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In situ observations of pyrosomes in the northern California Current

during an anomalous bloom year

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# Abstract

Pyrosomes (Pyrosoma atlanticum) are pelagic colonial tunicates that are typically found in tropical ocean waters. Research surveys from 2014 to 2017 conducted by the National Oceanic and Atmospheric Administration (NOAA) showed unusually high abundances of pyrosomes off the Oregon Coast, where they have not previously been observed, with the largest coastal blooms occurring in spring and summer of 2017. While pyrosomes can migrate to depths of 700 m over diel cycles in their normal range, nothing is known about their vertical distribution in the northern California Current. We made seven deployments of a stereo camera system equipped with a temperature data logger over a diurnal period at an off-shore location off the central Oregon coast and analyzed the video footage for pyrosome abundance, length, orientation, and density relative to temperature and depth. Results indicated that despite an observed temporal variation in pyrosome vertical distribution, across all deployments pyrosomes tended to be mainly distributed between 25 m and 35 m, with 53.6% of all pyrosomes observed aggregating in this depth range. Pyrosomes distributed between 25 m and 30 m were significantly shorter than pyrosomes between 30 m and 50+ m and tended to have a smaller nearest neighbor distance. Temperature did not appear to have an effect on pyrosome distribution. Pyrosomes oriented their bodies obliquely in the water column, which may provide additional insight into their swimming behaviors. By characterizing the swimming behaviors and abundance of pyrosomes over various depths in the northern California Current, better predictions can be made for how pyrosomes may impact the pelagic ecosystem of the North Pacific.

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#### Chapter 1

#### Background

#### 1.1 Overview

Pyrosomes (*Pyrosoma atlanticum*) are pelagic colonial tunicates that are typically found in tropical ocean waters. Research surveys from 2014 to 2017 conducted by the Northwest Fisheries Science Center, National Oceanic and Atmospheric Administration (NOAA) showed unusually high abundances of pyrosomes off the Oregon Coast, where they had not previously been observed, with the largest coastal blooms occurring in spring and summer of 2017 (Brodeur et al. 2018). While pyrosomes can migrate to depths of 700 m over diel cycles in their normal range (Angel 1989, Andersen et al. 1992), nothing is known about their vertical distribution in the northern California Current. Several deployments of a stereo camera system equipped with a temperature data logger were made over a diurnal period at an off-shore location off the central Oregon coast. The video footage was analyzed for pyrosome length, orientation, abundance, and density relative to temperature and depth. The results of this analysis provide new insights on fine-scale movements of pyrosomes throughout the day. By characterizing the swimming behaviors and abundance of pyrosomes over various depths in the northern California Current, better predictions can be made for how pyrosomes may impact the pelagic ecosystem of the North Pacific.

This thesis includes an in-depth evaluation of the underwater video camera systems used in my research to capture midwater ecological data. Each camera system presented multiple benefits and challenges to capturing the fine-scale interactions and distributions of gelatinous organisms, which should be considered as efforts are made to further improve the accuracy of these technologies as well as improve the current understanding of which system is best to use to collect these data. Another unique aspect of my research was that pyrosomes were kept alive in the laboratory for a brief time to perform an ex situ diel vertical migration experiment. The observations made during this experiment are noted to provide additional insight into measures that should be taken to keep these organisms alive in a laboratory setting. To conclude, I discuss how this anomalous bloom of pyrosomes may have long-term impacts on the pelagic marine ecosystems within the northern California Current and the direction future research should take to provide a better understanding of these effects.

# **1.2 Pyrosome taxonomy**

Part of the phylum Chordata, tunicates are characterized by a gelatinous body encased in an extracellular sheath or "tunic" comprised primarily of cellulose, a notochord and dorsal nerve cord that are typically only present in larval stages, and a U-shaped gut (Godeaux et al. 1998). The subphylum Tunicata contains three classes: Ascidiacea (sea squirts), Thaliacea (salps, doliolids, and pyrosomes), and Appendicularia (larvaceans). The Thaliacea and Appendicularia are important plankton grazers in marine ecosystems and collect their prey using mucus sheets and ciliary movement to filter water through their hollow, gelatinous bodies (Alldredge & Madin 1982). Pyrosomes (*Pyrosoma atlanticum*) are free-floating, colonial tunicates (Class: Thaliacea, Order: Pyrosomatida, Family: Pyrosomatidae, Subfamily: Pyrosomatinae). *P. atlanticum* have a cylindrical, hollow tube-shaped body that has a relatively narrower oral opening at the top of the body and a wider cloacal opening at the end of the body (van Soest 1981). Each pyrosome is comprised of thousands of individual organisms called zooids (Figure 1a), which are arranged in parallel rows and assist the pyrosome with suspension feeding and locomotion (Alldredge & Madin 1982). Each zooid also contains luminescent organs which can be stimulated by mechanical, chemical, electrical, or photic stimuli; this bioluminescence may be used to communicate with zooids further away within the colony and may assist the pyrosome with predator-avoidance (Bowlby et al. 1990). *P. atlanticum* have not been observed to be bioluminescent off the Oregon Coast (pers. obs.) Pink or yellowish pink in color, their colonies can reach lengths of a few centimeters (Figure 1b) to several meters, with pyrosomes in the Northeastern Pacific reaching well over 80 cm in length (Brodeur et al. 2018).



**Fig. 1a** Pyrosomes (*Pyrosoma atlanticum*) are gelatinous, colonial tunicates that have a hollow, tube-like body. Each round projection from the body is an individual zooid. **Fig. 1b** Pyrosomes can be from a few centimeters to several meters in length. (Photo Credits: Aminda Rainey).

# **1.3 Feeding behaviors**

Similar to other thaliaceans, pyrosomes produce a mucus net for prey-capture (Alldredge & Madin 1982). When larger particles collide with the oral opening, the pyrosome responds by contracting the oral siphon and utilizing the motion of cilia to pass water through the mucus net within the branchial basket (Alldredge & Madin 1982, Burighel et al. 1992, Caicci et al. 2013). Pyrosomes are important phytoplankton and microzooplankton consumers in tropical ocean waters, where their blooms remove substantial proportions of the productivity (Drits et al. 1992), and have been recorded to have some of the highest clearance rates of any pelagic grazer, with up to 351 h<sup>-1</sup> per colony (Perissinotto et al. 2007). Swarms of *P. atlanticum* near the surface of the water have also been found to remove >50% of phytoplankton standing stock from the 0 m to 10 m layer (Drits et al. 1992). This removal of phytoplankton standing stock within this depth layer was several times greater than within the 0 m to 50 m layer and when compared with only 4% removed by sparsely distributed pyrosomes, which may suggest that aggregations of pyrosomes create a patchiness in grazing pressure (Drits et al. 1992). Therefore, pyrosome grazing may have an impact on the vertical distribution of phytoplankton assemblages in marine communities (Drits et al. 1992).

An analysis of the fatty acid composition of *P. atlanticum* further supported that the primary diet of pyrosomes consists of phytoplankton and an examination of gut content revealed that 80% of their diet consisted of phytoplankton (Coccolithophoridae, Silicoflagellata, and Bacillariophyceae) and the remainder being Radiolaria and Tintinnidae (Culkin & Morris 1970). Gut content analyses have also suggested that pyrosomes tend to select phytoplankton > 10  $\mu$ m in size (Perissinotto 2007), but they have also been shown to retain particles as small as 3  $\mu$ m to 4  $\mu$ m (Drits et al. 1992). Pyrosomes were shown to have significantly higher gut pigment contents at nighttime than daytime, which supports observations that pyrosomes tend to aggregate and feed at the surface at night after undergoing diel vertical migration (DVM; Perissinotto 2007).

It is important to better understand the vertical distribution and swimming mechanisms of *P. atlanticum* to gain a greater understanding of the potential impact of pyrosome prey-selectivity within pelagic ecosystems. The long-term decline in the total zooplankton biomass in the northern California Current has been attributed to the long-term increase in the biomass of pelagic tunicates, such as pyrosomes (Lavaniegos & Ohman 2003). Aside from the potential to restructure the natural assemblage of zooplankton communities in marine ecosystems through predation, *P. atlanticum* have been shown to be a significant prey source for a variety of fish and turtle species (Harbison 1998, Brodeur et al. 2018). Further, other organisms have been found living within pyrosomes, such as the crustacean *Funchalia* spp. (Lindsey et al. 2001) and juvenile stages of fish species (Brodeur et al. 2018). This suggests that pyrosomes may play an important role in interactions within marine ecosystems that is currently not yet fully understood.

#### **1.4** Distribution and abundance

*Pyrosoma atlanticum* are the most wide spread and common of the Pyrosomatida (van Soest 1981). They typically occur between 50°N and 50°S and are located in all oceans,

primarily in tropical waters (van Soest 1981; Figure 2). When pyrosomes are recorded, they are typically seen in immense swarms (Drits et al. 1992, Andersen & Sardou 1994), which can cause mechanical damage to the rest of the catch when recorded in nets (Angel 1989). *P. atlanticum* have been found to be extensive diel vertical migrators, migrating up to depths of 700 m (Angel 1989, Andersen et al. 1992). At the Azores Front, instances of pyrosomes exceeding 1000 m in depth were recorded, with the average depth of pyrosomes during the day ranging from 500 m to 700 m (Angel 1989). Pyrosomes have mainly been observed to aggregate on the surface of the water at night (Drits et al. 1992), typically occupying the 0 m to 75 m zone only during the dark period (Andersen et al. 1992). Pyrosomes that had larger colony sizes tended to have greater DVMs than pyrosomes with smaller colony sizes (Andersen et al. 1992).



**Fig. 2** *Pyrosome atlanticum* are typically found between 50°N and 50°S (highlighted in yellow) and are located in all oceans, primarily in tropical waters (Figure from van Soest 1981). The red star indicates where Newport, Oregon is located.

Around the world, unprecedented blooms of pyrosomes have been recorded in areas where they have not previously been observed. For example, between February and March 2006, an extensive pyrosome bloom occurred off the Ivory Coast of West Africa, where carcasses were found at depths of over 1100 m (Lebrato & Jones 2009). Another unusual bloom of pyrosomes was recorded in August 2013 in the oligotrophic coral reef ecosystem of Nanwan Bay, southern Taiwan, where densities of up to 1500 carcasses m<sup>-2</sup> were distributed at 10 m along the sandy bottom of the reef edge (Kuo et al. 2015). Pyrosomes have been observed intermittently in the southern California Current from 1951-2002 (Lavaniegos & Ohman 2003), but had never been recorded off the Oregon Coast (in the northern California Current) until 2014 (Brodeur et al. 2018).

#### **1.5** Impact on carbon fluxes in deep-sea benthic ecosystems

Tunicates can impact the vertical flux of organic carbon within deep-sea benthic ecosystems through introducing benthic and pelagic detritus in the form of fecal pellets, mucus from discarded feeding structures, and decomposing carcasses (Robison et al. 2005, Billett et al. 2006). Pyrosomes have been found to produce a significant amount of fecal pellets, with the average defecation rate by a single zooid of 1.4 to 2.2 pellets h<sup>-1</sup> (Drits et al. 1992). When there are blooms of pyrosomes with larger colony sizes, this rate of defecation may increase the carbon export to benthic ecosystems. Mass die-offs and depositions of pyrosomes on the seabed floor have also been recorded and have shown a significant increase in the jelly-carbon accumulation in these environments (Lebrato et al. 2012). This means that there could be a large influx of organic carbon off the central Oregon coast when the pyrosomes in this bloom start to die-off. While the lifespan of a pyrosome is currently unknown, it is estimated to be approximately 1 year. This means that this pyrosome bloom may already be starting to have an impact on the carbon fluxes within these pelagic ecosystems.

# **1.6** Research questions

To better understand pyrosome ecology, I addressed research questions that focused on the in situ vertical distribution of pyrosomes in relation to potential physical drivers (i.e. temperature) in the northern California Current. Pyrosome length, nearest neighbor distance, and orientation were analyzed to better understand the aggregation patterns and fine-scale swimming behaviors of pyrosomes. To improve monitoring of gelatinous zooplankton blooms, I evaluated the underwater video camera systems that were deployed to collect pyrosome data for their advantages and disadvantages. Through this research, I sought to answer the following questions:

- 1. What are the advantages and disadvantages of the underwater video camera systems used in this study for capturing distributions and interactions between gelatinous zooplankton?
- 2. What is the vertical distribution of pyrosomes in the northern California Current by deployment time?
- 3. How does the distribution of pyrosome length differ, on average, by deployment time?
- 4. Does pyrosome nearest neighbor distance differ, on average, by depth?

- 5. How do pyrosomes orient their bodies in the water column?
- 6. Can pyrosomes be kept alive in a laboratory for ex situ experiments?

By characterizing the vertical distribution and aggregation patterns of the 2017 pyrosome bloom in the northern California Current, better predictions can be made for how pyrosomes may impact trophic interactions within pelagic ecosystems. By also evaluating the current camera systems that are used for monitoring gelatinous zooplankton blooms, efforts can be made to improve these systems for future research. If this pyrosome bloom persists in this region, this information will be crucial for understanding the potential impact on commercial fisheries and the overall food web.

# Chapter 2

#### Evaluating the underwater video systems used in this study

During this study, multiple underwater video camera systems were deployed to capture the vertical distribution of pyrosomes. The first camera system that was deployed was the Benthically Anchored Suspended Stereo Camera (BASS Cam) system (Figure 3). This camera system is equipped with three high-definition GoPro HERO4 Black Edition cameras, two forward-facing with an overlapping field-of-view and one downwardfacing, encased in Sexton GoDeep Acrylic housing (rated to a depth of 500 m). The forward-facing cameras are separated (measured at the center of the lens) at a baseline of 38.1 cm, tilted inward at 7°. This system is also fitted with four Bigblue LED lights (15000 lm for the lower lights and 72000 lm for the upper lights) that help to illuminate the field-of-view at depth. The BASS Cam weighs approximately 16.7 kg in air and has six non-compressible buoys, with a total positive buoyancy of 19 kg. This camera system can be deployed at any descent rate to a depth of 100 m from the deck of a small fishing or research vessel using a 12VDC motor and spool that are manipulated by an up and down momentary switch. As a benthically anchored system, the BASS Cam was designed to monitor fish aggregations near the sea floor, but it is beneficial for studying midwater ecology as it collects continuous footage of the water column until maximum depth is reached. This system is also capable of projecting a live feed of the footage collected, providing researchers with a more effective and efficient way to survey study areas by allowing them to determine where specimens are located while at sea. One of the challenges of this system is that the depth limitation of 100 m allows for only nearshore

study areas, preventing researchers from gaining a more holistic perspective of vertical distributions and diel vertical migration patterns of gelatinous zooplankton.

**Fig. 3** The Benthically Anchored Suspended Stereo Camera (BASS Cam) system is equipped with three high-definition GoPro HERO4 Black Edition cameras encased in Sexton GoDeep Acrylic housing. This system is also fitted with four Bigblue LED lights (15000 lm for the lower lights and 72000 lm for the upper lights) that help to illuminate the field-of-view at depth and it is equipped with a camera to provide a live feed (black camera in the center).



A smaller adaptation of the BASS stereo camera system (Figure 4) is equipped with two forward-facing GoPro HERO4 Black Edition cameras with an overlapping field-of-view, encased in Sexton GoDeep Acrylic housing (rated to a depth of 500 m). It also has two Bigblue LED lights (72000 lm) to illuminate the field-of-view at depth and can be deployed from a CTD (Conductivity, Temperature, Depth) wire at an average speed of 30 m/min. When deployed, this camera system is positioned vertically and weights are attached to the bottom so that it remains upright during the deployment. One of the benefits of using this smaller stereo camera system is that it can be easily deployed from smaller research and fishing vessels and does not require the extensive preparation or additional set-up that the BASS Cam requires to project a live feed. Disadvantages include that the camera tends to rotate continuously while being deployed due its vertical positioning, making the field-of-view less clear and measurements less accurate. Further, while the main benefit of this system is that it would allow researchers to mobilize more quickly in the face of a sudden bloom of gelatinous zooplankton, the deployment speed of the CTD cable needs to be slower to collect any meaningful data. At the normal rate of descent of a CTD (30 m/min), the field-of-view is not as clear and does not provide a sufficient resolution of the water column to provide accurate measurements of the vertical distribution of midwater organisms.



**Fig. 4** The smaller adaptation of the BASS cam is equipped with two GoPro HERO4 Black Edition cameras encased in Sexton GoDeep Acrylic housing. Two Bigblue LED lights (72000 lm) illuminate the field-of-view at depth. This camera system is deployed vertically, with one end attached to a CTD wire and the other end attached to various weights.

A very different camera system used in this study was the remotely operated vehicle (ROV) *Jason* (Figure 5). While the ROV *Jason* is not a stereo camera system, it is equipped with three Insite Mini-Zeus HD cameras (a Manipulator, Basket, and Aft-looking camera) which provide different perspectives for tether management, terrain identification, and visual location. This system is also equipped with sixteen 17700 lm LED lights, providing

over 283000 lm for excellent lighting at depth. The ROV Jason is 3.4 m long, 2.4 m high, and 2.2 m wide, weighing a total of 4,082 kg in air but being neutrally buoyant at depth. The ROV is connected to *Medea*, the partner vehicle to *Jason*, which serves as a neutrally buoyant tether and shock absorber, sending a live feed to the surface ship by an armored cable with three fibers and three electrical conductors. The maximum vehicle speed of the ROV Jason (on site, within tether range) is 1.5 knots forward, 0.5 knot lateral, and 1.0 knot vertical. This movement is powered by six brushless DC electric thrusters, each providing 113 N of thrust. One of the many benefits of using the ROV Jason to capture midwater footage is that the high definition cameras and optimal lighting conditions allow for high resolution footage to be captured, despite the relatively quick rate of descent of 30 m/min. This makes it easier for scientists to make accurate observations of organisms and their distributions. What would most improve this camera system is to make it stereo by either the addition of a camera so that at least two of the cameras have an overlapping field-ofview (which may create issues with the amount of information that is able to be sent over the current live feed system), or by changing the positions of two of the onboard cameras. Another easier way to obtain these measurements is by ensuring that an object of known length is in the camera frame at all times (the length of the object can be converted to pixels to ultimately determine the measurement of each individual pixel). While this may be a more cost-effective way to record additional measurements at depth, it ultimately is not as accurate as having the stereo camera system because it does not take into account the tilt of the ROV at any time, making it more challenging to acquire orientation measurements.



**Fig. 5** The Remotely Operated Vehicle (ROV) *Jason* is equipped with three Insite Mini-Zeus HD cameras (a Manipulator, Basket, and Aft-looking camera) which provide different perspectives for tether management, terrain identification, and visual location. This system is also equipped with sixteen 17700 lm LED lights, providing over 283000 lm for excellent lighting at depth. The ROV *Jason* is connected to *Medea*, which serves as a neutrally buoyant tether, and sends a live feed to the surface ship. This camera system can be "driven" at depth.

Another challenge to the ROV camera system is that it cannot be easily mobilized, weighing almost 245 times more than the BASS Cam and requiring the additional tethering system *Medea* for deployment and recovery. This means that in the face of a sudden bloom of gelatinous organisms, the ROV *Jason* would not be a feasible option because it cannot be deployed from smaller research and fishing vessels. In the time that it would take to make research cruise plans, it may be too late to fully capture the impact of the bloom. The benefits that the ROV *Jason* have over the BASS Cam is that is can far exceed the depth limitations of the BASS Cam (6500 m versus 100 m) and it can be manipulated and "driven" to obtain different perspectives of the same study site. By having a vehicle that can move in all directions, it allows scientists to fully capture midwater organism behaviors by allowing it to hover or change perspectives when needed. The BASS Cam only captures the organism from one direction as it is being deployed. Both cameras have the benefit of having a live feed, which allows scientists to know what video footage they are capturing while at sea, allowing them to alter their cruise plan to maximize the amount of valuable footage they are collecting. For example, if scientists are not seeing the organism that they were looking for at one study site, they may be able to move between locations to search for the organism there. While both the BASS Cam, the smaller adaptation of the BASS Cam, and the ROV *Jason* have benefits for observing midwater ecology, researchers should incorporate the most beneficial aspects of each of these systems into smaller camera systems that are more easily mobilized.

Camera System	Advantages	Disadvantages	
Benthically Anchored Suspended Stereo Camera (BASS Cam)	<ul> <li>Sends live feed to surface</li> <li>Stereo camera system</li> </ul>	<ul> <li>Not as easy to mobilize as the smaller BASS Cam adaptation</li> <li>Maximum depth is 100 m (relatively shallow)</li> </ul>	
Smaller BASS Cam Adaptation	<ul> <li>Easy to mobilize (not many people needed to deploy)</li> <li>Stereo camera system</li> </ul>	<ul> <li>Spins during deployment (needs more stability) for a steady shot</li> <li>Needs higher resolution cameras or slower deployment rate</li> <li>No live feed</li> <li>Not enough lighting for deeper depths</li> <li>Maximum depth is 500 m</li> </ul>	
Remotely Operated Vehicle (ROV) Jason	<ul> <li>Sends live feed to surface</li> <li>High definition cameras</li> <li>Optimum lighting</li> <li>Maximum depth is 6500 m</li> </ul>	<ul><li>Not a stereo camera system</li><li>Not easy to mobilize</li></ul>	

# **Table 1** Overview of the Advantages and Disadvantages of the Camera Systems Used in this Study

# Chapter 3

# Methods

## **3.1** Study site description

The California Current System (CCS) is an area of cold, nutrient-rich coastal upwelling waters that spans the entire western coast of the United States, extending, in the north, from the Transition Zone (~50°N, separating the North Pacific and Alaska gyres) to the southern Baja California Peninsula (Figure 6; Huyer 1983, Checkley & Barth 2009). Nutrient fluxes from upwelling in these regions help to stimulate high phytoplankton production, which can support rich coastal marine ecosystems and productive fisheries (Chelton et al. 1982). The Central Oregon coast is located in the northern California Current (NCC) and, similar to the rest of the CCS, is subject to substantial interannual variability (Chelton et al. 1982). The El Niño/Southern Oscillation (ENSO) is the appearance and persistence of anomalously warm water, which can reduce the strength of upwelling and the resultant primary productivity, leading to declines in zooplankton, fish, and seabird populations (Barber & Chavez 1983). From 2015-2016, the CCS experienced one of the strongest ENSOs on record and was comparable to the ENSO events of 1982-1983 and 1997-1998 (Jacox et al. 2016). In the 1997-1998 ENSO event, a dramatic recovery of biological productivity of the region occurred with La Niña conditions, with the resumption of increased upwelling leading to an extensive phytoplankton bloom (Chavez et al. 1999). As the CCS entered La Niña conditions in 2017, it remains unknown how these conditions impacted the primary productivity in the region.

Stonewall Bank is a rocky outcrop located on the continental shelf approximately 24 km from shore (44.550 N, 124.111 W). It is roughly 10 km long by 2 km wide and rises 20 m above the surrounding 60 m deep shelf waters off Newport, Oregon (Moum & Nash 2000). It consists of two high areas separated by a shallow submarine valley (Byrne 1962). Stonewall Bank is south of the Columbia River, the largest river on the Pacific coast of North America, which can have an average annual discharge of approximately 260 km<sup>3</sup> year<sup>-1</sup> (Thomas & Weatherbee 2006). The Columbia River Plume is a dominant hydrographic feature of the CCS (Hickey et al. 1998) and the warmer, lower salinity water it contains can settle over regions south of the plume, such as Stonewall Bank, during periods of high flow output.



**Fig. 6** The California Current System (CCS) spans the entire west coast of the United States, extending, in the north, from the Transition Zone separating the North Pacific and Alaska gyres to the southern Baja California Peninsula (Figure from Checkley & Barth 2009).

# **3.2** Data collection and analysis

On May 30, 2017, seven deployments of the Benthically Anchored Suspended Stereo Camera (BASS Cam) system equipped with a temperature data logger were made from the fishing vessel (F/V) Enterprise. Deployments were made at Stonewall Bank (Figure 7) over a 5 hr diurnal period (10:08-15:09). Due to the position of the vessel on the bank, the maximum deployment depth changed as some locations were shallower than others. Therefore, the shallowest maximum depth the BASS Cam was deployed was 35.4 m and the deepest maximum deployment depth was 54.9 m. Wind direction was from the NW and average wind speed was 3.7 m/s. Average wave period was 5.09 s with an average maximum wave height of 0.85 m (collected from Station 46050 (LLNR 641) Stonewall





**Fig. 7** Seven deployments of the Benthically Anchored Suspended Stereo Camera (BASS Cam) were made at Stonewall bank (44.550 N, 124.111 W) over a diurnal period.

Video footage was analyzed in EventMeasure (SeaGIS) for pyrosome abundance, length, orientation, and nearest neighbor distance relative to temperature and depth. To avoid recounting pyrosomes, only the downward cast was analyzed. Pyrosomes that were further than 4 m from the stereo camera system were counted, but not measured. In EventMeasure, measurements are determined by the number of pixels that are selected between two given points. To ensure accuracy and eliminate any human error when measuring pyrosome length, each pyrosome was measured three times and the average recorded. Nearest neighbor distances were determined by measuring the shortest distance between two pyrosomes within the same frame. Each nearest neighbor distance was measured three times and the average recorded. Depth was predicted from deployment rate and time using a linear model. To determine orientation, all pyrosomes were consistently measured from left to right. Since it is difficult to determine from the quality of the video footage the direction that each pyrosome is swimming (either up or down), all orientations can be signed and presented on a 2D (eliminating the z-axis), 180°-axis to determine whether pyrosomes are swimming more horizontally or vertically.

# **3.3** Statistical analysis

The following statistical analyses were conducted to address each of the research questions presented in Chapter 1.6 (excluding Question 1, which is addressed in Chapter 2, and Question 6, which is addressed in Chapter 5). Most statistical analyses were conducted in IBM SPSS Statistics 22 except for orientation, which was plotted in CircStat (MATLAB). For the graphs presenting these data, means are reported for the average surrounded by the standard error (SE).

- Question 2: A Chi-square test of independence was used to determine whether pyrosome vertical distribution varied by deployment time.
- Question 3: A one-way ANOVA with a Tukey HSD post-hoc test was used to determine whether average pyrosome length significantly differed by depth class.
- Question 4: A Kruskal-Wallis H test was conducted to determine whether there was a statistically significant impact of depth on nearest neighbor distance (a one-way ANOVA was not used since homogeneity of variances was not met).
- Question 5: Orientation was plotted to determine the mode angle pyrosomes were oriented in the water column.

#### Chapter 4

# Results

# 4.1 Vertical distribution of pyrosomes over a diurnal period

Across all seven deployments of the BASS Cam at Stonewall Bank, a total of 1172 pyrosomes were recorded (Figure 8). Pyrosomes were observed during each deployment to the maximum depth the BASS Cam was deployed, yet no pyrosomes were observed between the surface and 10 m. A Chi-square test of independence determined that pyrosome vertical distribution varied by deployment time  $(X^2_{48} (N = 1172) = 657.1, p < 100)$ 0.001). Despite the observed temporal variation in pyrosome vertical distribution, across all deployments pyrosomes were found to be distributed between 25 m and 35 m, with 53.6% of all pyrosomes observed aggregating in this depth range (Figure 9). A Chisquare test of independence revealed that when comparing the number of pyrosomes distributed between 25 m and 35 m and pyrosomes aggregating at all other depths by deployment time, there was variation in vertical distribution by time  $(X^2_6 (N = 1172) =$ 244.8, p < 0.001). This may indicate that pyrosomes are migrating in and out of this 10 m zone between 25 and 35 m. Comparing the number of pyrosomes for each deployment between 25 m and 35 m and the number of pyrosomes aggregating at all other depths, more than 50% of pyrosomes were found between 25 m and 35 m except for during one deployment (Table 2). Pyrosome vertical distribution was also observed to vary spatially for three deployments (Figure 8c, 8d, and 8e) spaced approximately 10 min apart. While there appeared to be a slight thermocline at 15 m to 20 m, temperature was linear and did not appear to be a significant driver of pyrosome distribution (Figure 9).



time ( $X^{2}_{48}$  (N = 1172) = 657.1, p < 0.001), indicating temporal variations in pyrosome vertical distribution. Pyrosome pyrosomes were observed between the surface (0 m) and 10 m. Pyrosome vertical distribution varied by deployment Fig. 8 Pyrosome vertical distribution for each of 7 deployments of the BASS Cam at Stonewall Bank (Oregon). No approximately 10 min apart for these three deployments. The black horizontal line indicates the bottom depth for vertical distribution was also observed to vary spatially (8c, 8d, and 8e) as the BASS Cam was deployed only each deployment.



**Fig. 9** Pyrosome vertical distribution in relation to the mean number of pyrosomes (+/-SE) and mean temperature (+/-SE) by 5 m depth bins. Pyrosomes were mainly distributed between 25 m and 35 m, with 53.6% of pyrosomes observed aggregating in this depth range. Temperature did not appear to be a significant driver of pyrosome distribution.

Table 2 Comparison of the Proportion of Pyrosomes Between $25 \text{ m} - 35 \text{ m}$ and at Ot	ther
Depths	

Deployment #	Proportion of Pyrosomes Between	Proportion of Pyrosomes at Other Depths
	25 m – 35 m	ut other Depths
1	33.0%	77.0%
2	51.2%	48.8%
3	74.3%	25.7%
4	80.7%	19.3%
5	56.0%	44.0%
6	77.9%	22.1%
7	66.7%	33.3%
TOTAL	53.6%	46.4%

4.2 Distribution of pyrosome length across varying depths and a diurnal period Pyrosome length was recorded for a total of 267 pyrosomes across all seven deployments. The smallest pyrosome recorded was 2.0 cm and the largest pyrosome measured was 92.5  $\rm cm^{1}$  (Figure 10). The average pyrosome length was 20.8 cm (± 0.8 cm). Observations over a diurnal period revealed that pyrosome length distribution varied by deployment time, with longer pyrosomes migrating between shallower and deeper depths (Figure 11). A one-way ANOVA confirmed that pyrosome length significantly differed by depth (F(8,(257) = 5.9, p < 0.001), with 18.3% of the variance in the depth distribution explained by pyrosome length (Figure 12). A Tukey HSD post-hoc analysis indicated that pyrosomes distributed between 25 m and 30 m were significantly shorter (mean =  $18.3 \pm 1.4$  cm) than pyrosomes distributed between 40 m and 45 m (mean =  $27.9 \pm 2.2$  cm; p = 0.004). Pyrosomes distributed between 30 m and 35 m were significantly shorter (mean =  $14.3 \pm$ 1.2 cm) than pyrosomes distributed between 35 m and 40 m (mean =  $22.9 \pm 2.3$  cm; p =0.015), 40 m and 45 m (mean = 27.9  $\pm$  2.2 cm; p < 0.001) and 50+ m (29.0  $\pm$  3.9 cm; p =0.007). Pyrosomes in this depth range also tended to be shorter than pyrosomes distributed between 45 m and 50 m (mean =  $26.3 \pm 4.2$  cm; p = 0.078). There appeared to be spatial differences in pyrosome length (Figure 11c, 11d, and 11e), with longer pyrosomes found at shallower or deeper depths depending on the deployment location. Temperature did not appear to have an effect on average pyrosome length (Figure 12).

<sup>&</sup>lt;sup>1</sup>An outlier pyrosome measuring 179.3 cm was excluded from this analysis. According to the results of the Levene's test when conducting a one-way ANOVA, homogeneity of variances was not met when including this pyrosome (F(8, 258) = 2.1, p = 0.034). After excluding this pyrosome from the analysis, the assumption of homogeneity of variances was met (F(8, 257) = 0.8, p = 0.536).



**Fig. 10** Pyrosome length (cm) versus frequency (N = 266). The shortest pyrosome recorded was 2.0 cm and the longest pyrosome used in this analysis was 92.5 cm. The mean pyrosome size was 20.8 cm ( $\pm$  0.8 cm)





**Fig. 12** Mean pyrosome length (cm) and mean temperature (+/- SE) by 5 m depth bins. Pyrosome length significantly differs by depth class (p < 0.001). Unique letters indicate significant difference with (B) representing only a trend (Tukey post-hoc analysis). Pyrosomes between 30 m and 35 m were significantly smaller than pyrosomes at deeper depths. Temperature does not appear to have an effect on average pyrosome size.

# 4.3 Pyrosome nearest neighbor distances

Nearest neighbor (NN) measurements were recorded for 192 pyrosomes. A Kruskal-

Wallis H test was conducted to determine that there was a significant difference in the

NN distance by depth (H(8) = 16.0, p = 0.042).<sup>2</sup> Pyrosomes distributed between 30 m and

<sup>&</sup>lt;sup>2</sup> A Bonferroni correction was not used for this analysis since the *p*-value would need to be less than 0.0056 (p = 0.05/9) for results to be statistically significant. All conclusions from this analysis are thus stated with caution.

35 m were more densely aggregated (mean NN = 94.6  $\pm$  11.9 cm) than pyrosomes distributed between 15 m and 20 m (mean = 169.2  $\pm$  31.5 cm; p = 0.033), 20 m and 25 m (mean = 180.7  $\pm$  34.0 cm ; p = 0.011), and 35 m and 40 m (mean = 160.9  $\pm$  36.0 cm; p = 0.012; Figure 13).



**Fig. 13** Mean nearest neighbor distance (cm) (+/- SE) by 5 m depth bins. There is a significant effect of depth on nearest neighbor distance. Unique letters indicate a significant difference (Tukey post-hoc analysis).

# 4.4 **Pyrosome orientation**

Pyrosome orientation was recorded for 267 pyrosomes on a  $180^{\circ}$ -axis (in 2D so as it does not include the z axis). Pyrosomes were generally obliquely oriented in the water column and the modal angle was  $30^{\circ}$  (Figure 14). Observations revealed that pyrosome orientation appeared to be random.



**Fig. 14** Pyrosome orientation in the water column (N = 267). Individuals were obliquely oriented (mode angle =  $30^{\circ}$ ). Red arrows illustrate the direction orientation was measured left to right.

#### Chapter 5

#### Ex situ diel vertical migration (DVM) experiment

As part of my research efforts during the Summer of 2017, I designed an ex situ experiment to collect video footage that would allow me to measure the swimming distances, orientations, and velocities of pyrosomes over a diel cycle to gain further information on their swimming behaviors. *Pyrosoma atlanticum* specimens were to be collected and placed in a 250 L cylindrical tank over a 12-hr light/ 12-hr dark cycle to determine if this species was responding to light when undergoing diel vertical migration. As pyrosomes have never been successfully held in a laboratory setting, this was a preliminary attempt at keeping these pelagic tunicates alive in an ex situ environment.

On June 13, 2017, our attempt to collect live pyrosomes at Stonewall Bank proved unsuccessful as no pyrosomes were present at this time for collection. An additional cruise on the R/V *Elakha* along the Newport Hydrographic Line on July 12, 2017 also did not provide sufficient pyrosomes for collection as the only pyrosomes that were observed on our stereo camera system were few and at deeper depths than could be collected. While living in Newport, I made connections with a local commercial fisherman who had observed pyrosomes while trolling for salmon and offered to bring back a few pyrosome specimens that came up on his lines. I provided him with dip nets and small containers for collecting and keeping the pyrosomes and instructed him to try to keep the containers as full of seawater as possible to avoid having bubbles in the containers (which can be deadly for gelatinous organisms). On July 17, 2017, he notified me that he had collected a few pyrosomes at approximately 10:00 and that I could retrieve them that afternoon. He had successfully collected four pyrosomes of medium length and placed them in individual containers. By 18:15, I had placed the pyrosomes in a Kreisel tank (Figure 15a) circulating on a low flow with water from the Yaquina Bay. At this point, two of the pyrosomes showed signs that they were alive and moved out of the flow into the center of the Kreisel tank, showing that they were actively swimming. The pyrosomes were left until 22:00 when they were placed into the 250 L cylindrical tank (Figure 15b) so that an acclimation period could begin before starting the experiments in the morning. Each pyrosome sank to the bottom and all four pyrosomes showed no signs of activity. By morning, the pyrosomes had not moved and were deemed dead. This was most likely due to the pyrosomes not being in water the same temperature and salinity that they were found in (the warmer and fresher intake water from Yaquina Bay water versus the cooler and saltier open ocean). While the ex situ experiment could not be performed, this did provide crucial information about the challenges of keeping pelagic tunicates alive in laboratory conditions. It also shows the importance of collaborating with the local fishing community to achieve research goals. In situations where funding and time can be short, as exemplified by the limited number of cruises we could sail on for our research, working with local fishers who are often out in our study sites fishing daily can be an excellent opportunity to collect further data or specimens.



**Fig. 15a** The four pyrosomes collected were placed in a Kreisel tank circulating on a low flow with water from the Yaquina Bay. Two of the pyrosomes moved out of the flow into the center of the Kreisel tank, showing signs that they were still alive and were actively swimming. **15b** After a 3.75 hr period in the Kreisel tank, pyrosomes were placed in 250 L cylindrical tank to conduct a diel vertical migration experiment. By this time, the pyrosomes were no longer alive (seen immobile on the bottom of the tank).

# Chapter 6

# Discussion

Through this study, I aimed to characterize the in situ vertical distribution, nearest neighbor distances, and swimming orientation of an unexpected bloom of Pyrosoma atlanticum in the northern California Current (NCC), where they have not historically been observed. As pyrosomes have been typically found in tropical ocean waters, this anomalous bloom of pyrosomes in the NCC may have resulted from the warmer waters present during the 2015-2016 El Niño/Southern Oscillation (ENSO), one of the strongest ENSOs on record in the California Current System (CCS; Chavez et al. 1999). If warmer waters continue to persist in the CCS, we may be documenting a range expansion of *Pyrosoma atlanticum* into regions that have been historically cooler in temperature. This study is also the first of its kind as pyrosome vertical distribution has previously been analyzed using vertical net tows (Angel 1989, Andersen & Sardou 1992), whereas I used a stereo camera system to analyze pyrosome vertical distribution as well as measure pyrosome length, orientation, and nearest neighbor distances during a diurnal period. As most studies have been conducted at night or early morning, this study provides new insight into where pyrosomes may be located during the day and the extent of which pyrosomes undergo a diel vertical migration. By continuing to develop and utilize new technologies like high definition camera systems to capture midwater ecology, more data can be collected when blooms of gelatinous zooplankton occur.

# 6.1 Bloom impacts on pelagic marine ecosystems in the North Pacific

Over a sampling period of 5 hours (10:09 to 15:09), we recorded a total of 1172 pyrosomes. From this sample, we can start to understand the immensity of the 2017 pyrosome bloom and predict the impacts it may have on the trophic dynamics within pelagic marine ecosystems in the NCC. As *P. atlanticum* are recorded to have some of the highest clearance rates of any pelagic grazer (Perissinotto et al. 2007), this bloom could be removing a substantial portion of the phytoplankton and microzooplankton that have previously sustained other invertebrate and commercial fish populations in these ecosystems. This is important when considering *P. atlanticum* have typically inhabited more tropical pelagic ecosystems (van Soest 1981), thus the impact on nearshore, temperate ecosystems in the Northeastern Pacific (such as Stonewall Bank) cannot yet be determined.

Observations that pyrosomes have been found in the stomach contents of widow rockfish (*Sebastes entomelas*; pers. comm. Kelly Lawrence) may indicate that organisms within these marine ecosystems are already responding to increased availability created by this anomalous pyrosome bloom. While rockfish in these regions have been observed to consume salps and other gelatinous organisms during previous El Niño conditions (Lee & Sampson 2009), pyrosomes may not be as nutritious a food source as the higher order prey species that rockfish normally consume. Thus, whether rockfish are actively selecting pyrosomes or are being forced to consume them due to a lack of availability of the prey species that they usually consume, rockfish that consume only pyrosomes (that have relatively little nutritional value) may not be gaining enough energy to support their survival and reproduction. If this pyrosome bloom persists, this may lead to declines in rockfish populations, and potentially the populations of other commercial fish species in the future.

# 6.2 Vertical distribution

Across each of the seven deployments of the BASS Cam, pyrosome vertical distribution varied by the deployment time. This may indicate that pyrosomes are actively migrating vertically throughout the day. Despite this observed temporal variation in pyrosome vertical distribution, pyrosomes tended to be mainly distributed between 25 m and 35 m, with 53.6% of all pyrosomes observed aggregating within this depth range. More than 50% of pyrosomes were observed between 25 m and 35 m for all but one deployment. Pyrosomes may be migrating through this relatively narrow 10 m depth range due to a physical driver, such as temperature, or due to there being a higher abundance of phytoplankton within this depth range. Despite a slight thermocline observed at 15 m to 20 m, temperature did not vary substantially with depth. While most of the pyrosomes were aggregated below this thermocline, it is difficult to conclude that a temperature difference of 0.5°C is the driver of this difference in pyrosome distribution, particularly considering pyrosomes undergo diel vertical migrations up to depths of 700 m (Angel 1989, Andersen et al. 1992), a depth range over which the temperature would be substantially more variable. Further, since this pyrosome bloom has effected regions from Alaska to northern California, which also vary greatly in temperature, it makes it more likely that a different physical or biological driver (such as phytoplankton availability)

may be driving pyrosome vertical distribution. As chlorophyll-*a* was not recorded for these deployments, I was unable to conclude whether this observation was due to there being higher abundances of phytoplankton in this region, possibly driving increased migration through this 10 m depth range to initiate feeding. This may be the most likely hypothesis since pyrosomes utilize the motion of cilia to pass water through their mucus net to capture prey (Alldredge & Madin 1982), necessitating increased swimming through the 25 m to 35 m depth range to initiate those feeding behaviors. For future research, a CTD (with an attached sensor to record chlorophyll-*a*) should be deployed alongside the BASS Cam so that a physical profile of the water column can be obtained with the video footage, providing additional insight to whether there are physical or biological drivers that may be driving pyrosome vertical distribution.

During each of the deployments, it was also observed that no pyrosomes were recorded between the surface to 10 m in depth during the diurnal period. Historically, pyrosomes have typically only been observed aggregating on the surface of the water at night (Drits et al. 1992), which may indicate that this species is sensitive to changes in light intensity or may have evolved to avoid visually-oriented predators that inhabit this depth range. Collecting the physical profile of the water column with a CTD during future deployments may also help to explore this observation in more detail, as well as conducting ex situ laboratory experiments where light intensity can be manipulated.

# 6.3 Length across varying depths

An analysis of pyrosome length provides additional support for the vertical migration of pyrosomes through the 25 m and 35 m layer due to an unknown physical or biological driver. Pyrosome length was distributed across a large range, with the shortest pyrosome recorded measuring 2.0 cm and the longest pyrosome included in my analysis measuring 92.5 cm. The average pyrosome length was 20.8 cm ( $\pm$  0.8 cm). This aligns with previous observations of pyrosomes recorded in the northern California Current, with the average pyrosome length measuring approximately 15 cm with some pyrosomes exceeding lengths of 80 cm (Brodeur et al. 2018). Results from the 2017 bloom indicate that pyrosome length significantly differed by depth, with pyrosomes distributed between 25 m and 30 m tending to be shorter (mean length =  $18.3 \pm 1.4$  cm) than pyrosomes between 30 m to 50+ m (mean =  $21.5 \pm 1.1$  cm). When pooling all of the data from each of the seven deployments for the average pyrosome length by depth, it appeared that on average, the longer pyrosomes tended to be distributed at depths surrounding the shorter pyrosomes. These shorter pyrosomes may be aggregating within this narrow 5 m depth range due to not being able to migrate as quickly as the longer pyrosomes. Andersen and Sardou (1994) found that shorter pyrosomes had a lower mean migration amplitude (MMA; 90 m MMA for 3-mm-length pyrosomes) over a diel cycle than longer pyrosomes (760 m MMA for 51-mm-length pyrosomes). This may indicate that the longer pyrosomes are able to vertically move through a potential chlorophyll-a layer (located within the 25 m to 30 m depth range) more effectively than the shorter pyrosomes, allowing for the larger pyrosomes to filter feed more efficiently. Shorter

pyrosomes may not be able to move as quickly through this range, leading to them form aggregations in the 25 m and 35 m depth range.

# 6.4 Nearest neighbor distances

Nearest neighbor measurements support the hypothesis that shorter pyrosomes may be staying within the narrow depth range between 25 m and 35 m due to not being able to migrate as efficiently as the longer pyrosomes. Our results indicated that pyrosomes in the 30 m to 35 m depth range tended to be more densely aggregated (mean NN = 94.6  $\pm$  11.9 cm) than pyrosomes at other depths. This may mean that the shorter pyrosomes are remaining within this narrow 5 m depth range while the longer pyrosomes are migrating vertically around them, allowing the longer pyrosomes to have a greater distance from other individual pyrosomes at both shallower and deeper depths. To fully understand what may be driving pyrosome vertical distribution and aggregation patterns during a bloom, it will be important for future research to have fine-scale physical data on the water column so that it can be compared to the video footage.

# 6.5 Orientation and ex situ laboratory experiment

A preliminary study of pyrosome orientation on a  $180^{\circ}$ -axis revealed that pyrosome orientation appears to be random. Pyrosomes were observed to be obliquely orientated in the water column (mode angle =  $30^{\circ}$ ). This may indicate that this angle is the most effective for filter-feeding or for undergoing diel vertical migration, but additional

statistical analyses should be conducted to confirm our observations. One way to better study the fine-scale swimming behaviors of pyrosomes is in an ex situ laboratory setting. I conducted an experiment in which pyrosomes were kept alive in the laboratory for a brief period (approximately 4 hrs), but I suspect that the water used in the tanks from the Yaquina Bay was not optimal for their survival as it differs from the open, offshore waters they typically inhabit. One way of overcoming this challenge would be to collect and study pyrosomes in tanks while at sea on a research vessel, which would allow for tank water conditions to be more similar to what the pyrosomes are adapted to and may lead to a greater success in pyrosome survival. This would also minimize the stress that transportation to a research facility may create for the pyrosomes. By understanding how pyrosomes undergo such extensive migrations daily, we may be able to incorporate their swimming techniques into the designs of future remotely operated vehicles and submersibles so that they can move more effectively through the water column.

#### 6.6 **Pyrosome patchiness**

One of the most challenging aspects of studying the 2017 pyrosome bloom was that pyrosomes tended to be extremely patchy both spatially and temporally. While this study's analysis is extracted from video footage collected on May 30, 2017, an additional research cruise was planned at Stonewall Bank on June 13, 2017 so that the BASS Cam could be deployed again over a diel cycle (14:00 to 2:00) to collect more information on pyrosome diel vertical migration. During this 12-hour cruise, no pyrosomes were observed despite there being over a thousand pyrosomes in this location only a few weeks prior. Our current hypothesis for the lack of pyrosomes on June 13 is that the Columbia River Plume, located just north of Stonewall Bank, had a large discharge with a strong output of warm, freshwater moving down the coast (Figure 16 and Figure 17). This may have led to the pyrosomes being pushed off the coast into deeper waters than what we would have observed at Stonewall Bank. The patchiness of this 2017 pyrosome bloom has also made it difficult for fishers to target where to fish to avoid pyrosomes and to optimize their catches, so it is important to collect physical data when pyrosomes are observed so that conclusions can be drawn on the ranges of environmental variables that pyrosomes prefer.



**Fig. 16** The strength of the output from the Columbia River on June 13, 2017 led to there being a body of warm water that moved down the central Oregon coast and settled over Stonewall Bank, possibly pushing any pyrosomes out of that region.



**Fig. 17** The strength of the output from the Columbia River on June 13, 2017 led to there being a body of freshwater that moved down the central Oregon coast and settled over Stonewall Bank, possibly pushing any pyrosomes out of that region.

# 6.7 Future research

in the narrow 25 m to 35 m depth layer is consistent at other study sites and at similar times. To confirm whether pyrosomes are migrating through the 25 m to 35 m depth layer, additional efforts should be made to tag pyrosomes alongside the deployment of a stereo camera system so that their fine-scale movements can be better tracked. In previous studies, attaching acoustic transmitters and a time-depth recorder to the bell or oral arms of jellies has proved successful in tracking the vertical swimming behaviors of a variety of jelly species (Fossette et al. 2016). By developing a way to attach an acoustic transmitter and a time-depth recorder to the gelatinous, tube-shaped body of a sample of pyrosomes ranging in length, information may be collected not only on their diel vertical migration patterns, but on how pyrosome length may influence swimming speeds.

If this pyrosome bloom continues to persist in 2018 in the NCC, additional deployments of high definition video camera systems should be made to collect more data on how this bloom is developing. If we continue to develop smaller stereo camera systems like the smaller adaptation of the BASS Cam, not only can we further our current understanding of pyrosome ecology, but these technologies will also be readily available for when other blooms of gelatinous zooplankton occur. It is also important that scientists in these regions collaborate with local fishers to collect more information on the locations where the pyrosomes are most and how the pyrosomes are impacting their catches. Having this additional data can help scientists know which study sites may be the best to deploy their equipment so that more data can be collected on the effects of this pyrosome bloom on the dynamics within these pelagic marine ecosystems. By studying the fine-scale swimming behaviors and vertical distribution of pyrosomes, we can gain a better

understanding of what may be driving range expansions for pyrosomes, such as observed along the central Oregon Coast in 2017, as well as how these blooms may impact these ecosystems over extended periods.

# 6.8 Conclusions

By studying the vertical distribution and swimming behaviors of an anomalous bloom of pyrosomes in the northern California Current, we are not only gaining new knowledge on an understudied marine organism, but are also collecting new data on how pyrosomes may be impacting the trophic dynamics within pelagic marine ecosystems. These data can help us understand the physical and biological drivers that may be leading to the range expansions and blooms of other gelatinous zooplankton around the world, helping us to predict what our future oceans may look like if events like the 2017 pyrosome bloom continue to occur. As our climate and oceans continue to change, the data we collect now may be invaluable in helping address many of the risks facing our marine resources, such as fisheries, in future years.

# Chapter 7

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