FINE-SCALE VERTICAL DISTRIBUTION AND DIEL MIGRATIONS OF

PYROSOMA ATLANTICUM IN THE NORTHERN

CALIFORNIA CURRENT

by

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A THESIS

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THESIS ABSTRACT

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Title: Fine-scale Vertical Distribution and Diel Migrations of *Pyrosoma atlanticum* in the
Northern California Current

An unusual marine heatwave preceded anomalous blooms of the colonial pelagic

tunicate *Pyrosoma atlanticum* in the Northern California Current (NCC) in 2014-2018.

Although aggregations of pyrosomes have the potential to shape marine trophic dynamics

through grazing and rapid reproduction, little is known about their vertical distribution

patterns. In February and July 2018, we sampled *P. atlanticum* colonies in the NCC.

Depth-stratified net tows provided volume-normalized abundance estimates that

complemented fine-scale counts by a vertically-deployed camera system. Pyrosome

distribution and size structure varied over space and time. Pyrosomes were distributed

non-uniformly in the water column with peak numbers associated with vertical gradients

in environmental parameters, notably density and fluorescence. Vertical distributions

shifted over the 24-hour period, indicative of diel vertical migration. Understanding the

distribution of these subtropical gelatinous grazers gives insight to their ecological role,

particularly related to carbon transfer, in the NCC as conditions become more favorable

for recurring blooms.

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CHAPTER I

FINE-SCALE VERTICAL DISTRIBUTION AND DIEL MIGRATIONS OF *PYROSOMA ATLANTICUM* IN THE NORTHERN CALIFORNIA CURRENT

Introduction

Pyrosomes are colonial pelagic tunicates made of hundreds or thousands of identical, millimeter-sized zooids connected by a gelatinous tunic. Each zooid uses cilia to drive continuous feeding currents through an internal branchial basket; a fine-mesh mucous sheet is secreted over this structure to capture prey particles prior to digestion (Alldredge & Madin, 1982). The zooids' excurrent siphons are oriented towards a common central cavity, open at one end, where a weakly propulsive jet of water is produced (Alldredge & Madin, 1982; Holland, 2016). Pyrosomes are among the most efficient pelagic herbivores; in high densities, *Pyrosoma atlanticum* has been documented to consume up to 95% of daily phytoplankton stock (Drits et al., 1992; Henschke et al., 2019). Their wide prey range includes cells larger than 10 μm (Perissinotto et al., 2007) and potentially as small as nano- and pico-plankton (Sutherland et al., 2018, Thompson et al., in review). Efficient consumption of small particles allows these large grazers to 'short-circuit' the microbial loop, bypassing lower trophic levels (Conley et al., 2018).

Pyrosoma atlanticum (Péron 1804) is a cosmopolitan species of pyrosome, found from 50°N to 50°S in the Atlantic, though uncommon north of southern California (Van Soest, 1981). Previously, pyrosomes (not identified to species, but including *P. atlanticum* and *P. adherniosum*) were seen in almost half of the annual zooplankton surveys off southern California performed by the California Cooperative Oceanic Fisheries Investigations (CALCOFI), with highest biomasses in the "cool-phase" regime (Lavaniegos & Ohman, 2003). Before 2014, few pyrosomes had been documented in the

Northern California Current (NCC), a temperate portion of the California Current north of Cape Mendocino, California (Brodeur et al., 2018). Unprecedented blooms of *P. atlanticum* began occurring in the NCC between 2016 and 2018, each year expanding incrementally northward into Pacific Northwest waters (Brodeur et al., 2018; Miller et al., 2019; Sutherland et al., 2018). In 2017, peak catches from midwater trawls off Oregon exceeded 60,000 kg km^{-3} (Brodeur et al., 2018). In such high densities, pyrosomes can impact carbon cycling in the open ocean through high clearance rates and fecal pellet production (Henschke et al., 2019; Steinberg et al., 2008). Brodeur et al. (2019) suggest the emergence of a marine heatwave (Bond et al., 2015; Di Lorenzo & Mantua, 2016) and strong El Niño (Jacox et al., 2016) created the appropriate conditions for a pyrosome bloom. Understanding the distribution of *P. atlanticum* during these bloom events may give insight to their ecological role in temperate ecosystems as conditions become more favorable for recurring blooms.

While the spatial distribution of *P. atlanticum* in the NCC has been described during bloom years (2016-2019) along the west coast of North America (e.g. Miller et al., 2019), seasonal and vertical distribution patterns have not yet been explored. In the Eastern Atlantic and tropical Pacific, pyrosomes have been documented undergoing large daily vertical migrations to nearly 1,000 meters (Andersen et al., 1992; Angel, 1989; Henschke et al., 2019). The only published study describing the vertical distribution of *P. atlanticum* in the Pacific was located in the Tasman Sea (Henschke et al., 2019); there are currently no published studies of this nature in the NCC region. The vertical structuring of plankton is often influenced by physical and biological features of the water column, particularly the thermocline and subsurface chlorophyll maximum (Harris, 1988;

Sameoto, 1986; Townsend et al., 1984). Vertically-migrating zooplankton can accelerate the biological pump through the physical transport of material to depth (i.e. "eat high, poop low"), impacting how carbon is sequestered in the deep ocean (Steinberg et al., 2008). If *P. atlanticum* in the NCC perform similar migrations, the collective effect on carbon export may be greater than previously predicted.

However, quantifying diel vertical migration (DVM) is a challenge as it requires capturing movements over a fine scale. The distribution of zooplankton is often vertically patchy, forming thin, distinct layers in association with the physical structure of the water column (McManus et al., 2003). Pelagic tunicates, specifically, may aggregate in layers less than two meters thick (Paffenhöfer et al., 1991). Traditional depth-stratified sampling methods (i.e. net tows) lack the resolution needed to identify detailed vertical structure over a large depth range. *In situ* video counts can resolve the location of pyrosome layers to the meter scale and have been used previously to quantify vertical distribution of gelatinous zooplankton (Bi et al., 2013; Silguero & Robison, 2000).

The aim of this study was to explore how *Pyrosoma atlanticum* colonies were distributed over space and time in the Northern California Current (NCC) in 2018. This broad goal was achieved by addressing the following questions: (1) Does the spatial distribution of *P. atlanticum* vary with oceanographic features? (2) Does vertical structuring of *P. atlanticum* vary with environmental parameters? (3) Do *P. atlanticum* in the NCC exhibit diel vertical migration (DVM)? (4) Are vertical distribution patterns consistent over time? Addressing these questions will give insight into the animal's ecological role in a changing ecosystem and may help predict future blooms.

Methods

Sampling sites

      As part of the MEsoZooplankton in the CALifornia Current (MEZCAL) project,

pyrosomes identified as *Pyrosoma atlanticum* were sampled during winter (February 15-

23, 2018) and summer (July 3-11, 2018) cruises on the on the R/V Sikuliaq and R/V

Sally Ride, respectively. Pyrosomes were sampled along transects off Newport, OR (NH;

45°N, 124°W) and Trinidad Head, CA (TR; 41°N, 124°W). Each transect had five

stations extending across the slope of the continental shelf (Table 1, Fig. 1). Sampling

occurred both day and night, avoiding the hour before or after sunset and sunrise.

Table 1. Sampling locations and bathymetric depth at stations along transects off Newport, Oregon (NH) and Trinidad Head, California (TR). The number of MOCNESS ("MOC") and camera deployments are listed for the winter and summer cruises. Parentheses denote the number of sampling events where pyrosomes were present for each station if different from total deployment number.

Transect	Station No.	Latitude	Longitude	Depth (m)	Winter 2018		Summer 2018	
					MOC	Camera	MOC	Camera
NH	1	44.652	-124.295	79	2	3	3(2)	4 (3)
NH	2	44.652	-124.412	86	1 (0)	2 (1)	2	3
NH	3	44.652	-124.650	293	2 (1)	2	3	4
NH	4	44.652	-124.883	434	0	1	2	3
NH	5	44.652	-125.117	704	1 (0)	3	2	4
TR	1	41.058	-124.267	80	2 (0)	2 (0)	3 (1)	3 (0)
TR	2	41.058	-124.342	148	1 (0)	1 (0)	2 (1)	2 (1)
TR	3	41.058	-124.433	462	2	2 (1)	4 (3)	3 (2)
TR	4	41.058	-124.583	763	0	0	2	2
TR	5	41.058	-124.750	870	2 (0)	2 (1)	3 (2)	3 (2)
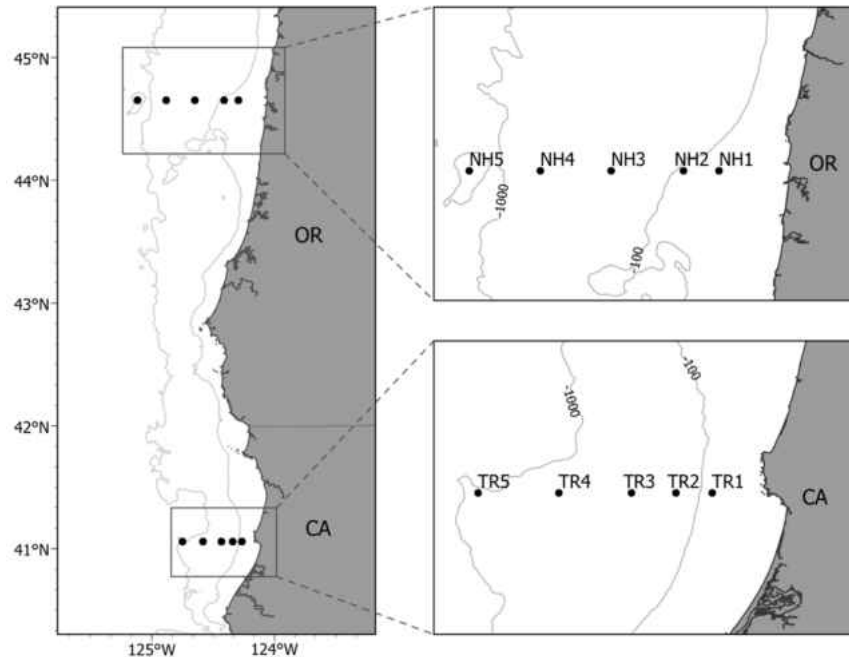
Figure 1. Study area and sampling stations off Newport, Oregon (NH) and Trinidad Head, California (TR). Gray lines show 100 m and 1000 m contours. See Table 1 for precise bathymetric depths by station.

Depth-stratified net tows

Pyrosoma atlanticum colonies were collected from coupled Multiple Opening and Closing Environmental Sensing System (MOCNESS) net tows (Guigand et al. 2005). The nets had openings of 1 m^2 and 4 m^2 with mesh sizes of 333μm and 1000μm, respectively. The pair of nets were used to sample 0-100 m in four 25 m bins, and a fifth net was towed to 100 m. Some stations were sampled twice within 48-72 hours and average abundance is presented in these cases. Due to a malfunctioning flowmeter on some deployments, the volume filtered by each net for all stations on both cruises was calculated using net opening size and pitch, ship speed, and duration of tow. Colonies were counted and their lengths recorded during the summer 2018 cruise. Colony biovolume was measured by displacement. If pyrosomes were too numerous to count, a subset of twenty from each depth bin were measured for biovolume.

CTD-mounted video camera

We mounted a GoPro Hero 4 (4K, 30fps) in a deep water housing (GoDeep Aluminum, Sexton Inc.) and two 7500 lumen lights (BigBlue VL7500P) to the frame of the ship's onboard CTD rosette frame. At each station, simultaneous CTD (SBE 911plus) and camera deployments captured fine-scale (1 m), *in situ* counts of pyrosomes to 100 m, or 5 m above the bottom at shallower stations. For casts in winter, we manually synchronized the video frames to the CTD sensor data by mapping camera motion to the motion of the CTD-rosette recorded by depth sensors. During the summer cruise, we used a stopwatch to synchronize the camera to the start of data logging on the CTD sensors. For each meter depth, we extracted a still frame from the video and counted all pyrosome colonies. We adjusted this count by subtracting colonies that were visible in the previous meter to avoid double-counts. Because visibility varied between stations, and the volume sampled in each video is not calculable, counts from individual casts were not directly comparable quantitatively. Instead, we looked qualitatively at the distribution of pyrosome colonies across the depth range to determine where peak counts occur. We identified the vertical distribution of colonies relative to features of the water column captured from the CTD sensors, and these relationships were used to compare distribution patterns across sampling stations.

Winter-summer comparison

The spatial distributions of pyrosomes may be affected by seasonal changes in oceanography. We identified oceanographic conditions during the winter and summer cruises in 2018. Regional sea-surface temperature (SST) maps were generated from a multi-sensor Geo-Polar blended analysis (Imager+AVHRR+VIIRS) at 5 km resolution

(NOAA CoastWatch/OceanWatch, Maturi et al., 2017). Representative SST values were calculated from averaging cells within 10 km of each transect.

We calculated a stratification index as previously used in zooplankton distribution studies to describe the change in seawater density between the surface and bottom (e.g. Júnior et al., 2015; Lavaniegos & Ohman, 2003):

$$\text{Stratification index} = \sigma_{t,\,100m} - \sigma_{t,\,5m}$$

We used the index to compare the degree of water column stratification to the numbers and distribution of pyrosomes around the pycnocline.

Spatial and vertical distribution

We used fine-scale counts from camera profiles to identify variation in vertical distribution from inshore to offshore. We observed aggregations of pyrosomes around the base of the surface mixed layer and fluorescence maximum at several stations. To test this relationship with the fluorescence maximum, we compared the depth at which the maximum count of pyrosome colonies occurred (i.e. the statistical mode) to the depth of the chlorophyll maximum.

Diel vertical migration

Weighted mean depth (WMD) is a common way to assess the vertical position of gelatinous zooplankton under depth-stratified sampling regimes (e.g. Andersen et al., 1992; Henschke et al., 2019; Júnior et al., 2015). WMD considers colony biovolume (as a proxy for biomass) to approximate the center of mass of colonies in the water column. WMD was calculated using the following equation:

$$WMD = \frac{\Sigma(b_i * d_i)}{\Sigma \, b_i}$$

where b_i is the biovolume (mL m^{-3}) and d_i is the midpoint of depth stratum (m). We tested differences in day-night pyrosome colony abundance in depth strata using a two-way ANOVA (Type III sum of squares).

In situ camera profiles supplied meter-by-meter colony counts. To compare profiles, we identified the mode pyrosome depth—that is, the depth at which the most colonies occur—for each camera deployment. We excluded profiles where the count at the mode depth was fewer than 2 colonies. Note that sampling depth was limited to 100 m, or 5 m above the seafloor at shallow stations.

Results

Winter-summer comparison

Oceanographic conditions varied between winter and summer 2018. In February, sea surface temperature (SST) was cool and somewhat consistent across the study region, decreasing from the southern transect to northern transect (Fig. 2a). In July, SST was higher offshore of Oregon, with cooler water extending south off the coast of Cape Blanco. On July 3, 2018, SST was higher within 10km of the northern transect ($18.00 \pm$ 0.35 ˚C; mean±SD, n=71) than the southern transect (13.84 ± 0.48 ˚C; mean±SD, n=51); cool surface waters south of Cape Blanco, OR suggest upwelling conditions near transect TR (Fig. 2b).
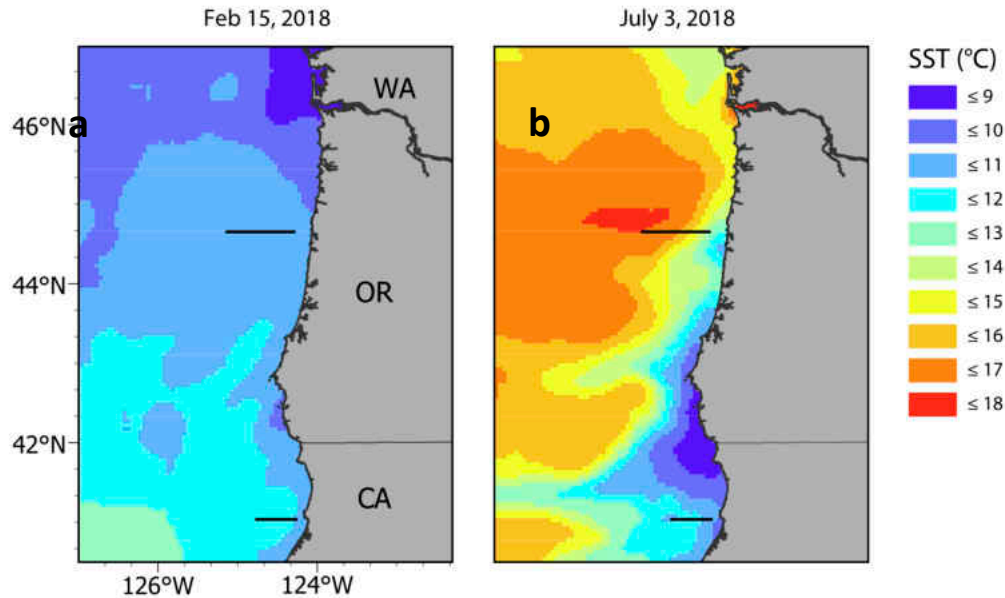
Figure 2. Regional sea-surface temperature (SST) offshore of Oregon and northern California during (a) February 15, 2018 (winter cruise, left) and (b) July 3, 2018 (summer cruise, right). SST data sourced from NOAA/OceanWatch Geo-Polar Blended (imager+AVHRR+VIIRS; 5km resolution).

In February, the mixed layer (ML) was deep along the NH (>30 m) and TR (>45 m) stations (Fig. 3a), and the fluorescence profile was multi-modal and often distributed throughout the ML. In July, the ML was relatively shallow (<20 m) along the NH stations, and a single subsurface fluorescence maximum was common, particularly at offshore stations (Fig. 3b). There was not a notable mixed layer at most TR stations in the summer; the fluorescence profile was often multimodal, reaching the highest values observed for the cruise (Fig. 3d).

The calculated stratification index showed that stratification on transect NH increased from winter (1.48 ± 0.17 kg m^{-3}; mean $\pm$ SE, n=11) to summer (3.12 ± 0.96 kg m^{-3}; mean $\pm$ SE, n=18). Overall, stratification was lower on transect TR and only marginally increased between the winter (0.68 ± 0.07 kg m^{-3}; mean $\pm$ SE, n=6) and summer (0.79 ± 0.11 kg m^{-3}; mean $\pm$ SE, n=13) cruises.

In general, there were more pyrosome colonies observed during the winter cruise than the summer cruise. On both winter and summer cruises, the most pyrosomes were observed at station NH5. The maximum colony count from whole vertical camera deployments occurred on the northern transect at station NH5 in winter (454 colonies) and summer (48 colonies) (Fig. 3a & 3b). The maximum count at any given meter interval occurred at station NH5 during winter (40 m, 119 colonies) and at station NH3 during summer (18 m, 6 colonies). The distribution at winter station NH5 was a particularly striking example of vertical patchiness because we observed a peak of 119 colonies at 40 m depth, while fewer than 3 total colonies were detected at shallower depths (Fig. 3a). Wintertime distributions tended to be more vertically clustered, presumably due to the higher numbers of colonies relative to summer (Figs. 3 & 9). There was variability between sampling events as we observed relatively few colonies during the second sampling effort in winter (Figs. 3a & 3e) and summer (Figs. 3b & 3f). On transect TR, colonies were sporadic and we only recorded single colonies in any given meter for stations TR3 and TR5; zero were recorded at TR1 (Fig. 3c and 3d).

Spatial distribution

Pyrosoma atlanticum colonies were not distributed uniformly over geographic space. In general, abundance of colonies increased from inshore to offshore (Fig. 4). The inshore stations on both transects (NH1 and TR1) had the lowest recorded abundances on average. During summer, the highest abundance (137 colonies 1000 m^{-3}) and biovolume (11.4 mL m^{-3}) was recorded during a nighttime tow at station NH5 within 25 m of the surface. Similarly, summed counts from camera profiles were highest at station NH5 in winter (454 colonies) and summer (48 colonies).

Winter 2018 - Newport, OR (February 16-17, 2018)
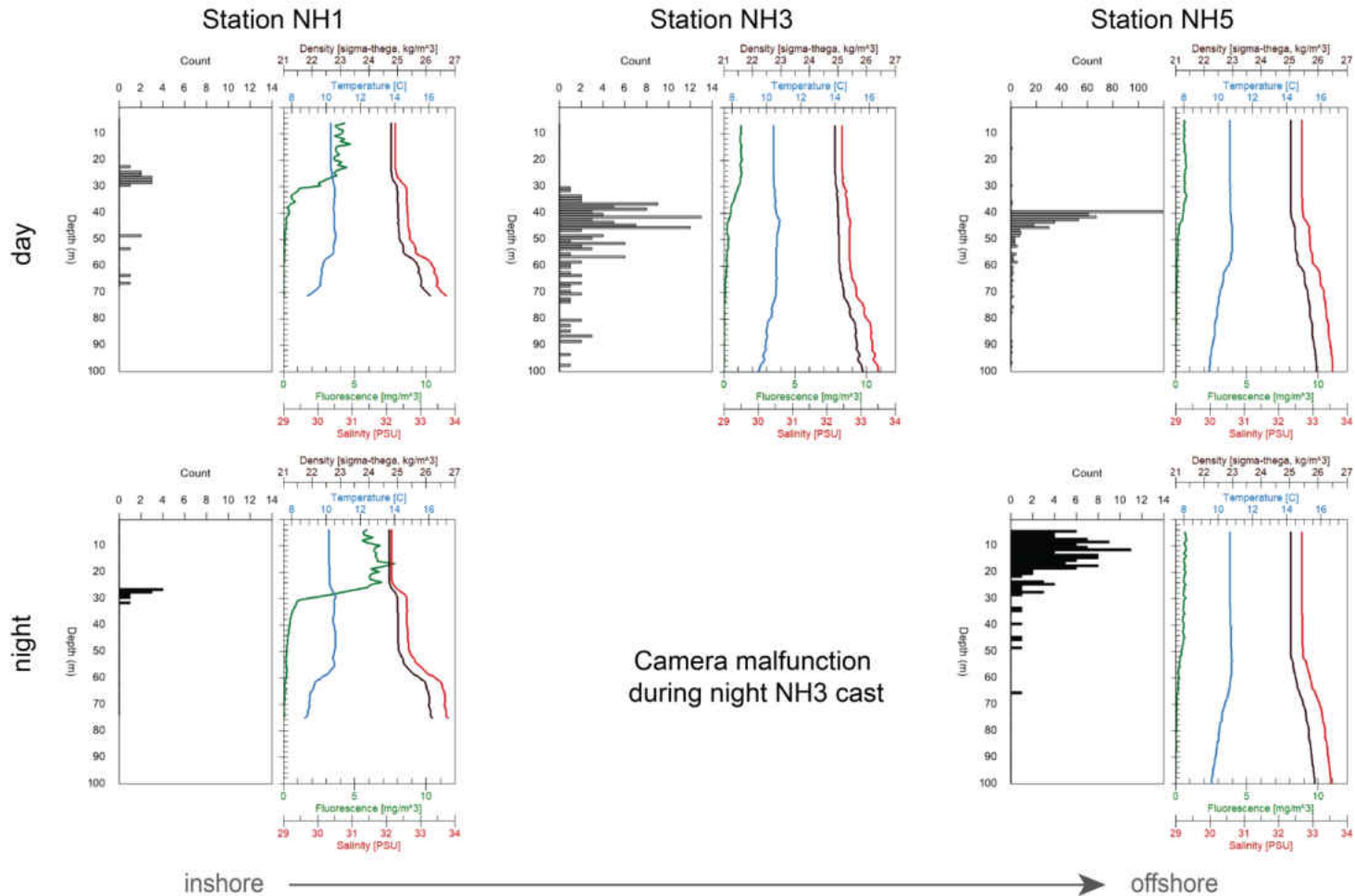
Figure 3a. Selected camera and environmental profiles from winter (February 16-17, 2018) on the Newport, OR (NH) transect. Day (grey bars) and night (black bars) profiles are displayed. Environmental data include temperature (blue), salinity (red), fluorescence (green), and density (black).

Summer 2018 - Newport, OR (July 9-10, 2018)

Figure 3b. Selected camera and environmental profiles from summer (July 9-10, 2018) on the Newport, OR (NH) transect. Day (grey bars) and night (black bars) profiles are displayed. Environmental data include temperature (blue), salinity (red), fluorescence (green), and density (black).

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Winter 2018 - Trinidad Head, CA (February 19-20, 2018)
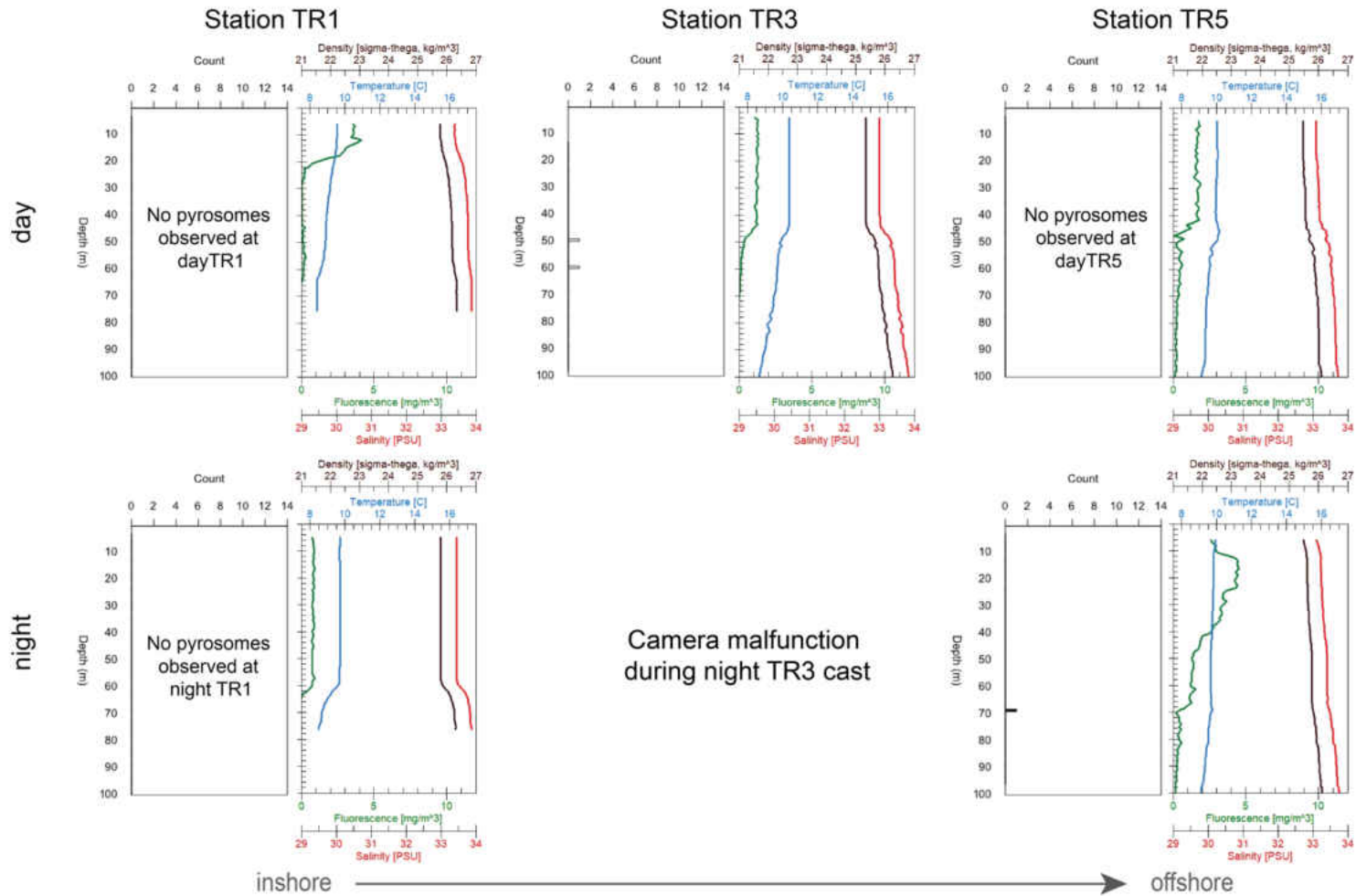
Figure 3c. Selected camera and environmental profiles from winter (February 19-20, 2018) on the Trinidad Head, CA (TR) transect. Day (grey bars) and night (black bars) profiles are displayed. Environmental data include temperature (blue), salinity (red), fluorescence (green), and density (black).

Summer 2018 - Trinidad Head, CA (July 6-7, 2018)

Station TR1

Station TR3

Station TR5

day

No pyrosomes observed at day TR1

night

No cast for night TR1

No cast for night TR3

inshore ———————————————→ offshore

Figure 3d. Selected camera and environmental profiles from summer (July 6-7, 2018) on the Newport, OR (NH) transect. Day (grey bars) and night (black bars) profiles are displayed. Environmental data include temperature (blue), salinity (red), fluorescence (green), and density (black).

Winter 2018 - Newport, OR (February 23, 2018)

Station NH1
Station NH3
Station NH5

day

No cast for
night NH1

No cast for
night NH3

No cast for
night NH5

night

inshore ⟶ offshore
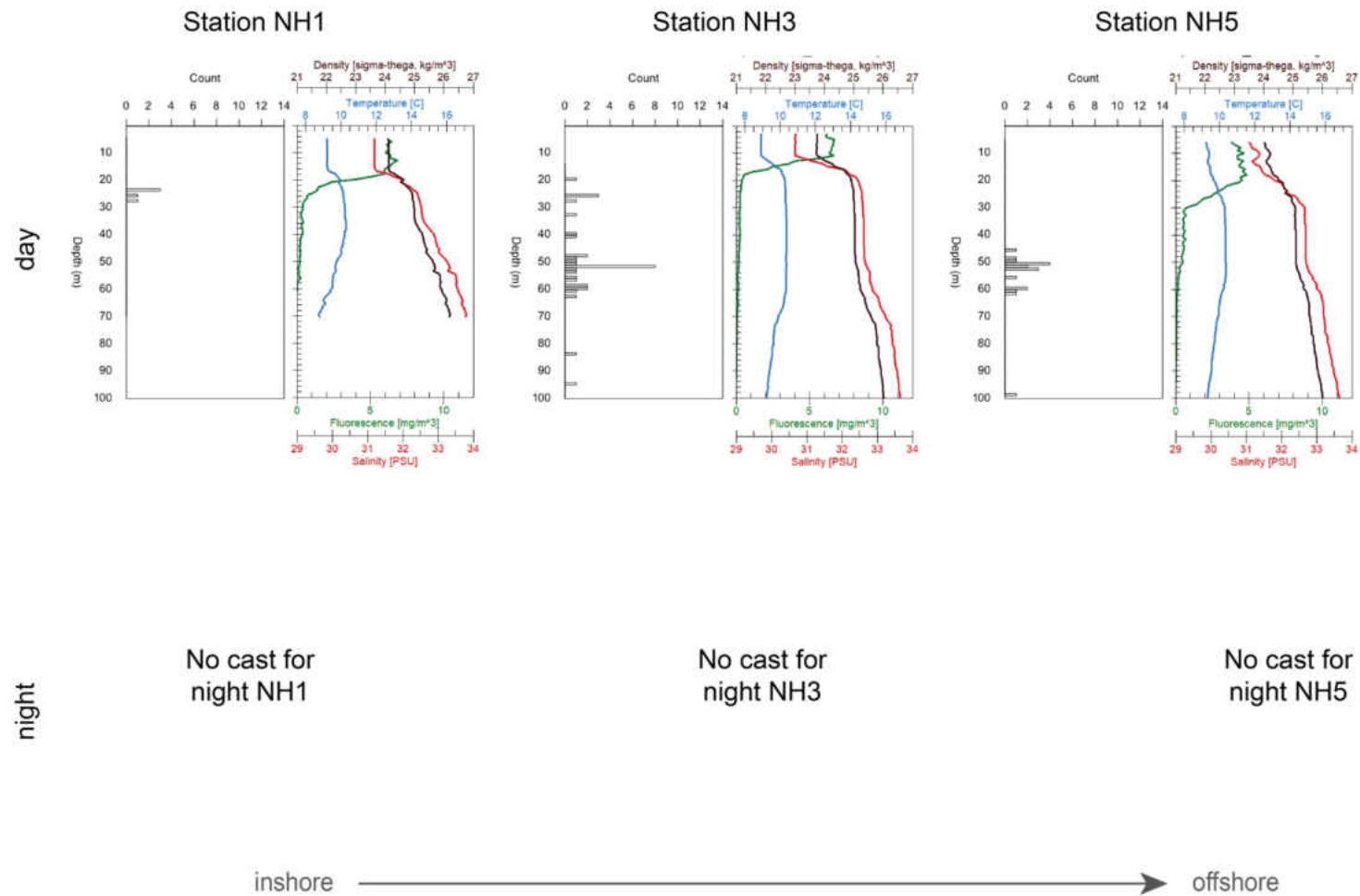
Figure 3e. Selected camera and environmental profiles from winter (February 23, 2018) on the Trinidad Head, CA (TR) transect. Day (grey bars) and night (black bars) profiles are displayed. Environmental data include temperature (blue), salinity (red), fluorescence (green), and density (black).

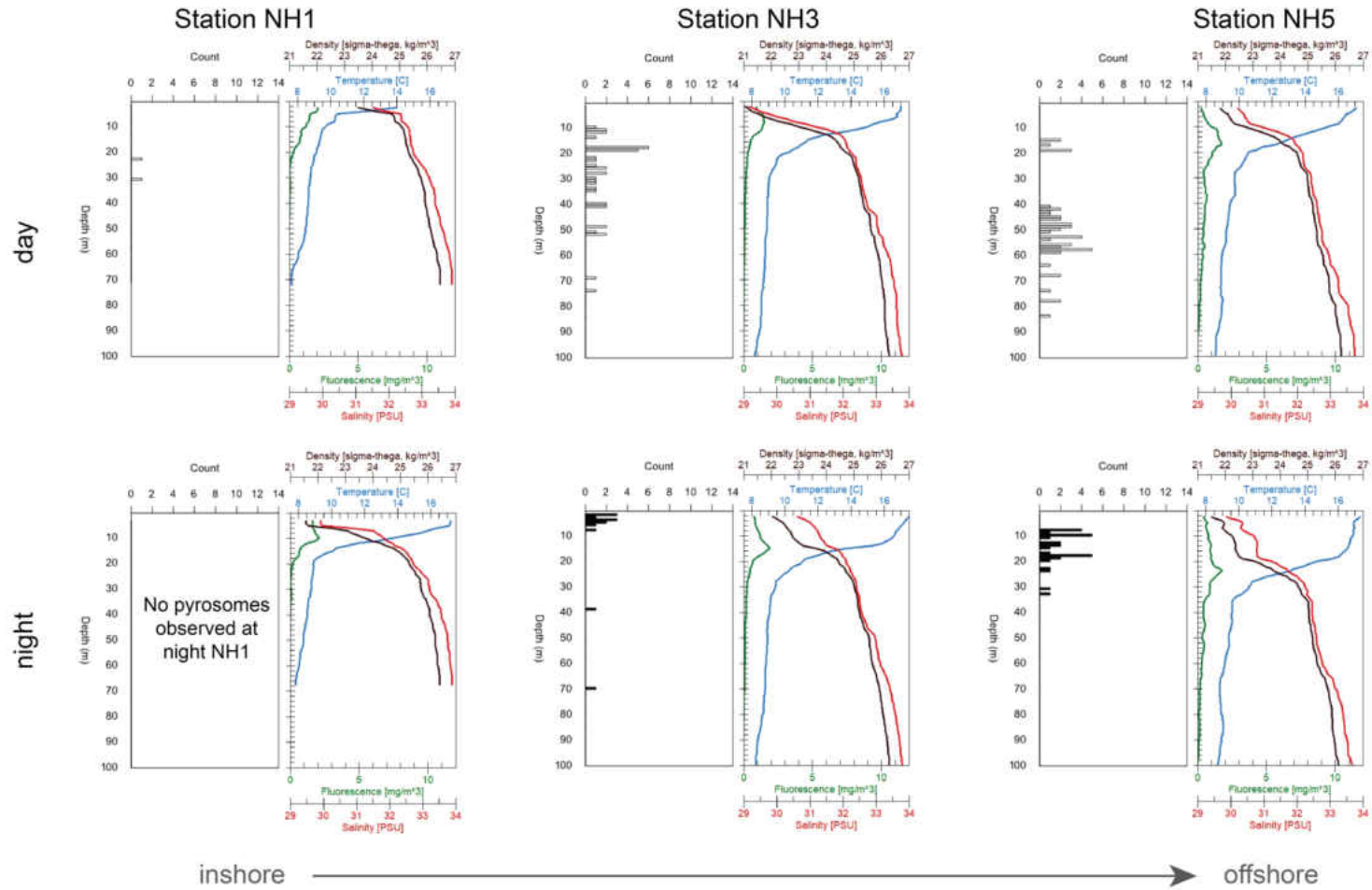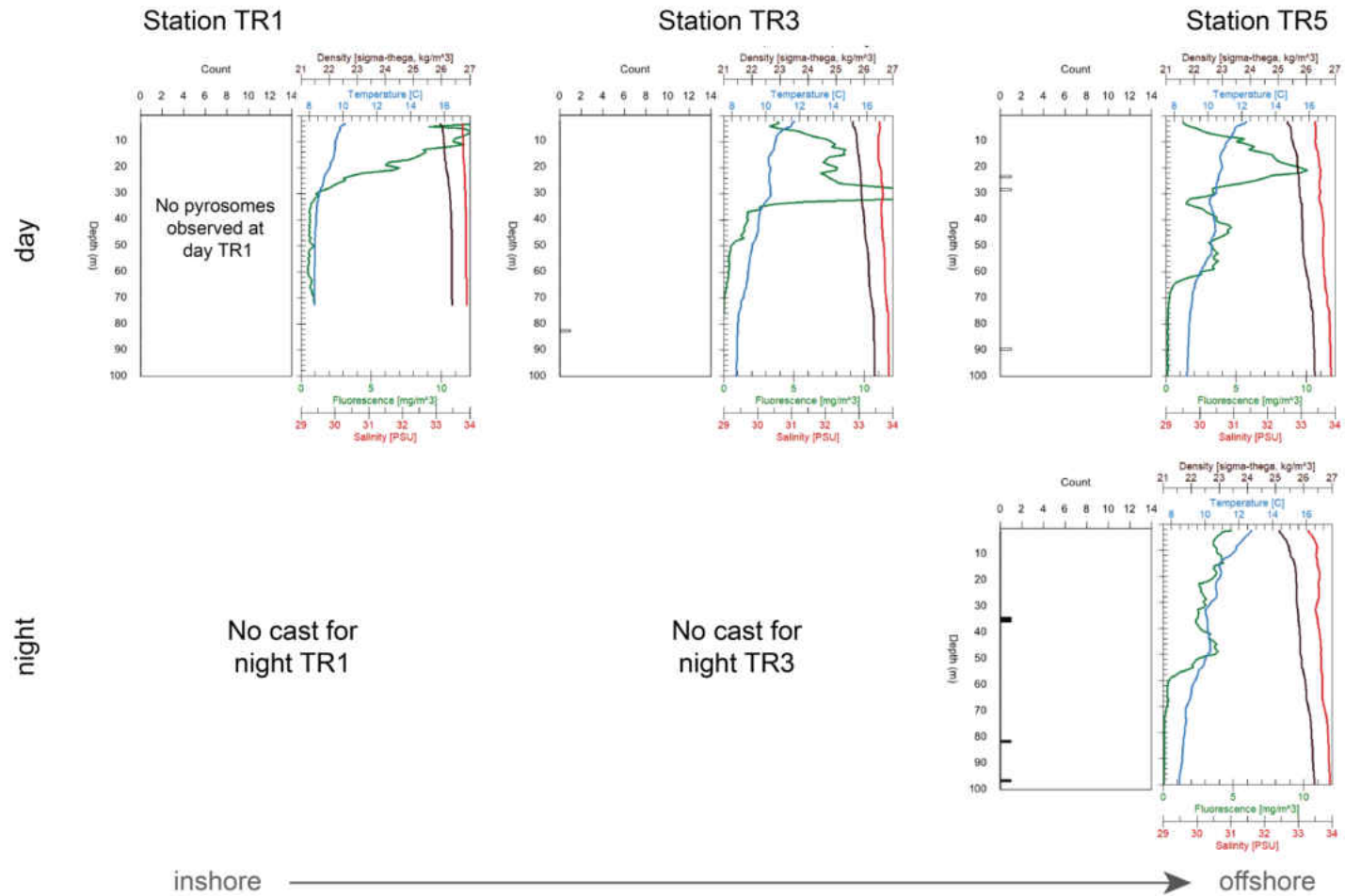## Summer 2018 - Newport, OR (July 11-12, 2018)
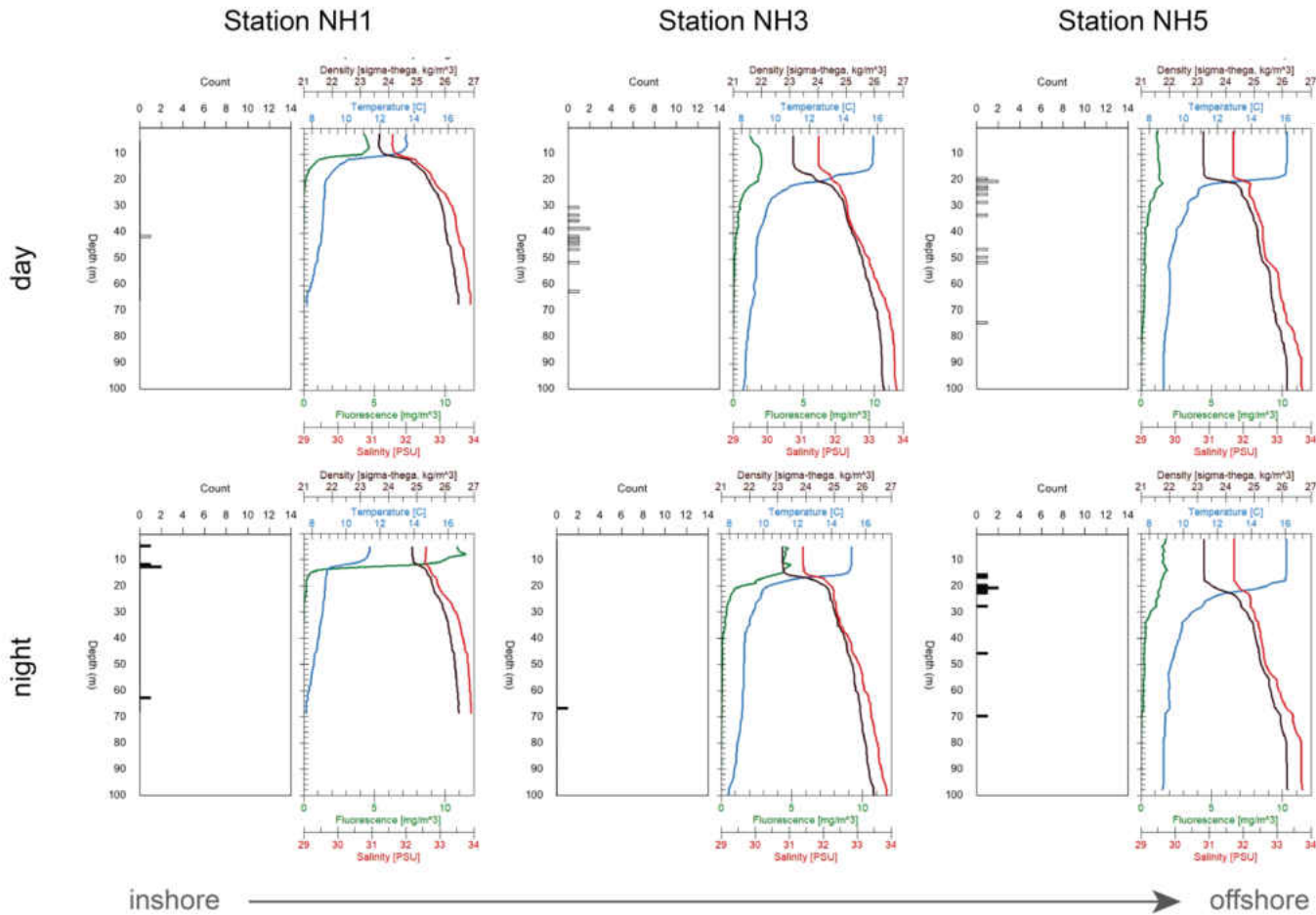
Figure 3f. Selected camera and environmental profiles from summer (July 11-12, 2018) on the Newport, OR (NH) transect. Day (grey bars) and night (black bars) profiles are displayed. Environmental data include temperature (blue), salinity (red), fluorescence (green), and density (black).

Few pyrosomes were observed in nets or camera profiles on the southern transect off Trinidad Head, CA (Fig. 4b). The maximum abundance (7.6 colonies 1000 m^{-3}) and biovolume (1.3 mL m^{-3}) recorded on transect TR in summer was a nighttime tow near the surface at TR5.
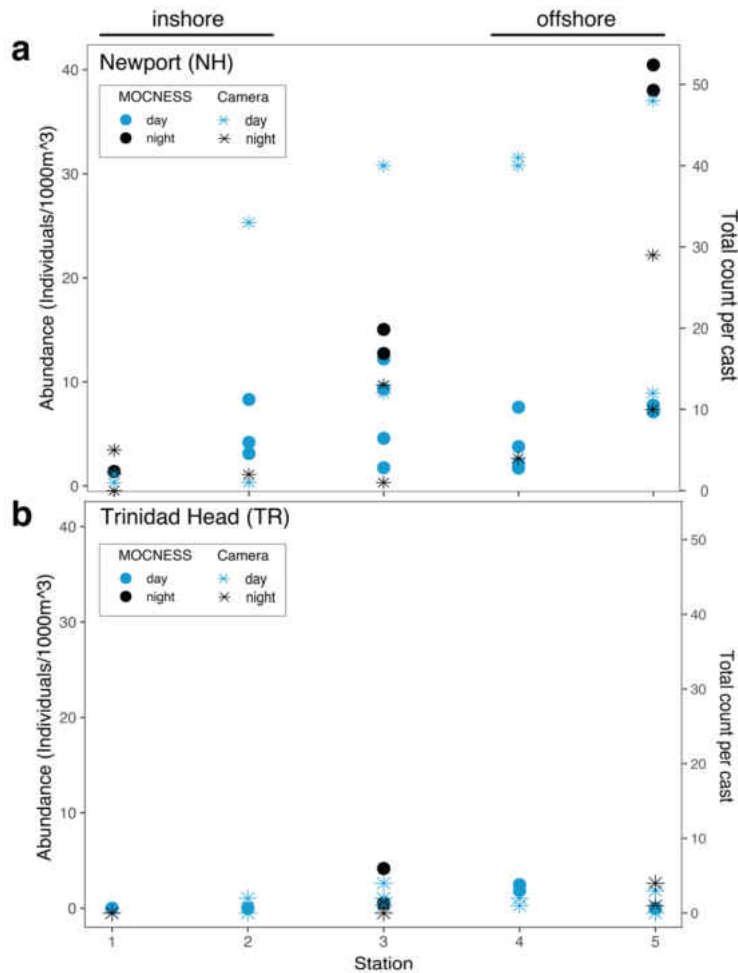
Figure 4. Spatial distribution of *Pyrosoma atlanticum* by station on the (a) Newport, OR (NH) (summer) and (b) Trinidad Head (TR) (summer and winter) transects. Abundances from MOCNESS 100 m tow are denoted by filled circles. Counts from vertically-deployed cameras are summed by cast and displayed as asterisks. Color represents time of deployment: night (black) and day (blue).

The colony size structure shifted from inshore (NH1 and NH2) to offshore (NH4 and NH5) in summer; pyrosomes caught inshore tended to be larger (18.1 ± 0.7 cm; mean ± SE, n=49) than offshore colonies (14.6 ± 0.3 cm; mean ± SE, n=229) (Fig. 5). Too few

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colonies were caught inshore on the TR transect to make a meaningful inshore to offshore

size comparison. The average size of colonies caught on TR transect (18.9 ± 1.1 cm;

mean ± SE, n=43) was similar to those caught offshore on the NH transect.
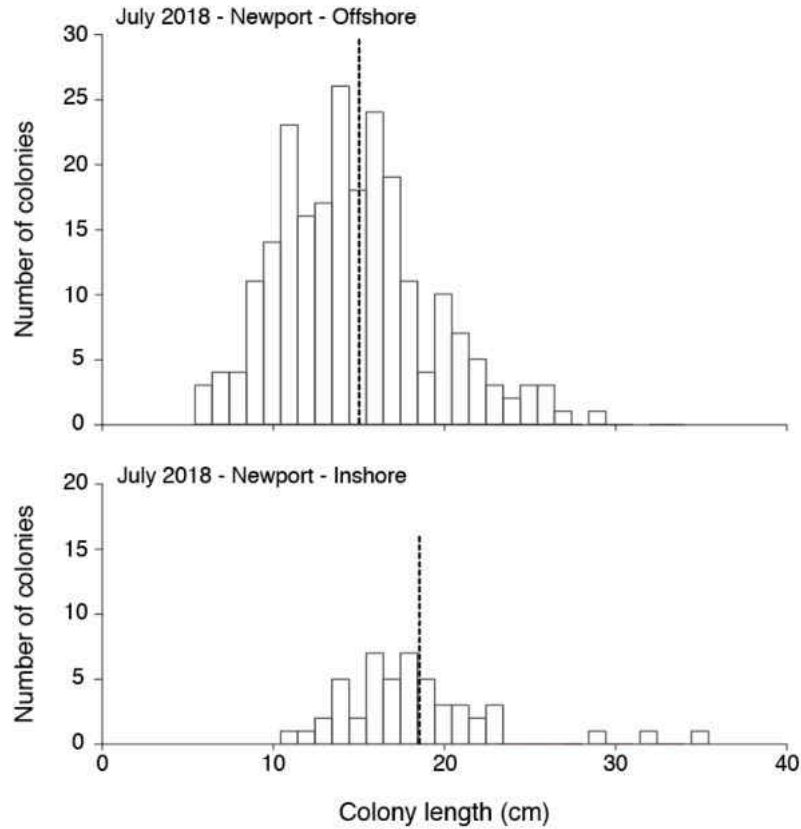
Figure 5. Histograms of colony lengths (in centimeters) from offshore (top, NH4 & NH5) and inshore (bottom, NH1 & NH2) stations in July 2018. Pyrosome colonies caught offshore were smaller (14.6 ± 0.3 cm; mean ± SE, n=229) than inshore colonies (18.1 ± 0.7 cm; mean ± SE, n=49). The vertical dotted line represents mean colony size for each group.

Vertical distribution

Pyrosomes were not distributed uniformly through the water column. Colonies

were often clustered near the base of the surface mixed layer. We rarely observed

pyrosomes within 5 m of the surface. Although colonies appeared to be distributed near

the fluorescence maximum (e.g. Fig. 6), there was not a direct relationship in a regression

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between the mode pyrosome depth and depth of fluorescence maximum during daytime ($R^2 = 0.0014$) or nighttime ($R^2 = 0.11$).
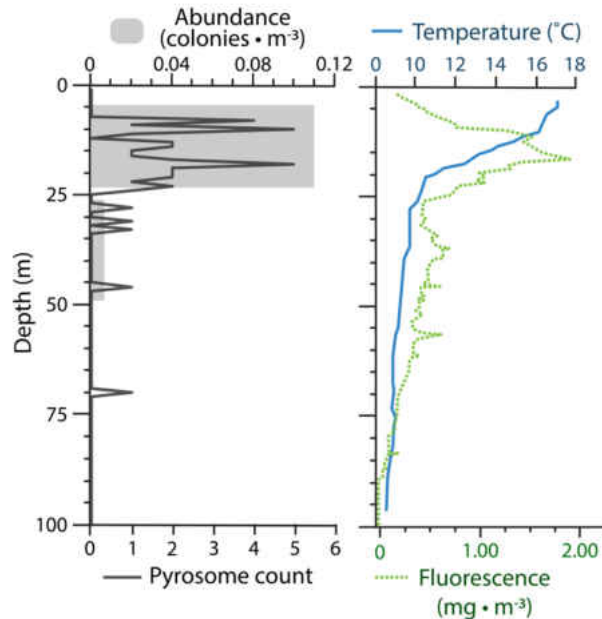
Figure 6. Representative plot showing comparison between the vertical distribution of pyrosomes and the temperature and fluorescence profiles at NH5 (July 9, 2018). Colony abundance was measured from MOCNESS tows (25 m bins). Colony counts were from *in situ* camera profiles (1 m bins). Fluorescence and temperature profiles were captured from CTD deployments (simultaneous with camera deployment).

Diel vertical migration

During the summer cruise, weighted mean depth (WMD) analysis of colonies collected in depth-stratified net tows revealed that the distribution of *P. atlanticum* colonies shifted towards the surface at night, evidenced by day-night differences in depth-stratified abundances and counts from video profiles (Fig. 7a). They were, on average, located deeper in the water column during the day (45.7 ± 3.4 m; WMD $\pm$ SE; n=53) than at night (16 ± 2.7 m; WMD±SE; n=16) at all stations on both transects during summer (Fig. 7b). WMD could not be calculated for the winter cruise due to a malfunction in the net opening mechanism on several nighttime tows. This day-night

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depth shift was most pronounced at offshore stations on transect NH (Fig. 8). On transect

TR, this pattern was not as clear, possibly due to overall lower colony abundances (Fig.

8).
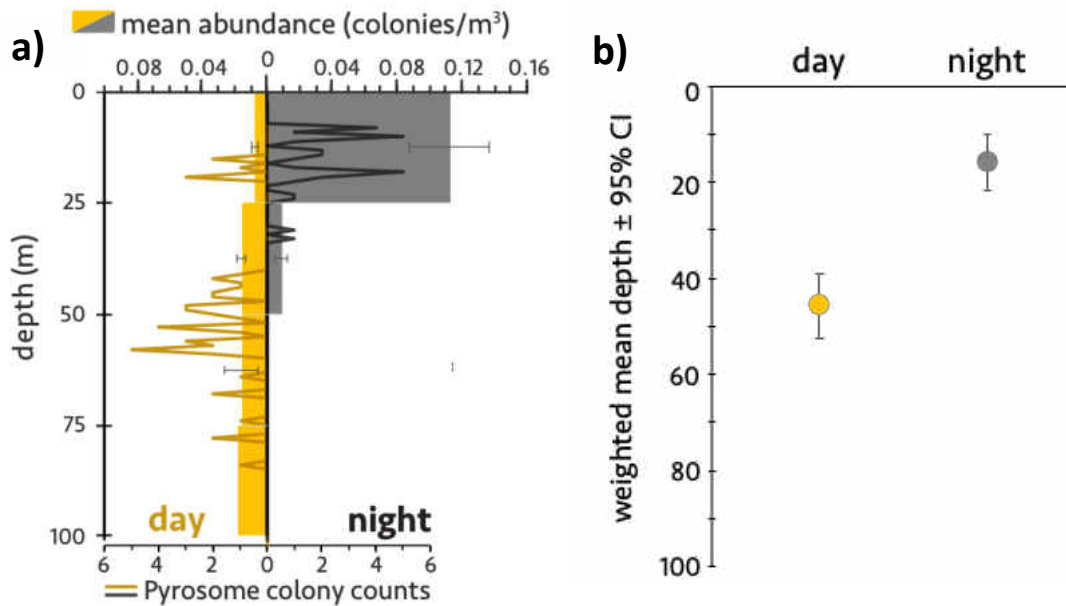
Figure 7. (a) Representative plot showing comparison between day and night distributions at the most offshore Oregon station (NH5) on July 9, 2018. Bars are abundances from MOCNESS tows averaged between the 1 m^2 and 4 m^2 nets (n=2). Lines are *in situ* counts from video frames (day: 48 colonies, night: 29 colonies). (b) Relative weighted mean depth (WMD) and 95% CI of *Pyrosoma atlanticum* from all day and night MOCNESS tows in summer 2018. Colonies were positioned at 45.7 ± 3.4 m (WMD ± SE; n=53) during the day vs. 16 ± 2.7 m (WMD±SE; n=16) at night.
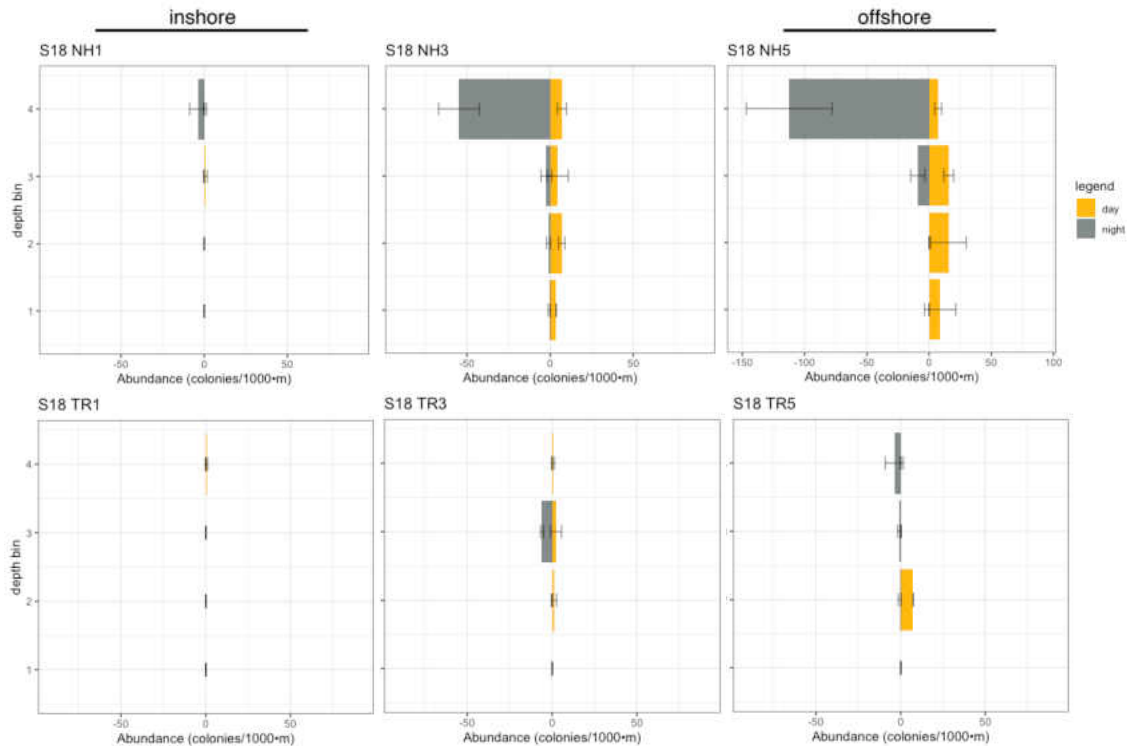
Figure 8. Average daytime and nighttime pyrosome colony abundances from coupled MOCNESS displayed by station (left: offshore, middle: slope, right: inshore) and transect (top: NH, bottom: TR). Error bars represent standard deviation. Negative abundance values denote night tows. Depth bins are 25 vertical meters from surface (bin 4) to 100 m depth (bin 1).

The following results correspond to statistical analysis of summer pyrosome abundances from MOCNESS tows on both transects. The pooled pyrosome abundance in the 100 m sampling range (4 depth bins) did not change significantly between day and night (two-way ANOVA; F=0.66, p=0.42, df=1). Pyrosome abundance differed significantly between depth strata (two-way ANOVA, F=5.89, p=0.0013, df=3). The interaction between time of sampling (day/night) and the distribution of colonies among depth bins was significant (F=8.02, p=0.00014, df=3).

This day-night pattern was also evident from the camera profiles on transect NH. The average mode pyrosome depth in winter and summer was shallower at night (18.7 ± 3.0 m; mean ± SE, n=10) than during the day (36.6 ± 3.5 m; mean ± SE, n=14). In winter,

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daytime and nighttime distributions were shallow at inshore stations NH1 and NH2; the distribution was deeper during the day at offshore station NH5 (Fig. 9a). In summer, daytime distributions of colonies were deeper and varied across a wide depth range, while nighttime distributions were shallow, over a relatively narrow depth range (Fig. 9b). Too few pyrosomes were observed on TR in winter to visualize distribution. In summer, the distribution of pyrosomes was deep but varied. Nighttime tows were only performed at stations TR3 and TR5, but pyrosomes were only observed offshore. At TR5, the nighttime distribution of colonies was deeper than daytime (Fig. 9c).

Comparison of sampling gear

The vertically-deployed camera reliably detected *Pyrosoma atlanticum* colonies relative to the MOCNESS net tows. Of 38 sampling stations that had both camera and net deployments, 31 stations showed agreement between the sampling gear, where the presence of colonies on video corresponded to presence in the nets. Only in three sampling events where pyrosomes were in low densities (≤ 4 colonies per cast) did we see pyrosome colonies on camera but did not catch them in nets. Similarly, there were only three instances where we saw colonies (≤ 3) in the nets, but not on camera. In summer, daytime camera profiles at NH stations tended to have higher total counts than nighttime casts (Fig. 4a).

The oblique tows to 100 m (MOCNESS downcast) tended to underestimate pyrosome abundance relative to the cumulative 25 m increment, depth-stratified tows, particularly when there were many colonies (>30) in a given tow (Appendix Figure 1). Vertical patchiness or differences in sampling physics (i.e. orientation of the net relative

to flow during upcast versus downcast) could explain this discrepancy (Burd & Thomson, 1993).
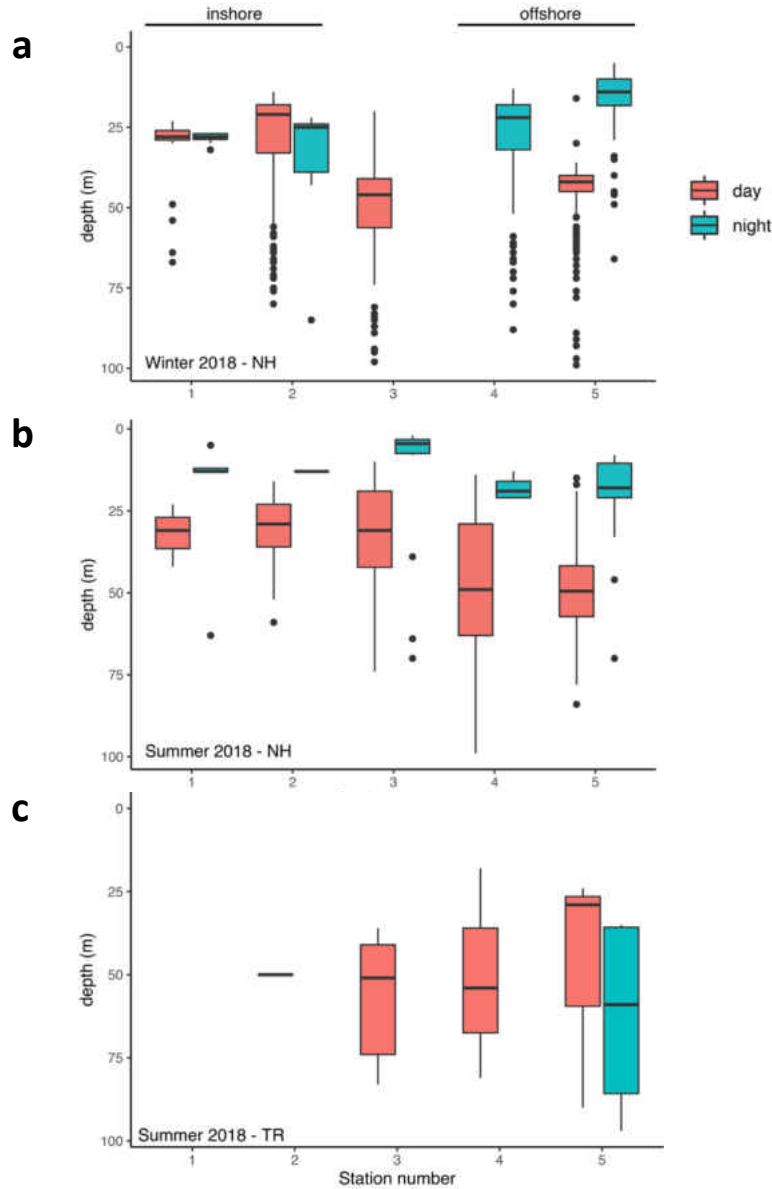
Figure 9. Daytime (red) and nighttime (blue) distribution of pyrosome colonies from camera profiles. Inshore stations are those where the bathymetric depth is <150 m and offshore stations are deeper than 400 m. Pyrosome distributions from Newport, Oregon (NH) transect are shown for winter (a) and summer (b). Note that in winter, stations NH3 and NH4 do not have day-night pairs due to camera malfunction and lack of daytime deployment, respectively. (C) Pyrosome distribution from Trinidad Head, California (TR) transect are shown. Nighttime tows were only performed at stations TR3 and TR5, and none were observed at station TR3. Zero pyrosomes were observed at station TR1.

Discussion

Winter-summer comparison

Pyrosoma atlanticum colonies were present during both winter and summer cruises in 2018 in the NCC. Both SST and stratification increased between winter and summer off Oregon. Fluorescence (an indicator of chlorophyll-a) was typically distributed throughout the surface mixed layer in winter but formed distinct peaks during the summer (Fig. 3). Winter storms generate deep mixing in the upper water column, creating a more uniform density profile (Fig 3a). Summer conditions, by contrast, tend to have a shallow pycnocline and increased stratification (Fig 3b), potentially concentrating pyrosome prey at the base of the surface mixed layer. By contrast, SST and stratification did not increase off northern California. The seasonal discrepancy between transects could be explained by strong, continuous upwelling south of Cape Blanco (Mann & Lazier, 2006).

In general, pyrosome abundances were highest at offshore stations than inshore. For both cruises, the most pyrosome colonies were observed at station NH5 offshore Oregon. The diel vertical distribution patterns were evident in both winter and summer. However, the overall numbers of pyrosomes we observed decreased dramatically between the winter and summer cruises (Appendix Figure 2). Changes in environmental parameters could account for this decrease as SST and surface salinity are positively correlated with pyrosome density in the NCC (Schram et al., 2020). It is important to note, however, in the context of the multi-year blooms, this study occurred during the bloom slow-down. Indeed, by early the following year, very few pyrosomes were in the NCC (Miller et al., 2019; O'Loughlin et al., 2020). Only a single colony was caught in

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our nets in March 2019 (personal observation). Future analysis on the environmental

drivers of pyrosome blooms is necessary.

Spatial distribution

Considerably more pyrosomes were observed off Oregon than northern California

(Fig. 4). Oceanographic conditions off Oregon's central coast are dependent on seasonal

winds, which drive summer upwelling, whereas upwelling is typically more continuous

in the region between Cape Blanco and Cape Mendocino (Longhurst, 2007), although

there is evidence that these dynamics are shifting due to climate change (Brady et al.,

2017). Waters around the Oregon transect were typically highly stratified, particularly in

the summer, relative to the southern transect. Reduced stratification could indicate

vertical mixing within surface waters, potentially preventing the formation of

phytoplankton layers (Chiswell et al., 2014) that grazers may rely on to efficiently

capture energy (Benoit-Bird & McManus, 2012). These environmental differences could

be key in understanding the conditions which drive or limit pyrosome blooms.

Stable isotope analysis by Schram et al. (2020) suggest that pyrosome colonies

collected in the NCC in 2017 likely grew and assimilated carbon offshore. Thus, colonies

collected at inshore stations may have been transported by advection onto the shelf.

Pyrosome colonies grow through asexual budding of additional zooids over time, and

new colonies are formed by sexual generation of tetrazooids (Holland, 2016). Miller et al.

(2019) proposed that the presence of small colonies may play a key role in seeding and

maintaining blooms off the west coast of North America. The increased frequency of

relatively small (i.e. younger) colonies observed offshore may suggest that sexual

reproduction occurs in waters far from shore. Although offshore colonies were small

relative to those caught inshore in July 2018, they were large (>140 mm) in the context of the Miller et al. (2019) study. This lack of small (<40 mm), newly budded colonies may have foreshadowed the bloom cessation in the coming months.

Vertical distribution

Pyrosoma atlanticum colonies were distributed non-uniformly in the water column with highest colony densities frequently associated with the base of the surface mixed layer, near the subsurface chlorophyll maximum (Figs. 3 & 6). Although colonies aggregated near fluorescence peaks at night, their distribution did not appear to track to the precise location of maximum fluorescence, suggesting that vertical position is likely influenced by multiple interacting factors. Our observations represent snapshots of the vertical distribution of colonies, and it is likely that the vertical positioning is the dynamic result of collective behavior interacting with physical features.

The association of colonies with the mixed layer and regions of elevated fluorescence is likely related to pyrosome targeting of photosynthetic prey taxa, including diatoms, dinoflagellates, prymnesiophytes, and picoeukaryotes (Perissinotto, 2007; Schram et al., 2020; Thompson et al., in review). The mucous-mesh of the pyrosome feeding mechanism seems to efficiently target cells >10 µm (Perissinotto et al., 2007), though may become clogged in high-particle waters close to shore (Harbison et al., 1986). Recent estimates suggest that NCC pyrosomes could consume up to a quarter of daily phytoplankton standing stock (O'Loughlin et al., 2020). Consequently, pyrosome feeding at a low trophic level could decrease the amount of food available to other zooplankton grazers in surface waters of the NCC (Conley et al., 2018; Schram et al., 2020).

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There are likely multiple passive and active aggregating mechanisms contributing to pyrosome colony clustering in the water column. A previous study of doliolids, another pelagic tunicate, concluded that aggregations were the result of directional swimming and rarely coincided with depths of high chlorophyll concentrations (Paffenhöfer et al., 1991). Sharp salinity gradients can be a physical barrier to the migration of small zooplankton (Lougee et al., 2002), although it is unclear whether these density gradients affect pyrosome swimming. Notably, we observed highest clustering during the winter cruise when density gradients were the most modest. Some gelatinous zooplankton aggregate around haloclines as a behavioral preference (Arai, 1973), but to our knowledge no one has studied pyrosome swimming dynamics in enough detail to evaluate whether pyrosomes exhibit similar behavior. Unfortunately, difficulty in keeping pyrosomes in captivity currently limits laboratory-based experimentation that would be necessary to explore these questions.

Diel vertical migration

Weighted mean depth analysis revealed a nighttime vertical shift of *P. atlanticum* colonies towards the surface (Fig. 7b). These results suggest that diel vertical migration (DVM) is the mechanism driving these changes in vertical structure, although the scale of migrations by NCC pyrosomes is yet unclear. Other studies have found *P. atlanticum* at depths of 700 m or more (e.g. Andersen et al., 1992). Because our sampling was limited to the top 100 m of the water column, we could only determine the position of colonies relative to the surface between day and night. We observed similar abundances of colonies within the 100 m sampling depth at night relative to the day, with the exception of summer station NH5 where the nighttime abundance increased (Fig. 4a). Except for

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colonies sampled at shallow inshore stations (<100 m), we cannot rule out the possibility that *P. atlanticum* is performing multi-hundred-meter migrations similar those shown in studies elsewhere in the world (Andersen et al., 1992; Angel, 1989; Henschke et al., 2019).

Diel vertical migrations may be the result of several mechanisms: light-avoidance, feeding, and reproduction. *Pyrosoma atlanticum*, like other vertically migrating zooplankton, may migrate up to the chlorophyll maximum at night (Harris, 1988) to feed in darkness, safe from visual predators (Lampert, 1989). Light may better penetrate the clear, oligotrophic waters of the tropics than the particle-filled waters of the NCC due to phytoplankton bloom shadowing (Kaartvedt et al., 1996; Sato et al., 2013). Thus the scale of these migrations we observed may be less extensive because the hypothesized cue to migrate (i.e. light) is relatively reduced close to the surface. Alternatively, pyrosomes may be aggregating near desirable grazing locations. Henschke et al. (2019) concluded that chlorophyll *a* levels were driving vertical distribution patterns of *P. atlanticum*; in a cold-core (upwelling) eddy, pyrosome colonies were distributed closer to the surface, even remaining in the top 100 m during the day. Finally, pelagic tunicates may aggregate to increase gamete concentrations during reproductive events (Purcell & Madin, 1991).

High grazing rates by NCC pyrosomes in surface waters (O'Loughlin et al., 2020) combined with daytime migration to depths could expedite carbon export via active transport (Steinberg et al., 2008). Thus, large aggregations of vertically-migrating pyrosomes have the potential to alter NCC trophic dynamics by short-circuiting the microbial loop and accelerating the biological pump. Pyrosomes and other pelagic tunicates use mucous mesh sieving to harvest small particles, removing available food for

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micro- and meso-zooplankton in surface waters, termed a "short-circuit" as it bypasses those lower trophic levels (Conley et al., 2018; Le Fèvre et al., 1998; Pomeroy et al., 2007). Active transport from fecal pellet production is one mechanism by which pelagic tunicates can accelerate carbon export. Recent estimates indicate that active transport by *P. atlanticum* has a minimal impact when the mixed layer is deep (>180 m) (Henschke et al., 2019), but likely plays a bigger role in the NCC where ML depth is often much shallower. Aggregations of pyrosomes may quickly assimilate carbon in surface waters then migrate to depth where they produce fecal pellets or are themselves ingested by mesopelagic or benthic consumers. These effects may be more pronounced offshore where colony abundances were higher and there is greater potential for pyrosome biomass to be transported to depth.

Comparison of sampling gear

The vertically deployed camera system was a reliable and cost-effective method to sample the vertical structure of conspicuous, abundant macrozooplankton. Cameras provided higher resolution *in situ* counts relative to the large ship-deployed MOCNESS net system that was constrained to the number of available nets and human processors. Although we deployed the camera from the shipboard CTD rosette, this method could be easily adapted for use with smaller CTD cages deployed off boats or docks. We were limited to sampling the top 100 m of the water column, but sampling depth could be expanded through use of shipboard acoustic backscatter to capture deep distributions and migration speeds (Henschke et al., 2019)

The main drawback of the present study is unknown sampling volume in video profiles, without which calculating abundance is impossible. This may be a particular

issue in comparing counts from video profiles under different lighting regimes. Our results suggest that the additional light from surface illumination during daytime camera profiles may increase visibility of distant colonies relative to nighttime (or deep) casts lit only by the mounted lights. One could reasonably create and apply a correction factor based on background light intensity and attenuation. Another solution is using calibrated stereo cameras where distance in three-dimensional space is measurable, allowing for *in situ* abundance calculations (Goetze et al., 2019). However, the single camera was sufficient to identify distribution patterns and make comparisons between deployments.

Implications for the NCC

Our findings suggest that blooms of *P. atlanticum* in the NCC may have the most prominent effects north of Cape Blanco in waters on the slope and offshore where colony abundances were highest. Large blooms of *P. atlanticum* similar to those seen in 2018 could affect pelagic food webs of the NCC due to increased grazing pressure (Drits et al., 1992; Henschke et al., 2019; O'Loughlin et al., 2020) that may restructure energy transfer. However, pyrosome biomass is not a trophic dead-end; pelagic fish and cetaceans have been recorded feeding on NCC pyrosomes (Brodeur et al., 2018). Additionally, jelly-falls composed of *P. atlanticum* in the NCC provide extra carbon input to benthic consumers such as crustaceans, sea stars, brittle stars, and anemones (Archer et al., 2018; Lebrato & Jones, 2009). Under bloom conditions, *P. atlanticum* aggregations undergoing diel vertical migration could accelerate the biological pump in the NCC by transporting surface carbon to depth via fecal pellets.

Despite its global distribution, little is understood about the basic biology and vertical dynamics of *P. atlanticum*. Identifying distribution patterns and migratory

behaviors is key to understanding how they fit into the NCC ecosystem, particularly

given recent evidence of a northward range expansion (Sutherland et al. 2018). The

unprecedented blooms of *P. atlanticum* in recent years are likely tied to a large-scale shift

in oceanographic conditions along the U.S. West Coast (Brodeur et al., 2019).

Understanding the distribution of these gelatinous grazers will give insight into their

ecological role in the Northern California Current as favorable bloom conditions become

more common.

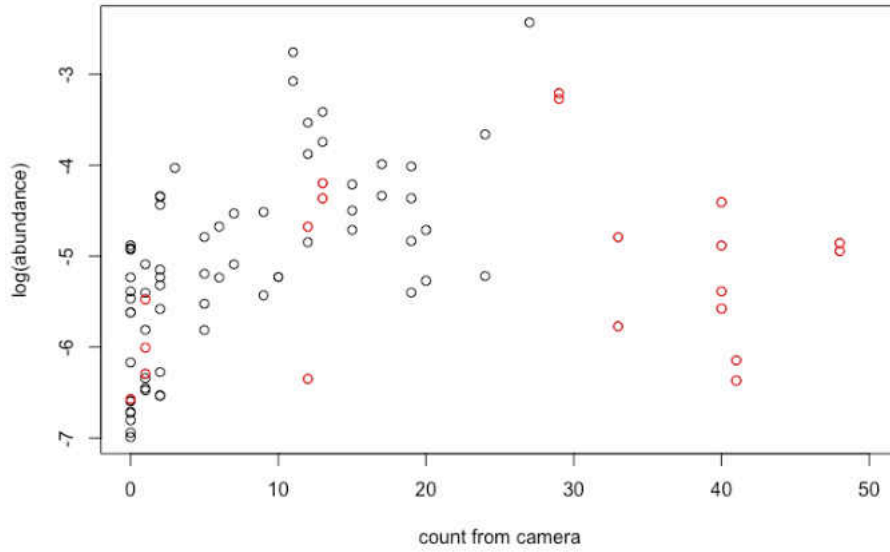Figure 1. Comparison between depth-stratified (25 m) and whole-column (100 m) tows. log(abundance) (colonies m^{-3}) from MOCNESS net tows plotted against pyrosome colony counts from camera and in summer 2018. Black and red symbols are from 25 m and 100 m vertical bins, respectively.
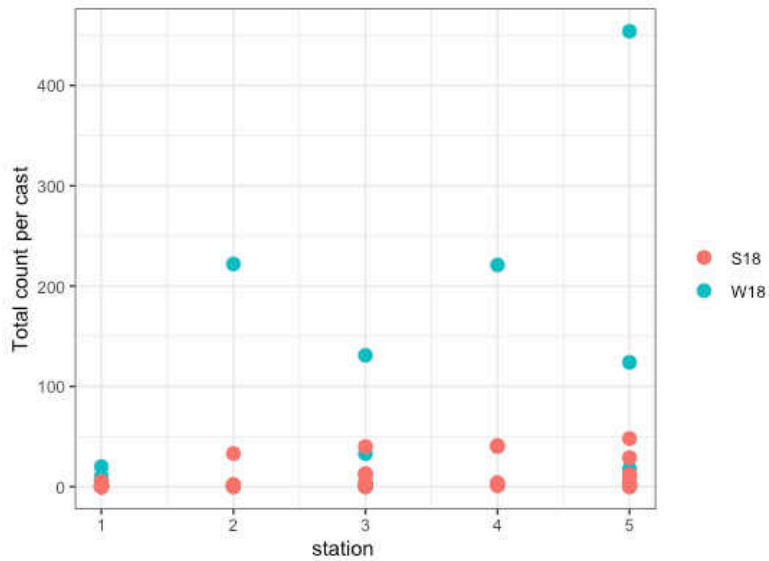

Figure 2. Comparison between pyrosome counts from camera deployments in winter ("W18", blue") and summer ("S18", red).

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