CURRENT EVIDENCE

A global review of pyrosomes: Shedding light on the ocean's elusive gelatinous "fire-bodies"

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Scientific Significance Statement

Massive blooms of pelagic tunicates are regular occurrences, but we know little about their causes and predictability. Recent attention has focused on seeming increases in blooms of pyrosomes, colonial tunicates closely related to salps and with the potential to impact many aspects of marine food webs. However, much remains unknown about pyrosomes, limiting our ability to incorporate them into food web models and forecasts. We synthesize current understanding of reproduction, habitat, feeding, predation, and carbon cycling, and use this knowledge to identify key scientific gaps essential for modeling and forecasting pyrosome blooms and food web impacts. We distill contradictory literature reports on habitat use and bloom formation of the most common species, *Pyrosoma atlanticum*, into a consistent hypothesis that the species forms blooms in high-productivity waters below 18°C and uses variable-depth diel vertical migration to adapt to a range of temperatures. Pyrosomes may not directly compete for prey with dominant zooplankton groups such as copepods, as previously thought, but blooms likely contribute substantially to carbon export to abyssal depths.

Abstract

Pyrosomes are colonial tunicates that form gelatinous tubes and occasionally produce bioluminescent swarms. The rapid "bloom-bust" dynamics of pyrosomes have the potential to outcompete other zooplankton, restructure marine food webs, enhance carbon export, and interfere with human activities. Pyrosomes have been recorded for at least two centuries, yet much remains unknown about their physiology, bloom mechanisms, and ecosystem impacts. Recent bloom reports prompt the question of whether frequencies or densities are

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increasing, and whether potential population changes are caused by ocean change. This review clarifies current information on pyrosome biology and ecology and explores apparent contradictions in habitat preferences and diel vertical migration (DVM). We posit that the dominant species, *Pyrosoma atlanticum*, may preferentially inhabit waters below 18°C and alter its DVM activity to maintain overall body temperature near this threshold. Expanding our knowledge of pyrosomes is needed to facilitate their inclusion in ecosystem models and forecasts of future population distributions.

Pyrosomes hold allure among zooplankton as the mysterious and elusive "fire-bodies" of nighttime seas, so named because vast numbers of the pink, tubular colonies can sometimes be seen bioluminescing a faint blue at the ocean surface ("pyro"—"some" is Greek for "fire"—"body"; Huxley 1851; Brodeur et al. 2018). Pyrosomes can grow to be some of the longest ocean animals: colonies of one species, *Pyrostremma spinosum*, often span 1–3 m (Gauns et al. 2015; Décima et al. 2019) and occasionally grow to 14–20 m (Tables 1, 2; Griffin and Yaldwyn 1970; Van Soest 1981).

Pyrosome blooms can form rapidly and decimate phytoplankton stocks (Drits et al. 1992; Henschke et al. 2019), potentially outcompeting other zooplankton groups. When pyrosomes die *en masse*, their fecal pellets and carcasses rapidly transport carbon to deeper waters (Lebrato and Jones 2009; Stenvers et al. 2021). Pyrosomes are known to beachcombers as novel phenomena that occasionally wash onto the shoreline after blooms. Recent pyrosome blooms have clogged fishing nets to the point of breaking and blocked coastal water intake systems of power plants (Kuo et al. 2015; Brodeur et al. 2018; Sutherland et al. 2018). These events have prompted closer

attention to the causes of pyrosome blooms, their predictability, and the question of whether blooms are increasing.

Although often grouped within the broad and ill-defined zooplankton category of "jellyfish," pyrosomes are pelagic colonial tunicates belonging to Chordata, making them the closest relatives of salps, doliolids, and larvaceans and among the closest living relatives of vertebrates (Milne-Edwards 1841). The order Pyrosomida belongs to the Class Thaliacea, along with Doliolida and Salpida, and contains two subfamilies (Pyrostremmatinae and Pyrosomatinae) that together encompass three genera and eight species (Table 1; Van Soest 1981; Govindarajan et al. 2011). *Pyrostremma* has developmental characteristics most similar to salps and doliolids and may be the most closely related genus to ancestral pyrosome forms (Govindarajan et al. 2011).

Records of pyrosomes, including descriptions of their morphology and reproduction, go back to at least the 1800s (Perón 1804; Huxley 1851; Joliet 1881; Salensky 1890). However, pyrosomes remain remarkably understudied, and little is known about the causes, timing, and ecological implications of their blooms. Further, much of the information that is known about pyrosomes is somewhat contradictory. For example, some studies show positive relationships between *Pyrosoma atlanticum*

Table 1. Subfamily divisions of the eight species of pyrosomes described by Van Soest (1981), with geographic distributions and length ranges.

Family	Species	Range	Maximum/new length (mm)
Pyrostremmatinae	*Pyrostremma spinosum*	Near-global (40° N–45° S)	20,000/5–6
Pyrostremmatinae	*Pyrostremma agassizi*	Near-global (40° N–45° S)	470/2–6
Pyrosomatinae	*Pyrosomella verticillata*	Indo-West Pacific (15° N–10° S) • Recent sighting in SW Atlantic (Rio de Janeiro, Brazil)*; molecular sequences from Celebes Sea, NW Australia[†]	50
Pyrosomatinae	*Pyrosomella operculata*	Indo-West Pacific (rare)	130
Pyrosomatinae	*Pyrosoma atlanticum*	Near-global (50° N–50° S, including Mediterranean Sea) • Additional records in Southern Ocean (Fig. 1)[‡]	600/40–60
Pyrosomatinae	*Pyrosoma aherniosum*	Near-global (30° N–30° S, rare)	25
Pyrosomatinae	*Pyrosoma ovatum*	S. Atlantic, S. Pacific, and Indian oceans	50
Pyrosomatinae	*Pyrosoma godeauxi*	12° S, 41° E; molecular sequence from NW Australia[†]	120

The first length value listed is the maximum (or only recorded) colony length; second value is the length of newly formed colonies. All information from Van Soest (1981).
*de Carvalho and Bonecker (2008).
[†]Govindarajan et al. (2011).
[‡]Pyrosome database records.

abundance and ocean temperature but no relationship with chlorophyll-*a* (Chl *a*; Lebrato et al. 2013; Schram et al. 2020), while others have found negative relationships with temperature but positive relationships with Chl *a* (Henschke et al. 2019; O'Loughlin et al. 2020; Stenvers et al. 2021). There are also contradictions in reported pyrosome preferred depth ranges and extent of diel vertical migration (DVM; Andersen et al. 1992; Andersen and Sardou 1994; Sutherland et al. 2018; Henschke et al. 2019; Miller et al. 2019; Lyle et al. 2022). Deciphering these seemingly contradictory findings might shed new light on our understanding of pyrosome blooms. Finally, recent pyrosome blooms across various ocean regions have prompted the question of whether bloom occurrences or spatiotemporal extents are increasing due to ocean changes or are simply better sampled and recorded as our understanding of gelatinous organisms evolves.

In this review, we first present the literature-based consensus knowledge on five key aspects of pyrosome biology and ecology: 1. Reproduction; 2. Habitat; 3. Feeding; 4. Predation; and 5. Carbon cycling. We then highlight several outstanding questions and possible methods to address them. We expand on two topics—(i) potential temperature preferences and (ii) drivers of blooms—by distilling consistent underlying patterns of habitat preference from seemingly contradictory literature. Finally, we discuss further research needs for modeling food web impacts of pyrosomes and forecasting blooms under current and future ocean conditions. We include information on all pyrosome species, where possible, but much of the focus is necessarily on the most well-studied species, *P. atlanticum*.

To summarize pyrosome sightings, blooms, habitat, and physiological characteristics, we draw upon a comprehensive body of scientific manuscripts identified using Google Scholar via variations on search terms including "Pyrosome," "Pyrosoma," "atlanticum," and others, as well as citations from other manuscripts (see Supplemental Information for full description of search methods). We also include pyrosome records from four databases: NOAA COPEPOD (NOAA 2022), BCO-DMO Jellyfish Database Initiative (JeDI; Condon et al. 2014), Global Biodiversity Information Facility (GBIF; GBIF.org 2023), and Ocean Biodiversity Information System (OBIS; IODE Programme 2023). Literature-based sources and the four databases span the period 1850-present. Literature records encapsulate 1–5 specific dates within a 1–2 yr span, while database records are for single dates. We developed preliminary habitat envelopes for pyrosome groups using both literature-based in situ and satellite-measured surface temperature and Chl *a* values (see Supplemental Information for details on data sources, extraction, and compilation).

Biology and ecology

Reproduction

Reproductive stages

Pyrosomes are hermaphroditic and show a two-part life cycle analogous to salps, although without alternation of generations (Huxley 1851; Thompson 1948; Andersen 1998). In the first part, a fertilized ovum develops to a "nurse-like" form, termed a "cyathozooid." In the second part, the four ascidiozooids (ascidian-shaped individuals), now known as the "tetrazooid" stage, are produced by the cyathozooid via gemmation and are deemed the "parents" of the subsequent asexually produced zooids in the colony (Huxley 1851; Salensky 1890; Thompson 1948). The orientation of additional ascidiozooids differs among the three genera: *Pyrostremma* shows a two-part addition of 30–80 primary ascidiozooids in a whorl-like arrangement followed by secondary zooids that remain in their budded positions; *Pyrosomella* produces ascidiozooids in parallel rows throughout the life of the colony; and *Pyrosoma* produces ascidiozooids in random, densely-packed arrangements (Van Soest 1981). The older (closed) end of a pyrosome colony is protandrous, while the younger end is protogynous, meaning that a colony may self-fertilize from one end to the other (Bone 1998).

Colony density

Blooms of two pyrosome species (*P. atlanticum* and *Pr. spinosum*) have been described from various locations, although information is relatively scant. *P. atlanticum* usually occurs as multiple colonies in an area, although occasional observations have noted single colonies, particularly on the benthos (Fig. 1 and references therein). *Pr. spinosum* is often observed as 1–2 colonies at a time (Griffin and Yaldwyn 1970; Marimuthu et al. 2021), although denser blooms have been observed (Gauns et al. 2015; Décima et al. 2019). There are fewer observations of *Pr. spinosum* than for *P. atlanticum*, so the preponderance of solitary colonies could be a sampling bias.

Habitat distributions

Spatial distribution

Pyrosomes are distributed across tropical, subtropical, and temperate waters globally, extending into the Southern Ocean but not yet recorded in Arctic seas (Fig. 1). They are found in both oceanic and neritic waters and across a range of depths, to 750 m based on literature records (Andersen and Sardou 1994), and even to depths of nearly 5000 m according to some database records (Condon et al. 2014). High concentration of *Pyrosoma* spp. observations from the COPEPOD and OBIS databases in the Indian Ocean (Fig. 1) is likely due to sampling bias rather than true population increases, as that region showed the highest overall zooplankton sampling effort in the COPEPOD database (Supporting Information Fig. S2).

P. atlanticum is the most ubiquitous pyrosome species. Van Soest (1981) described its range as 50° N to 50° S across all oceans, and it is the only species so far recorded in the Mediterranean Sea (Fig. 1; Table 1; Andersen et al. 1992; Andersen and Sardou 1994; Lebrato et al. 2013). It is likely that the true number of observations of *P. atlanticum* also includes many of the records for *Pyrosoma* spp. Since *P. atlanticum* is by far the most populous pyrosome species globally (4446 unique observations combined from literature sources and the four
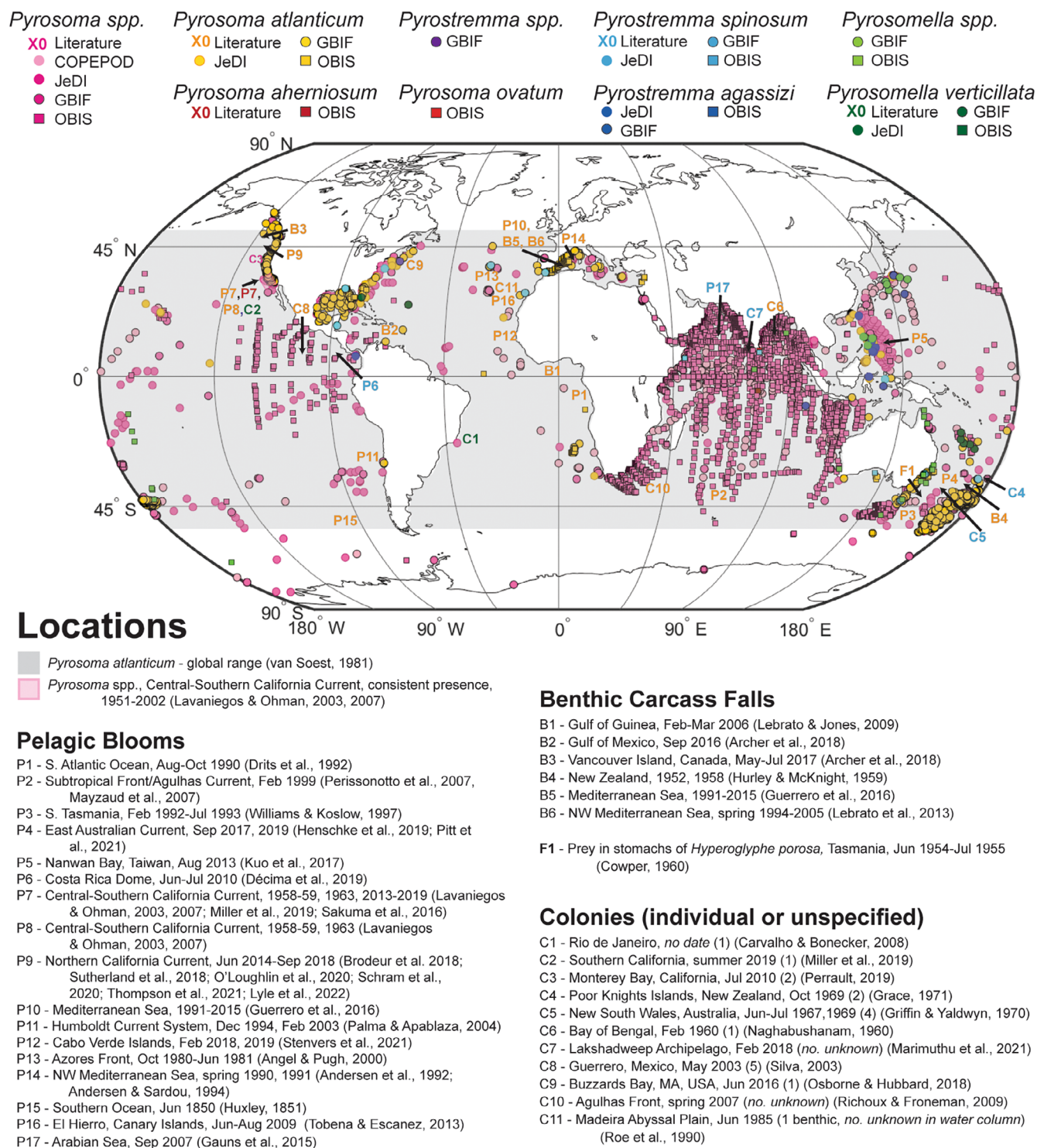
Fig. 1. Global records of pyrosome appearances from literature sources (letter–number symbols) and four databases (circles and squares): NOAA COPEPOD, BCO-DMO JeDI, GBIF, and OBIS (see Supplementary material for details of data sources and extraction; see Lilly 2023 for datasets and coding scripts used in figure creation). The COPEPOD database provides records only to *Pyrosoma* spp. level; all other data sources provide varying subsets of species- and genus-level records. Gray shading between 50° S and 50° N indicates the described range of *P. atlanticum* from Van Soest (1981). Pink shaded box off California indicates long-term observations of Pyrosoma species (*P. atlanticum* and *P. aherniosum*), as described by Lavaniegos and Ohman (2003). Literature-based records are divided into "Pelagic Blooms," "Benthic Carcass Falls," and "Individual Colonies" (COPEPOD > JeDI > GBIF > OBIS). The number of unique records for each pyrosome genus or species, summed across the literature and database sources is *Pyrosoma* spp. = 3861; *P. atlanticum* = 4446; *P. aherniosum* = 7; *P. ovatum* = 3; *Pyrostremma* spp. = 1; *Pr. spinosum* = 29; *Pr. agassizi* = 17; *Pyrosomella* spp. = 9; *Pl. verticillata* = 60.

databases, compared to 3861 observations for *Pyrosoma* spp. and 126 observations total for all other species and genera), we speculate that most of the "*Pyrosoma* spp." observations recorded in databases are likely to be *P. atlanticum*.

Pr. spinosum is the second most frequently recorded species, and, with its congener *Pr. agassizi*, has a narrower described range, from 40° N to 45° S (Table 1; Van Soest 1981). Two other pyrosome species (*Pyrosomella verticillata* [*Pl. verticillata*] and *Pyrosoma aherniosum* [*P. aherniosum*]) have been recorded in literature studies. Although Van Soest (1981) claimed *Pl. verticillata* went extinct in the Atlantic Ocean after the Miocene Epoch, one specimen was recorded off Rio de Janeiro, Brazil (de Carvalho and Bonecker 2008). The specimen was identified based on descriptions by Van Soest (1981) and Esnal (1999) and clear differences in the shape and size of the oral siphon compared to *P. atlanticum*. Another specimen of *Pl. verticillata* was observed off Southern California during the 2014–2015 marine heat wave (Miller et al. 2019). *P. aherniosum* has been recorded consistently alongside *P. atlanticum* in the southern California Current System since at least the 1950s (Fig. 1; Lavaniegos and Ohman 2003).

Van Soest (1981) claimed that "there are no neritic pyrosomes, [but] *P. spinosum* has been observed nearshore at times." However, blooms of both *P. atlanticum* and *Pr. spinosum* have been reported in coastal areas. Blooms of *P. atlanticum* occasionally wash up on beaches (Brodeur et al. 2018; Sutherland et al. 2018) and can clog coastal intake plants (Kuo et al. 2015), similar to salps (Lee et al. 2010; Henschke

et al. 2016). *Pr. spinosum* is often found associated with reefs or the benthos (Griffin and Yaldwyn 1970; Grace 1971; Marimuthu et al. 2021) (Box 1).

Habitat ranges

We developed "habitat envelopes" of temperature and Chl *a* for each pyrosome species to evaluate potential habitat range limits. For each species, we developed two sets of envelopes: one from literature-reported pyrosome observations paired with corresponding habitat measurements from the same studies (see Supplementary Table S1 for source studies), and a second from the matchup of database pyrosome observations with satellite-measured sea surface temperature (SST; OISST 2023) and Chl *a* (Melin 2013a,b) (Fig. 2; literature pairs and database-satellite matchups shown separately). We matched database pyrosome observations with monthly-averaged satellite values to utilize greatest temporal and spatial coverage of satellite measurements. Because satellite data are only available after certain dates, we used a two-part matchup approach. For database pyrosome records within the time-period of satellite measurements (SST: 1981–2020; Chl *a*: 2003–2017), we matched each pyrosome record to the corresponding year-month satellite value. For pyrosome records outside those periods, we matched to the corresponding climatological monthly mean of each variable (see Supplemental Information for data sources, extraction, and compilation methods, and Lilly 2023 for repository of all datasets used in analyses).

Box 1. What constitutes a pyrosome "bloom?"

There is no universal definition of a pyrosome bloom, which could limit comparative analyses across dates and regions. Studies describing pyrosome "blooms" report wide-ranging colony densities, from 0.03 to > 40 colonies m^{-3}. Lavaniegos and Ohman (2003) is the only study we know of that attempts to develop a concrete definition of a pyrosome bloom: >5 mg C m^{-2}. However, they did not specify the basis for this delineation, and many blooms are reported in various units of abundance other than carbon biomass (e.g., col m^{-3}, col m^{-2}, col L^{-1}). We suggest that developing a consistent definition of "pyrosome bloom" is a valuable first step toward enhancing our ability to compare pyrosome dynamics across regions. Colony size and sampling mesh size are important caveats to the definition of a bloom.

One study in the Eastern Atlantic reported extremely high bloom densities: 9.5–41 col m^{-3} (Drits et al. 1992). Studies of the 2014–2018 *P. atlanticum* bloom in the Northern California Current System reported densities ranging from 0.14 col m^{-3} (Lyle et al. 2022) to 0.4–0.7 col m^{-3} (O'Loughlin et al. 2020) to 3–5 col m^{-3} (Sutherland et al. 2018; Schram et al. 2020). An observation of a *P. atlanticum* bloom off Chile reported densities of 35–215 col/1000 m^{-3} (0.035–0.22 col m^{-3}; Palma and Apablaza 2004), while a comparison study of high *P. atlanticum* densities in a cold-core eddy of the East Australia Current compared to neighboring warm-core eddies reported highest densities of 2.85 col/1000 m^3 (0.0029 col m^{-3}) of pyrosomes > 10 cm in length (Henschke et al. 2019). These lower densities, reported as col/1000 m^3, often come from studies that use larger-mesh sampling nets and thus only target larger pyrosome colonies (> 10 cm in length), biasing reports toward lower concentrations. Based on these numbers, we suggest a threshold of 0.1 col m^{-3} as constituting a "bloom" of large-size pyrosomes (> 10 cm) and > 1 col m^{-3} for smaller colonies (< 10 cm). "Bloom" is likely used to refer to differing densities among regions, particularly where pyrosome expansions are a novel occurrence.

Van Soest (1981) noted seasonality of pyrosome abundances in some regions: *P. atlanticum* in the Mediterranean Sea (highest in autumn) and off Bermuda (winter); *Pr. agassizi* off Bermuda (autumn); *Pr. spinosum* off Bermuda (late winter). Thompson (1948) similarly noted a steep rise in *P. atlanticum* abundances off Australia in autumn but low abundances in spring. Pyrosome blooms may thus be a regular seasonal occurrence in some regions.
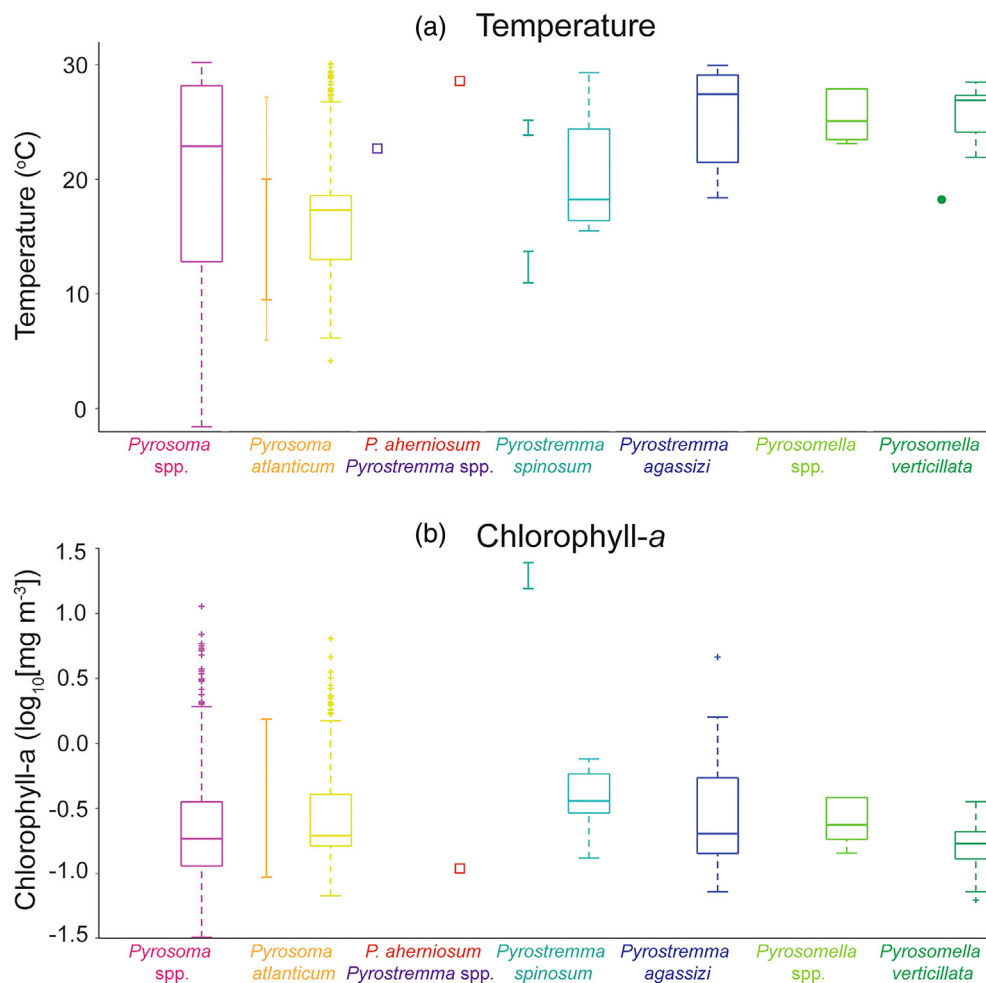

Fig. 2. Habitat envelopes of (**a**) temperature and (**b**) Chl *a* for each pyrosome group, color-coded as in Fig. 1. Boxplots and square symbols depict values from database pyrosome-satellite habitat matchups; square symbols depict single-point values for species with insufficient data for boxplots. Horizontal lines inside boxplots are median values. Solid vertical lines and circular symbol to the left of boxplots indicate literature-based ranges (*P. atlanticum*, *Pr. spinosum*, and *Pl. verticillata* only). Thin extension lines for *P. atlanticum* literature-based temperature range indicate the full 7–30°C range originally described by Thompson (1948). *P. ovatum* is not shown for habitat ranges due to lack of sample overlap with habitat variables. Literature-based pyrosome records were compared to corresponding in situ temperature and/or Chl *a* measurements from the same studies. Database pyrosome records were compared to satellite-measured monthly means of SST (NOAA OISST V2) or Chl *a* (MODIS-AQUA). See Supplementary Table S1 for source references of literature values and supplementary material for additional information on satellite data sources and extraction.

Literature-based and database-satellite envelopes both indicate that pyrosome distributions span broad ranges of temperature and Chl *a* (Fig. 2); there is only limited literature information on salinity and oxygen. Thompson (1948) described a temperature range of 7–30°C for *P. atlanticum* across the global oceans. Subsequent literature records of in situ temperature measurements have reported *P. atlanticum* in the range of 10–22°C (Fig. 2a; Supplementary Table S1). The records further subset into three categories within that range: 10–14°C (Tobena and Escanez 2013; Sutherland et al. 2018; Lyle et al. 2022), 14–18°C (Perissinotto et al. 2007; Henschke et al. 2019; Lyle et al. 2022), and 18–22°C (Richoux and Froneman 2009; Henschke et al. 2019; Pitt et al. 2021;

Stenvers et al. 2021). Database-satellite matchups show a comparable temperature range for *P. atlanticum*, with an interquartile range spanning 13–18°C and median of 17°C (Fig. 2a). Database-satellite matchups for *Pyrosoma* spp., which we hypothesize to be comprised mostly of *P. atlanticum*, show a comparable range to *P. atlanticum*, although with an overall warmer interquartile range of 13–28°C and median of 23°C (Fig. 2a).

Pr. spinosum has narrower, warmer temperature envelopes. Literature studies report thermal ranges of 26–27°C for near-surface habitat in both the Arabian Sea (Gauns et al. 2015) and Eastern Tropical Pacific (Décima et al. 2019), although the latter study found that *Pr. spinosum* also migrates below the mixed

layer to or through waters of 12–15°C (Fig. 2a; Supplementary Table S1). Database-satellite matchups for *Pr. spinosum* show a similar range of 15–29°C with a median of 18°C. The lack of cooler temperature matchups for database *Pr. spinosum* records may reflect the surface bias of satellites, which cannot provide information on sub-mixed layer habitat. A third species, *Pl. verticillata*, was only reported in one literature study at 19.7°C off Rio de Janeiro, Brazil (de Carvalho and Bonecker 2008), but shows database-satellite matchups ranging from 22°C to 28°C (Fig. 2a). Several other species (*Pyrostremma* spp., *P. aherniosum*, *Pr. agassizi*, and *Pyrosomella* spp.) do not have literature-reported habitat information but have database-satellite matchups showing temperature envelopes within 20–30°C (Fig. 2a).

Literature studies of *P. atlanticum* give Chl *a* ranges of −1 to −0.15 $\log_{10}(\text{mg m}^{-3})$ (Andersen and Sardou 1994; Perissinotto et al. 2007; Richoux and Froneman 2009; Henschke et al. 2019; O'Loughlin et al. 2020; Pitt et al. 2021) and occasionally up to 0–0.12 $\log_{10}(\text{mg m}^{-3})$ (Andersen and Sardou 1994; Henschke et al. 2019) (Fig. 2b; Supplementary Table S1). Database-satellite matchups of both *Pyrosoma* spp. and *P. atlanticum* with Chl *a* show similar ranges, although with lower interquartile ranges than literature studies, between −0.9 and −0.5 $\log_{10}(\text{mg m}^{-3})$. However, outlier values from database-satellite matchups extend to > 1 $\log_{10}(\text{mg m}^{-3})$ for *Pyrosoma* spp. and > 0.5 $\log_{10}(\text{mg m}^{-3})$ for *P. atlanticum* (Fig. 2b).

Literature studies of *Pr. spinosum* report substantially higher Chl *a* ranges, between 1.2 and 1.4 $\log_{10}(\text{mg m}^{-3})$ (Gauns et al. 2015; Marimuthu et al. 2021; Fig. 2b; Supplementary Table S1). However, database-satellite matchups for *Pr. spinosum* yield comparable ranges to those for *P. atlanticum*, between 0.1 and 0.8 $\log_{10}(\text{mg m}^{-3})$. No other species has literature-reported Chl *a* habitat. Database-satellite matchups for two species (*Pr. agassizi* and *Pyrosomella* spp.) with Chl *a* show comparable ranges to *Pr. spinosum*, while *P. aherniosum* and *Pl. verticillata* only occur in waters ≤ −0.5 $\log_{10}(\text{mg m}^{-3})$ (Fig. 2b).

Discrepancies in habitat envelopes between literature and satellite matchups likely reflect differences in depth resolution of sampling. Many in vivo literature studies sample temperature and Chl *a* at the same depths where pyrosomes are observed. Satellites only measure surface ocean conditions and are thus biased toward warmer, lower-productivity values in most ocean regions. The warmer temperature envelope of *Pyrosoma* spp. compared to *P. atlanticum* may reflect the high proportion of database samples for *Pyrosoma* spp. in the Indian Ocean, which is among the warmest average ocean regions globally (NOAA 2022).

Only four literature studies report habitat salinity for *P. atlanticum*. One study in the northern California Current System observed *P. atlanticum* in relatively fresh waters (31–33 PSU) typical of that region (Schram et al. 2020), while studies in the Canary Islands upwelling region (Tobena and Escanez 2013) and subtropical western boundary currents (Richoux and Froneman 2009; Pitt et al. 2021) observed colonies in salty waters of 35–36 PSU. *Pl. verticillata* was described at a salinity of 36.4 PSU off Rio de Janeiro, Brazil (de Carvalho and Bonecker 2008). Only one study described oxygen ranges for *P. atlanticum*, noting that colonies associate in daytime with the local oxygen minimum zone (300–400 m), although the relationship may reflect vertical migration preferences unrelated to oxygen levels (Stenvers et al. 2021). We did not match pyrosome database samples with oxygen or salinity.

Vertical distribution and DVM

P. atlanticum is most often recorded in the upper 75 m of the water column at night (Andersen and Sardou 1994; Angel and Pugh 2000; Stenvers et al. 2021) and occasionally in the upper 20 m (Drits et al. 1992; Lyle et al. 2022). Daytime distributions of all pyrosome groups span a broad range of depths (Fig. 3a,b, Supporting Information Fig. S3a,b). Blooms of *P. atlanticum* in the cool California Current System (Miller et al. 2019; Lyle et al. 2022) and southeast Atlantic (Drits et al. 1992) inhabited daytime distributions between 10 and 35 m, showing little change from night depths. However, the majority of literature studies, as well as a high proportion of database records, indicate pyrosomes deeper than 100 m during the day, most often between 100 and 500 m (Andersen et al. 1992; Andersen and Sardou 1994; Henschke et al. 2019; Stenvers et al. 2021) and occasionally deeper than 700 m (Fig. 3, Supporting Information Fig. S3; Angel and Pugh 2000). There are numerous records in the JeDI, GBIF, and OBIS databases of pyrosomes at >1000 m depth, although to our knowledge no such observations have been recorded in literature studies.

P. atlanticum thus exhibits extensive yet variable DVM by region, traveling anywhere from 20 m to ≥ 500 m through the water column between day and night (Fig. 3c). Andersen and Sardou (1994) also noted evidence for size-related DVM; colonies of 3 mm length only migrated on average 90 m, while 51 mm colonies migrated 760 m and tended to arrive in surface waters slightly later at night. As for most zooplankton, pyrosome DVM is likely linked to feeding: in one study, gut pigment levels in colonies were 1.8 times higher at night than during the day, presumably from nocturnal surface feeding (Perissinotto et al. 2007).

Feeding and growth
Feeding

Pyrosomes, similar to other filter-feeding tunicates, have huge predator–prey mass ratios, on the order of 50 million : 1 (Heneghan et al. 2020; for comparison, carnivorous copepods have ratios of 50 : 1 and herbivorous copepods of 50,000 : 1). Thus, despite their large size, pyrosomes consume relatively small particles, ingesting a wide range of types and sizes of phytoplankton and detrital matter. Records of specific prey types for *P. atlanticum* include prymnesiophytes (predominantly coccolithophores), dinoflagellates, centric diatoms, and
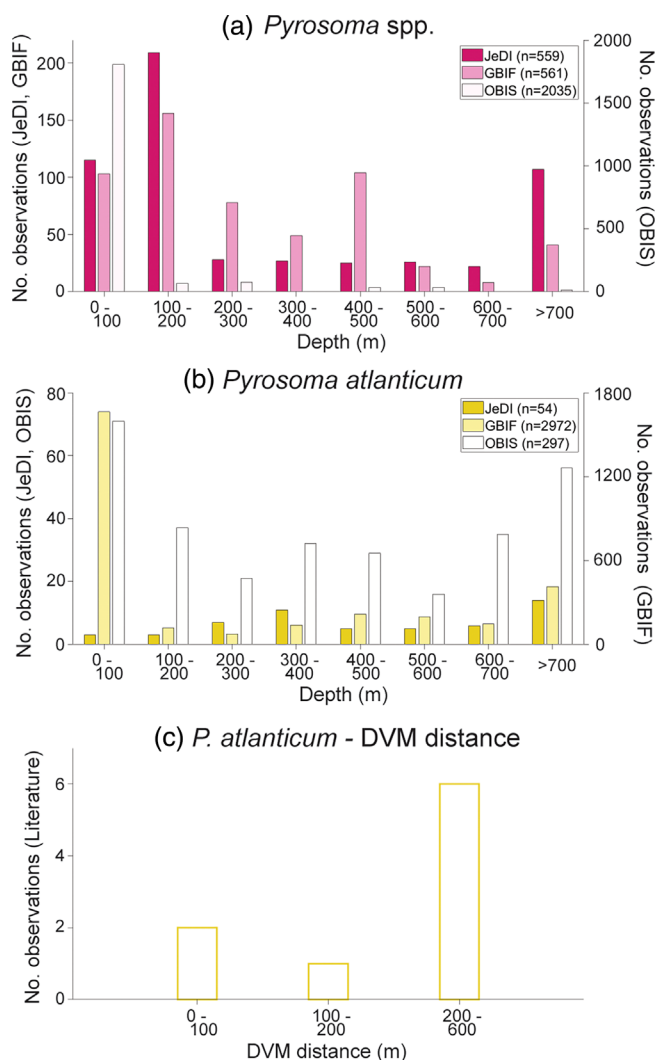
Fig. 3. (**a,b**) Daytime depth distributions for (**a**) *Pyrosoma* spp. and (**b**) *P. atlanticum*. Bars are separated by data source (JeDI—dark; GBIF—medium; OBIS—light), with total number of records listed in parentheses. Depths are binned by 100-m group; all observations deeper than 700 m are binned together. (**c**) DVM distances for *P. atlanticum* from literature sources (*n* = 9), as reported or calculated from differences between day and night mean depths.

crustacean fragments and eggs (Drits et al. 1992; Mayzaud et al. 2007; Perissinotto et al. 2007; Schram et al. 2020). There is some evidence that *P. atlanticum* consumes highest levels of prymnesiophytes and dinoflagellates, as indicated by elevated levels of corresponding fatty acid signatures, but fewer diatoms (Perissinotto et al. 2007; Schram et al. 2020). Documented prey sizes range from 3 μm to 150 μm (Drits et al. 1992). Some studies record preferential consumption of smaller prey (generally <10 μm; Palma and Apablaza 2004; O'Loughlin et al. 2020), whereas others note evidence for higher consumption of particles >10 μm (Perissinotto et al. 2007; Henschke et al. 2019). *P. atlanticum* thus appears

capable of tolerating, and even benefiting from, a wide range of prey types and sizes.

Diet preferences of *Pr. spinosum* are less clear. The species has been documented to feed predominantly on flagellates and cyanobacteria, but occasionally on diatoms and dinoflagellates, where available (Gauns et al. 2015). One study hypothesized that a *Pr. spinosum* bloom in the Arabian Sea benefited from a corresponding bloom of the small (< 1.5 μm) unicellular cyanobacterium *Synechococcus* (Gauns et al. 2015), although the authors did not analyze gut contents for proof of consumption and the blooms may have been coincidental. A separate study in the Eastern Tropical Pacific found that, although a *Pr. spinosum* bloom coincided with high levels of *Synechococcus*, gut contents of *Pr. spinosum* contained low phaeopigment markers for *Synechococcus* compared to the overall phytoplankton community (Décima et al. 2019). They therefore hypothesized that *Pr. spinosum* may have been feeding deeper than the *Synechococcus* bloom. However, considering the open-ocean environments of both these blooms, we suggest that *Pr. spinosum* generally feeds predominantly on small-celled phytoplankton (e.g., cyanobacteria and prymnesiophytes) that would be expected to dominate such waters.

Impact on phytoplankton

The combination of high colony densities and fast clearance rates (Table 2) results in pyrosome blooms substantially impacting phytoplankton stocks. Studies of the highest-density blooms of *P. atlanticum* estimated removal of 53–95% of the total phytoplankton stock (Drits et al. 1992; Henschke et al. 2019), even though pyrosome colonies only had an energy requirement for ~20% of the phytoplankton biomass (Henschke et al. 2019). The only estimate for percent removal of phytoplankton standing stocks by *Pr. spinosum* is 0.7–17.5%, with a single location value recorded at 36.2% (Décima et al. 2019). At times, pyrosome blooms may thus be substantial competitors for phytoplankton with other zooplankton groups.

However, both *P. atlanticum* and *Pr. spinosum* tend to feed at a lower trophic position than most zooplankton groups, particularly crustaceans such as copepods and euphausiids (Schram et al. 2020). Trophic positions of both pyrosome species are comparable to salps (Richoux and Froneman 2009) but lower than doliolids, appendicularians, and all other zooplankton (Décima et al. 2019). Décima et al. (2019) observed *Pr. spinosum* feeding slightly deeper in the water column, at the 20–40 m depth mixed layer, than surface feeding by other zooplankton groups. They hypothesized that the species may thus form a completely different feeding loop that does not directly compete for prey.

Growth rates

To our knowledge, no laboratory study has successfully measured pyrosome growth rates, although two studies have estimated *P. atlanticum* growth rates from field observations.

Table 2. Ranges of biological and ecological characteristics of *P. atlanticum* and *Pr. spinosum*.

Category	*P. atlanticum*	*Pr. spinosum*
Colony density		
Low	0.002–1 col m^{-3}[1a1, 1a6, 1a14, 1a2, 1a8, 1a9, 1a12]	0.04 L m^{-2}[2a1]
High	3–41 col m^{-3}[1a1]	2.7 L m^{-2}[2a1]
Colony length (mm)		
Pelagic	6–260[1a1, 1a2, 1a4, 1a5, 1a6, 1a8]	500–2000[2a1, 2a2]
Benthic	145–400[1b1, 1b2, 1b3, 1b4]	3700–20,000[2a3, 2a4]
Ingestion rate (μg col^{-1} d^{-1})	3.8–19.8[1a9], 39.6–41.3[1a1, 1a7]	19,200[2a1]*
% Phytoplankton grazed		
Low	0.01–5%[1a1, 1a2, 1a7, 1a9]	0.7–17.5%[2a1]
High	22–95%[1a1, 1a2, 1a9]	36.2%[2a1]
Phytoplankton cell sizes (μm)	3–150[1a1, 1a7, 1a10, 1a12, 1a13]	0.8 to > 2[2a1, 2a2]
Clearance rate (L col^{-1} h^{-1})	3.6–13.6[1a1, 1a2, 1a9]	3 × 10^3[2a1]§
Gut turnover time (h)	0.75–2.6[1a1, 1a7, 1a9]	–
DW/WW (g)	1.1–3.6/22–64[1a7]	0.2 g m^{-2} (DW only)[2a1]
% Lipid or nitrogen	Lipid: 5–7[1a7, 1a10]	Nitrogen: 8.8[2a2]
Carbon flux (mg C m^{-2} d^{-1})		
Low	10–15[1a2, 1a3, 1a6]	18.9[2a1]
Bloom	300–1000[1a1]	
Fecal pellet production (pel h^{-1})		70 × 10^3–108 × 10^3[2a2]
Low	338[1b1]	
Bloom	1729[1a1]	

Description of units: "Colony density" is colonies per cubic meter for *P. atlanticum* and liters per meter squared for *Pr. spinosum* for either low-density ("non-bloom") or high-density ("bloom") observations; "Colony length" is in millimeters, for either pelagic blooms or benthic carcass falls; "Ingestion rate" is micrograms of pigment per colony per day ("*" indicates values were converted from milligrams per colony per hour); "%Phytoplankton grazed" is the percentage of the phytoplankton population that was grazed by pyrosomes during either low or high concentrations; "Phytoplankton cell sizes" is the range of reported phytoplankton cell sizes (diameter) ingested, in microns; "Clearance rate" is the amount of water that pyrosome colonies were measured to filter, as liters per colony per hour ("§" indicates values were converted from meters cubed per colony per hour); "Gut turnover time" is the amount of time, in hours, for pyrosome colonies to completely empty their guts; "DW/WW" are the respective values of ash-free DW and wet weight, in grams, reported separately; "%lipid or nitrogen" is the percentage of dry-weight body mass comprised of lipids (*P. atlanticum* only) or nitrogen (*Pr. spinosum* only); "Carbon flux" is the amount of carbon, in milligrams per meter squared per day, exported below the mixed layer (variable depth by study location and water feature), from either low-density or high-density pyrosome occurrences; "Fecal pellet production" refers to the number of fecal pellets per colony per hour. Reference key: [1a1]Drits et al. (1992), [1a2]Henschke et al. (2019), [1a3]Stenvers et al. (2021), [1a4]Andersen et al. (1992), [1a5]Andersen and Sardou (1994), [1a6]Lyle et al. (2022), [1a7]Perissinotto et al. (2007), [1a8]Sutherland et al. (2018), [1a9]O'Loughlin et al. (2020), [1a10]Mayzaud et al. (2007), [1a11]Davenport and Balazs (1991), [1a12]Schram et al. (2020), [1a13]Palma and Apablaza (2004), [1a14]Guerrero et al. (2016), [1b1]Lebrato and Jones (2009), [1b2]Hurley and McKnight (1959), [1b3]Osborne and Hubbard (2018), [1b4]Roe et al. (1990), [2a1]Décima et al. (2019), [2a2]Gauns et al. (2015), [2a3]Griffin and Yaldwyn (1970), [2a4]Grace (1971).

Andersen and Sardou (1994) observed pyrosome colonies in the Northwestern Mediterranean increasing from 6–7 mm to 14–16 mm length across 24-h and 69-h windows, resulting in growth rates of 24–75% of colony length per day. Henschke et al. (2019) estimated growth rates of pyrosome colonies in the East Australian Current from percentages of phytoplankton clearance and approximate assimilation and respiration coefficients. Pyrosomes had potential growth rates of 0.6% of body C d^{-1} in a high-productivity cold-core eddy but only 0.02–0.05% body C d^{-1} in two neighboring low-productivity warm-core eddies. Pyrosomes in the two regions thus showed a 100-fold difference in growth rates, even though Chl *a* concentrations were only three times higher in the cold-core eddy (0.12 vs. −0.36 log$_{10}$[mg m^{-3}]; Henschke et al. 2019).

Predation
Predators

By incorporating carbon from tiny particles (nanoplankton and picoplankton) into their relatively large-bodied colonies, pyrosomes make energy directly available to much larger predators, often at the highest trophic levels (Sutherland and Thompson 2022). A variety of pelagic predators consume pyrosomes, including 62 fish species, 3 turtle species (Harbison 1998), 2 albatross species (James and Stahl 2000), 1 sea lion species (Childerhouse et al. 2001), and zooplankton and ciliate parasites (Perissinotto et al. 2007). Specific fish predators include walleye pollock, Arctic cod, giant grenadier, prowfish, various species of rockfishes, and sablefish in the Gulf of Alaska (Brodeur et al. 2021). Trevally (*Hyperglyphe*

porosa) off Australia and New Zealand were observed with their stomachs full of pyrosomes (Cowper 1960). Pyrosome falls in the Mediterranean Sea, Gulf of Alaska, and Gulf of Mexico are frequently consumed by benthic predators, particularly dominant species of echinoderms, cnidaria, and arthropods (Lebrato and Jones 2009; Lebrato et al. 2013), including 11 species not previously recorded as feeding on pyrosomes (Archer et al. 2018).

Nutritional content

Pyrosomes, with their gelatinous and watery bodies, have often been dismissed as low-nutrient trophic dead-ends similar to other gelatinous zooplankton such as salps (Henschke et al. 2016) and jellyfish (Lamb et al. 2019). However, *P. atlanticum* and *Pr. spinosum* appear to have among the highest carbon contents of gelatinous zooplankton, on a dry weight (DW) basis: 9.4–39.2% for *P. atlanticum* and 9.2–37.7% for *Pr. spinosum* (see Supplementary Table S2 for source references for ranges). These values extend substantially higher than the < 20% body carbon observed for salps and many other gelatinous taxa, although not as high as for

chaetognaths (39–52%) and appendicularians (50–62%; Fig. 4; Supplementary Table S2).

Conley et al. (2018) noted that mucous-mesh gelatinous grazers (pyrosomes, salps, doliolids, and appendicularians) can have high water content and low overall caloric value but still have high carbon and nutrient contents in terms of DW. Regardless, pyrosomes likely preferentially employ high biomass turnover rather than lipid storage as their primary mechanism of energy storage and use, as demonstrated by their high water content (Mayzaud et al. 2007; Perissinotto et al. 2007).

Carbon cycling

The heavy tunics, large colony sizes, and dense fecal pellets of pyrosomes could provide a rapid means of exporting carbon through the water column and delivering food to benthic communities, although limited information is available (Table 2; Lebrato and Jones 2009; Lebrato et al. 2013; Conley et al. 2018). Fecal pellets of *P. atlanticum* have a measured sinking rate of 70 m d^{-1} and carbon content of 22% (Drits et al. 1992). This sinking rate is substantially slower than those recorded for salps (320–2700 m d^{-1}; Bruland and Silver 1981; Madin 1982), copepods (120–220 m d^{-1}; Honjo
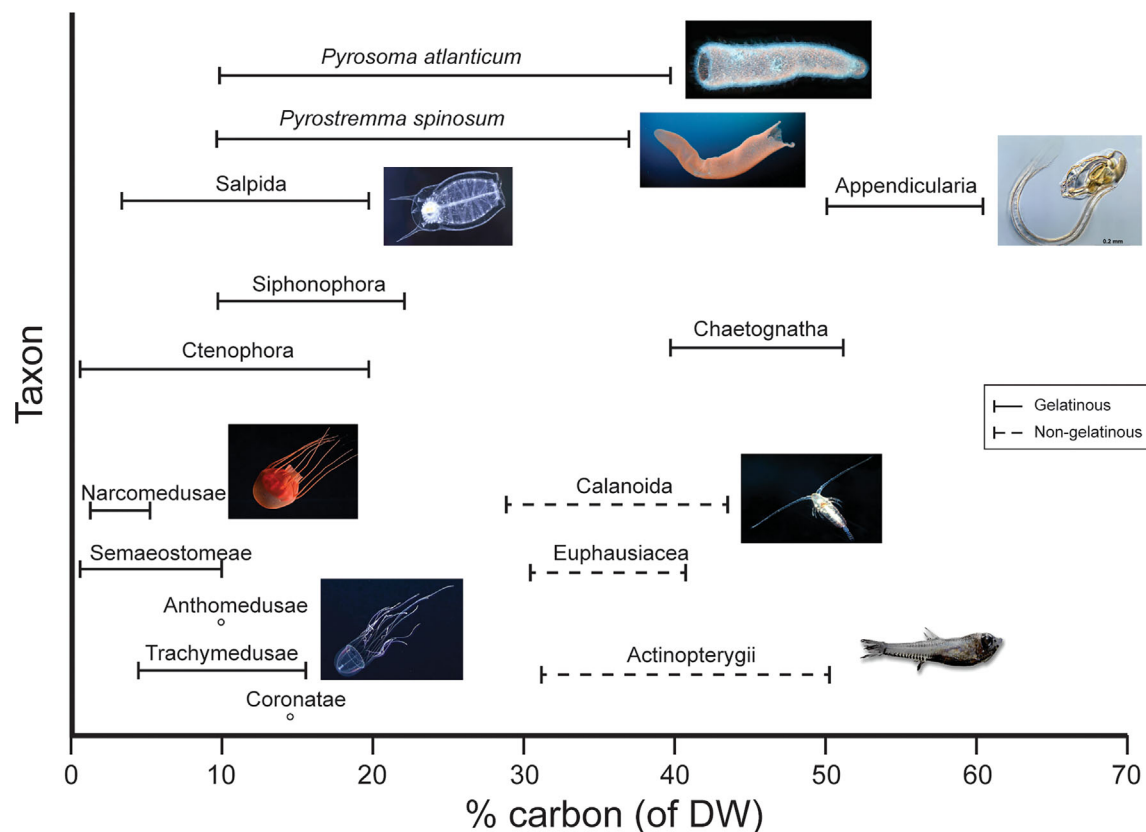

Fig. 4. Percent carbon content (%C) of body DW for gelatinous (solid lines) and nongelatinous (dashed lines) zooplankton orders. *P. atlanticum* and *Pr. spinosum* are shown individually. Exact ranges of %C and source references for each range are listed in Supplementary Table **S2**. Image references: *P. atlanticum*—McDaniel (2022); *Pr. spinosum*—DORIS (2022); *Thalia democratica*—Oceana (2022); *Oikopleura dioica*—SIO (2022); *Aeginura grimaldii*—Shale (2022); *Colobonema sericeum*—Schmidt (2020); *Calanus helgolandicus*—PML (2018); *Vinciguerria attenuata*—Costa (2018).

and Roman [1978]; Stamieszkin et al. [2015]), and even doliolids (up to 200 m d^{-1}; Bruland and Silver [1981]). However, the pyrosome pellet rate was extrapolated from experiments in a graduated cylinder, so it may not accurately capture in vivo sinking rates. We also did not find any published estimates of tunic sinking rates, which limits our ability to model pyrosome-based carbon sequestration.

The large colony sizes and dense blooms of pyrosomes can, however, lead to large amounts of carbon export to deep waters and the benthos, similar to other gelatinous zooplankton such as salps (Henschke et al. [2013]; Smith et al. [2014]; Luo et al. [2020]). Off the Cabo Verde Islands, a *P. atlanticum* bloom produced a three-fold increase in carbon export compared to the particulate organic carbon concentration in surrounding waters, via the sum of fecal and respiratory fluxes (Stenvers et al. [2021]). A separate bloom off the Ivory Coast produced benthic carbon levels of up to 22 g m^{-2}, representing a 20-fold increase in carbon compared to nearby areas (Lebrato and Jones [2009]).

Magnitudes of carbon removal by pyrosome blooms vary among studies and regions. Highest reported fluxes are 300–1000 mg C m^{-2} d^{-1} from fecal pellets alone (Drits et al. [1992]); other literature sources report lower values, around 10 mg C m^{-2} d^{-1} (Andersen and Sardou [1994]; Henschke et al. [2019]), while still other studies report intermediate values of 15–485 mg C m^{-2} d^{-1} from fecal pellets (Table [2]; Stenvers et al. [2021]). However, differential depths of DVM can have a confounding effect on active carbon transport. Henschke et al. ([2019]) found that, although total pyrosome biomass (and thus feeding and excretion) was significantly higher in a cold-core eddy of the East Australian Current compared to neighboring warm-core eddies, 70% of the carbon flux in the cold-core eddy was likely excreted and recycled in the mixed layer, rather than at depth, because pyrosomes were not migrating as deep as in the warm-core eddies.

Future research directions

Many aspects of pyrosome biology and ecology remain poorly described. In particular, apparent contradictions in temperature/Chl *a* relationships and DVM distances of *P. atlanticum* among different regions present valuable opportunities for future research. We pose two questions on thermal preferences of pyrosomes and drivers of *P. atlanticum* blooms and examine potential patterns of coherence across studies despite seeming differences. We then present additional questions that we deem essential for expanding our understanding of pyrosomes and ability to incorporate them into ecological models and future predictions.

Do pyrosomes preferentially inhabit cool-to-temperate waters?

Based on literature-described patterns of habitat use, *P. atlanticum* may preferentially be a temperate species that can tolerate warm temperatures but requires regular immersion in cool waters. Six literature studies describe elevated *P. atlanticum* abundances at temperatures below 18°C (Perissinotto et al. [2007]; Tobena and Escanez [2013]; Sutherland et al. [2018]; Henschke et al. [2019]; Schram et al. [2020]; Lyle et al. [2022]), while only three studies observed elevated *P. atlanticum* in 18–22°C waters (Richoux and Froneman [2009]; Pitt et al. [2021]; Stenvers et al. [2021]). Notably, Henschke et al. ([2019]) observed 1000 times greater *P. atlanticum* biomass in an upwelling cold-core eddy at 16°C (mean upper 100 m temperature) compared to two neighboring warm-core eddies > 18.5°C. Additionally, while *P. atlanticum* bloom abundance in the Northern California Current System showed a positive relationship with temperature, that relationship only extended up to 12–14°C (Schram et al. [2020]), well below the 18°C threshold we identify here. Matching database records of *P. atlanticum* to satellite SST corroborates this trend, with an interquartile range of 13–18°C. Both literature and database records of *P. atlanticum* range up to 30°C, and the interquartile range of *Pyrosoma* spp. database-satellite comparisons encompasses temperatures up to 28°C, indicating that *P. atlanticum* certainly inhabits waters > 18°C. However, we posit that, while *P. atlanticum* can tolerate a wide range of temperatures for certain periods, it preferentially inhabits waters < 18°C.

We hypothesize that *P. atlanticum* employs DVM to return to its optimal cool sub-surface temperature range after nighttime upper ocean feeding in warmer waters. Studies report significant differences in DVM distance for cool-water and warm-water systems, with DVM to warm surface waters ranging from 2 to 10 times the distances of cool-water systems (see Section [1.2.3]; Andersen et al. [1992]; Andersen and Sardou [1994]; Sutherland et al. [2018]; Henschke et al. [2019]; Stenvers et al. [2021]; Lyle et al. [2022]). *P. atlanticum* may need to migrate substantially deeper in warm-water systems to reach its optimal temperatures, whereas cool-water systems already have optimal conditions in near-surface waters.

There are two records of *Pr. spinosum* in surface waters 26–27°C (Gauns et al. [2015]; Décima et al. [2019]), substantially warmer than *P. atlanticum*. However, the question of true thermal ranges for *Pr. spinosum* again arises. In a *Pr. spinosum* bloom on the Costa Rica Dome, Décima et al. ([2019]) noted that mixed layer temperatures, which the pyrosomes presumably moved into or through during DVM, were 12–15°C. Several *Pr. spinosum* sightings, though not blooms, have also occurred off southeastern Australia and New Zealand in the relatively cool Tasman Sea (Griffin and Yaldwyn [1970]; Grace [1971]). Although the temperature range for *Pr. spinosum* database samples extends to 29°C, its lower end encompasses cooler waters comparable to the range of *P. atlanticum*. *Pr. spinosum* may thus prefer warmer temperatures than *P. atlanticum* or inhabit a wide range of temperatures equally, or it may similarly tolerate warm temperatures for certain periods before migrating to cooler waters.

We recommend several methods to test thermal preferences of pyrosomes. The first step is to increase depth-resolved

sampling, which will allow us to better constrain the true habitat ranges of pyrosomes and examine whether they spend time preferentially at certain temperatures. Depth-resolved sampling requires making a concerted effort to conduct depth-stratified (e.g., MOCNESS) tows, both day and night, when pyrosome blooms are encountered. Depth-resolved sampling can also be increased via in situ water column imaging technologies such as the Underwater Vision Profiler (Picheral et al. 2010), Zooglider (Ohman et al. 2019), and In situ Ichthyoplankton Imaging System (Cowen and Guigand 2008), although these technologies are limited in the organism sizes they can image. A second method is to measure physiological rates (e.g., growth and reproduction) at various temperatures to determine optimal thermal conditions for those processes. Rate measurements can be approximated from repeat high-temporal-resolution in situ sampling of blooms (i.e., Andersen and Sardou 1994; see Section 1.3.3) or via shipboard or laboratory experimentation (see Henschke et al. 2019; O'Loughlin et al. 2020).

Do certain combinations of conditions induce *P. atlanticum* blooms?

Rapid population increases of *P. atlanticum* are likely to occur in response to optimal combinations of temperature, Chl *a* concentration, and other factors such as additional relevant habitat conditions, specific prey types or sizes, absence of predators, or favorable advection. Three studies that developed statistical models of *P. atlanticum* from habitat variables found negative or neutral relationships with temperature and positive relationships with Chl *a* (Henschke et al. 2019; O'Loughlin et al. 2020; Stenvers et al. 2021). Elevated Chl *a* conditions often coincide with cooler temperatures, so it is difficult to separate the effect of each variable on pyrosome blooms. However, occurrences of several large blooms in high-chlorophyll conditions suggest that *P. atlanticum* is not a predominantly oligotrophic species and may benefit from high-productivity conditions to form bloom-level densities.

Advection may also induce *P. atlanticum* blooms. Some blooms may occur due to advection transporting seed populations into an area of favorable conditions, while other blooms may occur solely via in situ populations responding to altered conditions. Whether advection is an essential component for bloom formation depends on whether a region already has a seed *P. atlanticum* population. One outstanding question related to advection is whether regions of apparently novel *P. atlanticum* appearances (e.g., the Northern California Current), where no pyrosome blooms were recorded before 2015, actually had novel population advection or simply lacked prior observations in pyrosome habitat.

One method for analyzing bloom evolution and responses to varying habitat conditions is to conduct high-resolution repeat sampling of *P. atlanticum* blooms (e.g., Andersen and Sardou 1994). Such samples could be linked to corresponding habitat data, using statistical modeling (e.g., generalized additive models, species distribution models) to identify trends. Modeled relationships could be compared among geographic regions and habitat ranges to determine overall patterns of pyrosome environmental preferences, as well as location- or condition-specific responses. Modeled pyrosome-habitat relationships could be valuable for incorporation into ecosystem models and future predictions. Additional existing datasets (e.g., many listed in the EcoTaxa data exploration platform, https://ecotaxa.obs-vlfr.fr/explore/), particularly from region-specific repeat sampling, can also be analyzed for environmental patterns.

A second method is particle tracking and population models. Particle tracking models are useful for determining bloom origins and proportions of bloom evolution caused by advection (see Dorman et al. 2011; Lilly et al. 2022 for examples with euphausiids), particularly in instances where there are relatively few observations. Size-structured population models are also valuable for evaluating population growth and potential future changes (e.g., Henschke et al. 2015; Henschke et al. 2018 for salp blooms), although these require estimates of growth rates under varying habitat conditions. Specific questions for any short-term sampling or modeling efforts are: How quickly do *P. atlanticum* blooms respond to short-term changes in habitat conditions? Do *P. atlanticum* blooms respond non-linearly to environmental conditions beyond certain thresholds? What factors cause bloom die-off?

What are the basic process rates and genetic diversity of *P. atlanticum*?

A first step toward improved understanding of *P. atlanticum* bloom appearance and evolution is to better quantify basic process rates (e.g., colony growth rate, maximum age, reproductive rates, feeding, and excretion). As part of this focus on process rates, the global population of *P. atlanticum* could be evaluated for genetic structure, particularly region-specific physiological adaptations, since the rapid growth and reproductive rates of zooplankton make them prime candidates for regional evolution (Dawson and Hamner 2005). Genetic diversity under different conditions could explain why *P. atlanticum* appears to bloom in such disparate ocean environments.

Fundamental to quantifying basic process rates is refining our ability to maintain pyrosomes alive in captivity, even short-term (12–24 h). No land-based laboratory experiment successfully rearing pyrosomes has yet been reported, although several short-term shipboard experiments have shown success (Perissinotto et al. 2007; Décima et al. 2019; O'Loughlin et al. 2020). Second, conducting more shipboard captivity experiments will allow us to better measure physiological rates and test potential preferences for prey types and cell sizes via consumption of fluorescent abiotic particles (see Perissinotto et al. 2007). As noted in Section 2.2, a second method is to conduct short-interval repeat in situ sampling of evolving pyrosome blooms, which can also shed light on reproductive rates and timing.

Third, tissue samples of pyrosomes from various regions could be analyzed for possible underlying genetic variation in

physiological responses. Govindarajan et al. (2011) provided genetic insights into differentiation between Pyrostremmatidae and Pyrosomatidae but did not comment on possible genetic structure. We suggest genetic analysis as part of an integrated morphological and molecular approach, with particular focus on region-specific analysis of DNA barcodes, as advocated by the Census of Marine Zooplankton (Bucklin et al. 2010). A similar global population analysis was recently conducted on two species of ctenophores using a combination of whole-genome, mitochondrial, and nuclear sequencing (Johnson et al. 2022), and found instances of both genetic similarity despite seeming barriers and genetic distinction despite apparent lack of barriers. The question of regional genetic variation in pyrosomes thus remains ripe for study.

Do pyrosome blooms alter food web dynamics and carbon export pathways?

Ranges of prey types and sizes for *P. atlanticum* are large (3–150 μm) and vague (coccolithophores to diatoms), and diet preferences of *Pr. spinosum* have only been described in two studies. Several studies have recorded pyrosomes at one of the lowest trophic positions within the zooplankton (Richoux and Froneman 2009; Décima et al. 2019; Schram et al. 2020). Pyrosomes are thus unlikely to directly compete with other zooplankton groups for prey, but we do not know whether they can change their feeding level depending on prey types or other factors. Additionally, does rapid consumption by pyrosomes of small phytoplankton alter microzooplankton feeding and thus indirectly impact other mesozooplankton? How do pyrosomes compete with heterotrophic protists such as the protozoa, which can filter 10^5 body volumes per hour (Fenchel 1987)?

We first suggest additional stable isotope and fatty acid analyses to understand pyrosome trophic positions and feeding preferences. Second, to determine whether zooplankton predators substantially change their diets when pyrosome blooms occur, we suggest comparing predator diets (via stomach contents and stable isotopes) and nutritional composition (via tissue analysis) in the presence and absence of pyrosomes. Third, newer methods (e.g., sequencing and quantitative PCR for prey identification and concentrations) and novel applications of existing methods (e.g., flow cytometry to distinguish pyrosome tissue from prey cells) hold potential to more fully examine prey composition and concentrations of pyrosomes (Thompson et al. 2021; Sutherland and Thompson 2022). Finally, we suggest a comparative analysis of the feeding biometrics of pyrosomes vs. other major filter-feeding components (e.g., protozoans, salps, and appendicularians) to help contextualize pyrosome roles and impacts within marine food webs.

Impacts of pyrosome blooms on carbon export pathways also need to be further measured. Ranges of percent body carbon and nitrogen, as well as sinking rates of fecal pellets and carcasses, are poorly constrained or only described by single studies. Further, under what conditions are pyrosome carcasses remineralized in the upper layers of the water column rather than sinking to sufficient depth for carbon sequestration? How much does DVM contribute to active carbon transport? We suggest additional fecal pellet experiments similar to those conducted for salps and doliolids (Bruland and Silver 1981). Finally, depth-resolved sampling of pyrosomes (as mentioned in Section 2.1) can help estimate relative proportions of active carbon transport and upper ocean remineralization (sensu Henschke et al. 2019).

Will *P. atlanticum* blooms increase and encroach on human activities in the future?

The recent increase in worldwide reports of pyrosome blooms raises the question of whether pyrosome abundance has increased in the last decade or has only appeared to increase due to improved sampling and greater scientific attention (e.g., in situ imaging that does not result in organism destruction; improved recordkeeping of large pyrosomes discarded at sea). Interest in pyrosomes does appear to show some increase. Searches for the term "Pyrosome" across all English literature using Google Ngram Viewer yield a minor increase since 2015, compared to a slight long-term decrease in the "Zooplankton" term (Supporting Information Fig. S1), although a quantitative analysis of whether pyrosome occurrences are increasing is not possible because of insufficient long-term data on pyrosome abundances.

In terms of actual population increases, recent mesocosm studies involving a closely-related tunicate, the appendicularian *Oikopleura dioica*, observed populations increases under warmer temperatures and lower pH (Troedsson et al. 2013; Winder et al. 2017). These studies hypothesized that increasing temperatures preferentially speed up biological rates of heterotrophs over autotrophs, which, combined with apparent tolerance by appendicularians for low pH, allow their populations to increase. Shifts toward oligotrophic phytoplankton communities further favor filter-feeding mesozooplankton such as appendicularians and pyrosomes. Robust quantitative analysis of whether pyrosome blooms are increasing in occurrence or density is not currently possible because of lack of available abundance data. It would help to standardize records among sampling types and efforts.

Because the basic habitat and bloom conditions of pyrosomes are poorly described, any current hypotheses about their global population changes are almost purely speculative. If *P. atlanticum* does favor waters below 18°C and elevated primary production, then many parts of the ocean may become uninhabitable. However, physical changes in some regions, such as Eastern Boundary Upwelling Systems, are themselves largely uncertain. There is some evidence that upwelling may intensify at the poleward ends of certain upwelling systems (e.g., the California Current System), although surface warming and reduced primary production are also projected (Garcia-Reyes et al. 2015; Rykaczewski et al. 2015; Bograd et al. 2023). Western Boundary Currents are similarly poorly projected, although there is evidence that the East Australian Current is strengthening and

leading to warming of the Tasman Sea (Suthers et al. 2011), which may alter pyrosome seeding via advection. Better constraining the habitat conditions of pyrosome blooms will allow us to better forecast when and where future blooms may occur, as global physical ocean forecasts also improve in accuracy.

Conclusions

While pyrosomes remain mysterious, this review has collated the known information on their reproduction, habitat use, feeding, predation, and carbon cycling. We suggest that the seemingly broad thermal range of *P. atlanticum* may belie a preference for habitats below 18°C, and that differential DVM distances among regions highlight how modifying this behavior helps position *P. atlanticum* in its optimal thermal range. Additional conditions that promote pyrosome blooms may involve elevated Chl *a* levels and advection by region.

Relatively little information exists on pyrosomes because, to date, these organisms have rarely compelled enough interest to warrant researchers to measure their population densities, reproduction, habitat, predation, and carbon export. This lack of information is a common theme across gelatinous taxa, including salps (Henschke et al. 2016) and siphonophores (Hetherington et al. 2022). Much additional information could be compiled simply by making additional in situ measurements when blooms occur and sampling time permits, allowing us to better understand the broader roles and impacts of *P. atlanticum* and other pyrosome species in marine ecosystems.

Only by refining our understanding of *P. atlanticum* can we hope to predict how its populations might change in the future. Such questions are key as we continue to debate potential long-term increases (Richardson et al. 2009) vs. cyclicality (Condon et al. 2012) in various gelatinous taxa across the global oceans, as well as biologically mediated contributions to oceanic carbon sequestration (Steinberg and Landry 2017; Luo et al. 2020). With many physical changes to ocean systems already occurring, we must define our baseline understanding of the mechanisms, frequency, and extent of pyrosome blooms to determine whether they will change significantly in coming decades and what impacts they may have on other plankton and the larger food web.

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Conflict of Interest

None declared.