciliary beating within the zooids achieves both suspension feeding and locomotion (Alldredge and Madin 1982). Each zooid contains luminous organs that may be used to communicate with zooids further away within the colony in response to mechanical or light stimuli (Bowlby et al. 1990).

Pyrosomes remain one of the least-studied planktonic grazers in spite of their widespread distribution and ecological significance. Like other pelagic tunicates, pyrosomes are known to form high density blooms reaching tens of individuals m^{-3}, with swarms of *P. atlanticum* removing >50% of phytoplankton standing stock in the 0-10 m layer (Drits et al. 1992). Most species, including *P. atlanticum,* have been considered tropical to subtropical in their distribution (van Soest 1981) with blooms previously reported in the southeast Atlantic (Drits et al 1992) and the northwest Mediterranean (Anderson and Sardou 1994).

Pyrosomes are relatively common off of the California coast south of Cape Mendicino; for example, in a time series of planktonic abundance *P. atlanticum* was reported about half the time during annual sampling off the coast of southern California from 1951 to 2002 (Lavaniegos and

Ohman 2003), within its known latitudinal range. In 2014 scientists, fishermen, and beachgoers first started reporting the appearance of *P. atlanticum* in coastal waters near northern California, Oregon and Washington north of their previously reported range. The pyrosomes appeared again in 2015 and 2016. By the summer of 2017, they appeared in unprecedented numbers along the entire west coast, reaching the Western Gulf of Alaska, but showed some of their highest abundances off Oregon (Brodeur et al. 2018) clogging nets and disrupting marine activities such as commercial and sport fisheries (Kaety Jacobson, Oregon Sea Grant, pers. comm.). During two research cruises off the Pacific Northwest coast, USA in summer of 2017, colonies were 4-26 cm long and occurred in densities up to 3 m^{-3}. Vertical video camera profiles and corresponding environmental data (temperature, salinity and fluorescence) indicated that layers of pyrosomes were distributed at ~60 m depth, at the base of the surface mixed layer. These observations were made during ecosystem survey cruises in May 2017 from Bodega Bay, CA (38˚N) to Cape Meares, OR (45.5˚N), and August 2017 from Newport, OR, to the north end of Vancouver Island (44ºN-49ºN).

The appearance of such high densities of tropical pyrosomes in the temperate Northeast Pacific presents interesting research questions about the physical oceanographic features that led to their northerly expansion, and the environmental drivers that have allowed their populations to persist for multiple years. Beginning in 2014, an unusually warm and stable water mass termed the 'warm blob' formed in the North Pacific and lasted several years, and then was replaced by the northward progression of a strong El Niño in 2016 (Di Lorenzo and Mantua 2016), which may have facilitated the survival of this tropical species well north of their normal range. Furthermore, onshore flow may have pushed them closer to the shore than normal, leading to numerous reports of beached pyrosomes from 2014 to 2018 (Fig. 1d). During a February 2018 cruise, we again observed pyrosomes in large numbers during day and night at three stations (10, 25 and 45 km off shore) along the Newport, OR Hydrographic line (44ºN), where temperatures ranged from 10 to 10.8 ºC (Fig. 1a, b; Video S1). Similar to the summer cruise observations, video footage showed that pyrosomes were absent in surface waters but aggregated in a layer near the base of the surface mixed layer at ~40 m depth.

More generally, physical environmental parameters including temperature, light, salinity, dissolved oxygen (DO), and currents have significant impacts on the biology and behavior of gelatinous zooplankton aggregations (Graham et al. 2001). Like other pelagic tunicates, pyrosomes are filter feeders that use cilia to pump water into their mucous filters to consume planktonic microorganisms (Mayzaud et al. 2007). *P. atlanticum* have been recorded to have some of the highest clearance rates of any pelagic grazer, with up to 35 l h^{-1} per colony (Perissinotto et al. 2007). Their high filtration rates allow them to feed efficiently on small planktonic microorganisms (Lavaniegos & Ohman 2003) down to the submicron size scale (Sutherland et al. 2010). These high filtration rates coupled with rapid reproduction and growth capabilities enable pelagic tunicates to be highly responsive to environmental fluctuations (Alldredge & Madin 1982). During blooms, they may have significant impacts on food web dynamics through grazing and fecal pellet production (Drits et al. 1992). *P. atlanticum* can undertake extensive diel vertical migrations, migrating up to depths of 700 m (Angel 1989), potentially accelerating vertical flux to the benthos.

The impacts of a bloom of this density and extent on ecological interactions are unknown. In spite of their widespread distributions (Van Soest 1981), there are very few studies on the dietary impact of pyrosomes. Analysis of pyrosome fecal pellets suggested they consume small phytoplankton (3-5 μm), coccolithophores, centric diatoms, and silicoflagellates (Drits et al. 1992). However, based on their measured mesh opening dimensions (0.6 μm, Bone et al. 2010) and the data supporting that other pelagic tunicates with larger meshes consume submicron particles (Sutherland et al. 2010), it is likely that they consume organisms in the nano- and picoplankton size range with relatively high efficiencies. This may allow them to persist during relatively oligotrophic conditions that favor smaller cells as evidenced by their presence during the ‘warm blob’ event and also during winter off the Oregon coast. Both of these phenomena represent periods of increased stratification and reduced upwelling favoring smaller phytoplankton and bacterioplankton. It is presently unknown how these recent pyrosome blooms may interact with or affect the dynamics of nutritionally valuable, lipid-rich plankton in the California Current.

Once present in the ecosystem, pyrosomes may be predated upon or eventually sink to the bottom, serving as a benthic food source. A number of organisms, including sea turtles and sea birds, have been observed feeding on pyrosomes and other pelagic tunicates (e.g. Harbison 1998, Mayzaud et al. 1992) and they can comprise a primary prey source for a number of fish species

(Harbison 1998). However, reports are mostly descriptive owing to the challenges of conducting quantitative feeding studies with such rapidly digested organisms. The sinking of dead and dying pyrosomes occurred on a large scale during summer 2017 and were captured in benthic trawls and images of the sea floor (Fig. 1d). Observations in the Gulf of Mexico and off the coast of British Columbia have shown invertebrates, including anemones, sea urchins and crabs directly consuming pyrosomes (Archer et al. 2018). Until recently, jelly falls have been mostly overlooked as a source of carbon deposition to the sea floor (Lebrato et al. 2012).

The appearance of pyrosomes in temperate and subpolar latitudes challenges assumptions about their temperature tolerance. Moreover, their appearance in multiple years and the capacity to reach bloom proportions suggests that they may even thrive in colder waters, especially during more oligotrophic conditions, and could become more permanent residents in the California Current marine ecosystem. Their continued presence will likely become a nuisance for certain fishing activities, causing fishers to relocate or spend extra time sorting their catch. Large pyrosome aggregations have the potential to restructure energy flows through food webs via efficient removal of photosynthetic plankton and subsequent fecal pellet production, consumption by higher trophic levels, or sinking to depth.

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Figure 1. Pyrosome bloom in the northeast Pacific Ocean. a) Large densities of *P. atlanticum* observed at ~60 m depth during a February 2018 cruise off of Newport, Oregon, USA (also see Video S1), b) pyrosome colonies from a net tow on the same cruise (M. Farley), c) pyrsomes washed up on beach in Newport, November 2017 (A. Rainey) and, d) dead pyrosomes on the sea floor (~50 m) at Cape Perpetua reef, Oregon, May 2017 (S. Marion).

Figure 1.