Range expansion of tropical pyrosomes in the northeast Pacific Ocean

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 Ascidiaeae). 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 per cubic meter, 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 dis-
tribution (Van Soest 1981) with blooms previously reported in
the southeast Atlantic (Drits et al. 1992) and the northwest
Mediterranean (Andersen and Sardou 1994).

Pyrosomes are relatively common off the California
coast south of Cape Mendocino; for example, in a time seri-
es 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 report-
ing 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,
personal communication). During two research cruises off
the Pacific Northwest coast, USA in the summer of 2017,
colonies were 4–26 cm long and occurred in densities up to
3 colonies/m³. Vertical video camera profiles and corre-
sponding environmental data (temperature, salinity, and
fluorescence) indicated that layers of pyrosomes were dis-
tributed at ~60 m depth, at the base of the surface mixed
layer. These observations were made during ecosystem sur-
voy cruises in May 2017 from Bodega Bay, California
(38° N) to Cape Meares, Oregon (45.5° N), and August
2017 from Newport, Oregon, to the north end of Vancouver
Island, British Columbia, Canada (44° N–49° N).

The appearance of such high densities of tropical pyro-
somes in the temperate northeast Pacific presents interesting
research questions about the physical oceanographic fea-
tures that led to their northerly expansion, and the envi-
ronmental 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. 1c). 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,
Oregon Hydrographic line (44.40° N), where temperatures
ranged from 10° to 10.8°C (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, pyro-
somes 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 gra-
zier, with up to 35 L/h per colony (Perissinotto et al. 2007).
Their high filtration rates allow them to feed efficiently on
small planktonic microorganisms (Lavaniegos and Ohman
2003) down to the submicron 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 and
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 verti-
cal flux to the benthos.

The impacts of a bloom of this density and extent on eco-
logical 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 pyosome fecal
pellets suggested they consume small phytoplankton (3–
5 μm), cocolithophores, centric diatoms, and silicoflagellates
(Drits et al. 1992). However, based on their measured mesh
opening dimensions (0.6 μm; Bone et al. 2000) 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 con-
ditions 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 pre-
dated 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, Perissinoto et al. 2007) and they can comprise a primary
prey source for a number of fish species (Harbison
1998). However, reports are mostly descriptive owing to the chal-
lenge 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 consum-
ing pyrosomes (Archer et al. 2018). Until recently, jelly falls
have been mostly overlooked as a source of carbon deposi-
tion 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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