POPULATION DYNAMICS AND VARIABILITY OF TWO GELATINOUS ZOOPLANKTERS (*AEQUOREA* & *PYROSOMA ATLANTICUM*) IN THE NORTHERN CALIFORNIA CURRENT

by

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THESIS ABSTRACT

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September 2018

Title: Population Dynamics and Variability of Two Gelatinous Zooplankters (*Aequorea* & *Pyrosoma atlanticum*) in the Northern California Current

This research focused on population dynamics of two gelatinous zooplankters (*Aequorea* & *Pyrosoma atlanticum*) in the northern California Current to assess their relationship to environmental conditions and role in the pelagic ecosystem. Data collected since 1999 showed seasonal and interannual fluctuations in the abundance and distribution of *Aequorea* in the NCC, with a positive correlation with sea surface temperature and salinity. *Pyrosoma atlanticum*, which are typically found in tropical waters, have only been observed in high abundances in the NCC since 2014 and their role in the pelagic ecosystem is not well understood. Pyrosome abundance related to *in situ* environmental variables showed a positive correlation with warmer SST. We also used fatty acids as trophic markers to better understand pyrosome trophic ecology in the NCC. FA biomarkers suggest that pyrosomes have a broad phytoplankton diet, which may indicate an ability to inhabit warmer, lower nutrient zones.

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CHAPTER I

GENERAL INTRODUCTION

Gelatinous zooplankton are an important component of marine ecosystems through their efficient feeding behaviors and ability to adapt to a variety of environmental conditions (Graham et al. 2001). Gelatinous zooplankton are influenced by small and large scale environmental fluctuations (Suchman et al. 2012) and their interannual and seasonal variability offers unique insight into the relationship between physical environmental conditions and population dynamics (Brodeur et al. 2008, Brotz et al. 2012).

The California Current is an eastern boundary current that flows southward from southern British Columbia to Baja California (50 ^{o}N to 30 ^{o}N respectively). Episodic and seasonal upwelling support a biologically productive area and a fisheries hot spot (Checkley & Barth 2009). Throughout spring and summer, winds blowing from the northwest generate upwelling of cold, nutrient rich water into the euphotic zone leading to an increase in primary productivity that supports a robust fisheries industry (Ruzicka et al. 2012, Conley & Sutherland 2015). The strength, timing, and duration of this seasonal upwelling is influenced by large-scale ocean and atmospheric indicators such as El Niño Southern Oscillation (ENSO) and the Pacific Decadal Oscillation (PDO) (Bi et al. 2011; Shanks & Roegner 2007; Checkley & Barth 2009).

The northern California Current (NCC; 42-48 ^{o}N), where the wind stress alternates from a northward and southward direction (Shanks & Roegner 2007, Checkley & Barth 2009), is an informative system to study the relationships between environmental variables and gelatinous zooplankton due to the dynamic seasonal

upwelling, which is sensitive to regional oceanographic indices and drives biological productivity (Bograd et al. 2009). In the NCC, seasonal and interannual environmental variability (temperature, salinity, dissolved oxygen, fluorescence) can lead to blooms of gelatinous zooplankton including cnidarian jellyfish and pelagic tunicates (Lavaniegos & Ohman 2003, Purcell et. al 2007, Suchman et al. 2012). Frequent blooms and broader distributions of certain gelatinous zooplankters have been observed in many marine ecosystems including the NCC (Purcell et al. 2007, Sutherland et al. 2018, Zeman et al. 2018) and these blooms can have lasting impacts on ecosystem dynamics and human activities (Graham et al. 2014).

Climate regimes in the North Pacific (periods of 1-3 decades; Lavaniegos & Ohman 2003), influence pelagic ecosystem dynamics through changes in sea surface temperature (SST), salinity, dissolved oxygen (DO), and currents all of which drive the timing and distribution of species in a given area. In the NCC, oceanographic influences on zooplankton populations include ENSO, PDO, and more recently, there have been unique environmental conditions impacting ecosystem dynamics such as the anomalously warm ocean conditions, termed “the Blob” that began in 2013 in the NE Pacific (Bond et al. 2015, Kintisch 2015; DiLorenzo and Mantua 2016). The 1-4˚C warming of ocean temperatures continued through 2015 followed by a major ENSO event in 2016 (Jacox et al. 2016; Peterson et al. 2017). Ecosystem impacts from these warmer ocean temperatures are not fully understood (Bond et al. 2015); however, warming sea surface waters have been linked to an increase in frequency of occurrence and abundance of several species of gelatinous zooplankton including pelagic tunicates and cnidarians (Peterson et al. 2017,

Brodeur et al. 2018). The two focal organisms for this research were the hydrozoan jellyfish, *Aequorea*, and the pelagic tunicate, *Pyrosoma atlanticum*.

This research first looked at interannual and seasonal variability in the abundance and distribution of *Aequorea* related to environmental variables in the NCC over an 18-year time period (1999-2017). We then focused on the 2017 bloom of *Pyrosoma atlanticum* in the NCC in the context of environmental parameters (temperature, salinity and fluorescence) and explored their feeding ecology through fatty acid analysis.

CHAPTER II

LONG-TERM CHANGES IN ABUNDANCE OF THE HYDROMEDUSA *AEQUOREA* IN RELATION TO ENVIRONMENTAL VARIABLES IN THE NORTHERN CALIFORNIA CURRENT (1999-2017)

Introduction

Cnidarian medusae are highly responsive to environmental fluctuations (temperature, salinity, dissolved oxygen and chlorophyll-a (Graham et al. 2003), have rapid growth, reproduction (Purcell, 2017), and therefore, are able to take advantage of conditions where other marine organisms may exhibit stress (Robinson et al. 2014). Cnidarian 'jellyfish' (i.e., medusae) are known to form dense aggregations known as "blooms" as part of their life cycle, however, increased climate variability in recent decades may contribute to an increase in bloom events of gelatinous zooplankton in some regions (Attrill et al. 2007, Brotz et al. 2012). This phenomenon has contributed to growing concern regarding the potential for gelatinous zooplankton to alter the marine food web (Brotz et al. 2012, Suchman et al. 2012), particularly, their potential negative impacts on key fish species and fishery operations (Purcell, 2012, Brodeur et al., 2016). For this study, we explored the relationship between *in situ* environmental variables and distribution and abundance patterns of the hydromedusan jellyfish *Aequorea* in the NCC (42-48˚N). We focused on the genus *Aequorea* because of their regular presence in the northern California Current and availability of time series data on their abundance, size, and distribution collected by annual NOAA fisheries surveys. The northern California Current is an ideal system to study the relationships between environmental variables and

zooplankton due to the dynamic and strong episodic seasonal upwelling signal, which drives biological productivity (Hickey et al. 2010).

Aequorea, commonly referred to as "crystal jellies" are bioluminescent hydrozoan jellyfish in the phylum Cnidaria. *Aequorea* have a benthic hydroid stage and a free-swimming medusae stage, which develop from asexually produced buds released from the hydroids. Medusae are sexually reproductive and fertilized eggs produce free-swimming larvae that settle into new benthic polyps within a few days of being released into the water column (Purcell 2017). The adult medusae are conspicuous in the pelagic environment due to their broad, cross-shelf distribution and frequency of being caught in surface trawl nets. Medusae grow rapidly going from bell diameters of a few cm in the spring to almost 40 cm in the fall (Suchman et al. 2012, Purcell 2017). Their relatively large size has led to their inclusion in studies focusing on larger scyphozoan jellyfish such as *Chrysaora fuscescens* and *Aurelia labiata* as key predators in the pelagic ecosystem (Suchman et al. 2012).

Aequorea in the NCC have previously been shown to feed on copepods, other hydromedusae, appendicularians, fish eggs and larvae (Purcell 1989). Gut content analysis of *Aequorea* in British Columbia in 1983 revealed few crustaceans, and large amounts of larvaceans, hydromedusae and siphonophores as well as herring larvae and flatfish eggs (Purcell 1989, Ruzicka 2007, Uye & Brodeur 2017). *Aequorea* predation on herring larvae can have detrimental consequences to the herring fishery due to the spatial overlap of *Aequorea* and herring spawning areas (Purcell et al. 1989).

Aequorea populations typically go through interannual and seasonal fluctuations with peak abundance in June followed by a decline throughout the summer with lower

abundances by September (Suchman et al. 2012, Purcell 2017). There are approximately 30 species of *Aequorea* worldwide (Purcell et al. 2015) which have a broad global distribution. *Aequorea victoria*, is the most common species along the west coast of North America from the Bering Sea to southern California as well as the Mexican Caribbean Sea, North Sea fjord systems, the Yellow Sea in China and the Catalan Sea in Spain. For this study we did not identify specimens collected in the NCC to species and therefore will refer to the genus *Aequorea* throughout. *Aequorea* have a much broader cross-shelf distribution than other large cnidarian jellyfish such as *Chrysaora fuscescens* (Suchman et al. 2012) and can be a nuisance for fisheries operations during bloom events by interfering with equipment as well as out-competing other taxa for food and habitat (Purcell et al. 2007, Conley & Sutherland 2015). Visual studies in the Bering Sea showed that *Aequorea* vertically migrate from deeper waters (~100 m) during daylight hours toward the surface at night (Purcell 2017) at a mean depth of 24 m (Uye & Brodeur 2017).

Due to the interannual and seasonal variability in abundance and distribution of gelatinous zooplankton and the recent blooms of *Aequorea* in 2015 and 2016 in the NCC, we sought to better understand which *in situ* environmental variables related to their population dynamics. We used NOAA annual fishery survey data to collected since 1999 to identify patterns in interannual and seasonal abundance and size of *Aequorea* related to large-and local-scale oceanographic indices.

Methods

Data Collection

Data used for this analysis were collected by NOAA Northwest Fisheries Science Center (NWFSC) annual surveys in the northern California Current off Washington and Oregon (~45°N-48°N) from 1999 to 2017. Surveys were conducted during the second half of June 1999-present and during late September from 1999-2012. Surveys sampled along eight cross-shelf (124.0°W-124.7°W) transects each containing 6-8 stations from Newport, Oregon to Father and Son, Washington. At each station, the upper 20 m of the water column was sampled with a Nordic 264 rope trawl with a 336 m^2 mouth opening (Nor-Eastern Trawl Systems, Inc.). Mesh size ranged from 162.6 cm at the mouth to 8.9 cm at the cod end. Trawls were towed for 30 minutes at approximately 6 km hr^1 (Suchman et al. 2012, Barcelo et al. 2018).

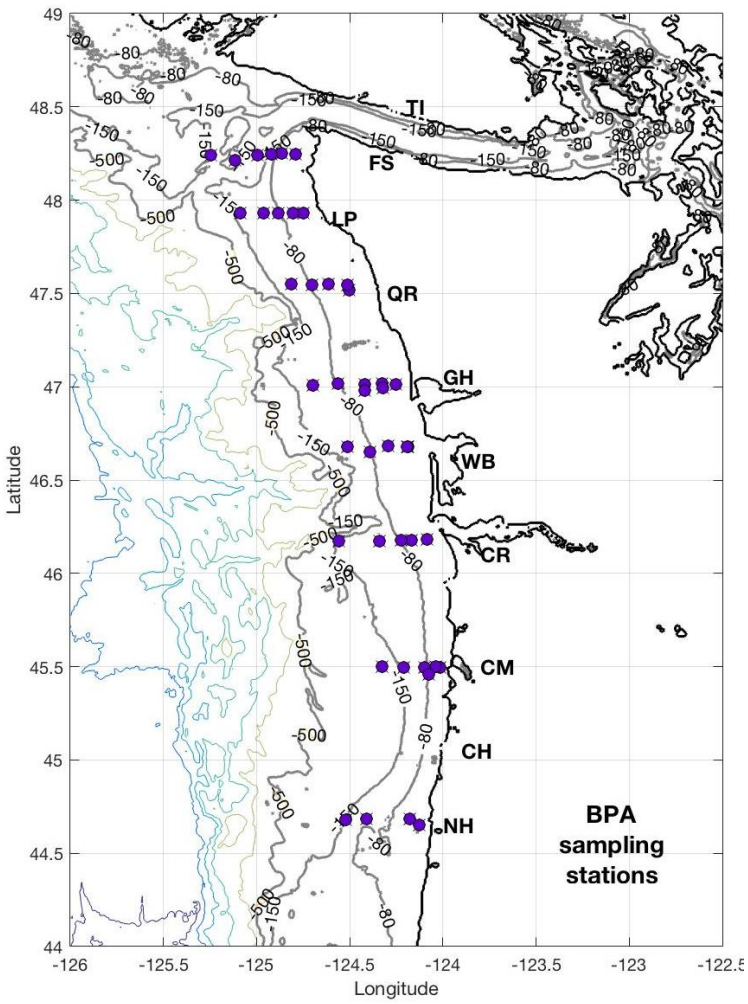


Figure 2.1 NOAA fishery survey-sampling stations 1999-2017 for the northern California Current off Washington and Oregon, USA shown with depth contours. Each circle represents the target sampling stations for each year. Transect acronyms are listed from north to south: Father and Son (FS), La Push (LP), Queets River (QR), Grays Harbor (GH), Willapa Bay (WB), Columbia River (CR), Cape Meares (CM), Newport Hydrographic (NH). Not all stations were sampled every year 1999-2017.

Large medusae, including *Aequorea* were identified, counted, weighed and, bell diameters were measured immediately after collection (Suchman et al. 2012). For large hauls, a random sub-sample of 50 medusae were counted, weighed and measured (Suchman et al. 2012). Abundance of *Aequorea.* were calculated by the area trawled and recorded as number of individuals per square km (Suchman et al. 2012).

In situ environmental conditions (temperature, salinity, dissolved oxygen) were collected at each sampled station with a conductivity-temperature-depth (CTD) unit (Sea Bird Electronics) deployed to 100 m at deep stations and to 5 m off the bottom at shallow stations. For the analysis of *Aeqourea* distribution, the sampled area was partitioned into three depth bins representing near shore (<75 m), shelf (75-150 m) and off-shore (>150 m). Chlorophyll *a* was sampled at 3 m depth with Niskin bottles (Suchman et al. 2012). Environmental indices including the Pacific Decadal Oscillation (PDO), upwelling, and Columbia River discharge were also examined over the same 18-year period. PDO data were obtained from http://research.jisao.washington.edu/pdo/, upwelling indices from: https://www.pfeg.noaa.gov/products/PFEL/modeled/indices/upwelling/upwelling.html , and river discharge data from USGS at the Dalles, Oregon: https://waterdata.usgs.gov/usa/nwis/uv?14105700. Environmental indices data were not lagged for this study.

Statistical Analysis

We used Generalized additive models (GAM) to identify and measure non-linear relationships between abundance and distribution of *Aequorea* and *in situ* environmental variables. GAMs are a non-parametric, additive, regression tool because they do not assume linear relationships between the dependent variable (*Aequorea* abundance) and the covariates (temperature °C, salinity ppt, chlorophyll a, distance from shore km). The relationships between variables were modeled with smoothing functions (Ciannelli et al. 2010, Suchman et al. 2012). Due to the spatial variability and high number of zero counts in the data, a Delta-GAM model with a binomial family was applied. Model goodness of fit was selected by working backward from an initial model containing all covariates and

removing covariates one by one while examining the model summary output p-value, equivalent degrees of freedom (EDF), and generalized cross validation (GCV) which measures model prediction error (Drexler & Ainsworth 2013). GAMs were run using the mgcv package in R version 3.3.2. Graphics were generated in MATLAB. The relationship between *Aequorea* abundance and bell diameter was analyzed using Poisson-family generalized linear models (GLMs). The models produced were compared using Aikaike's Information Criterion (AIC) and the model with the lowest AIC was considered to be the best model.

Results

Interannual variability

Over the 18-year time series (1999-2017), abundance of *Aequorea* per square km varied interanually, seasonally and across stations with the highest abundances recorded in 2015 and 2016, reaching more than 16,000 km^2 at some locations. Variability in abundance was highest in the near shore region (depths <75 m) for all sampled latitudes (Figure 2A). However, in the shelf region (75-150 m depth) abundance remained fairly consistent from year to year (Figure 2B).

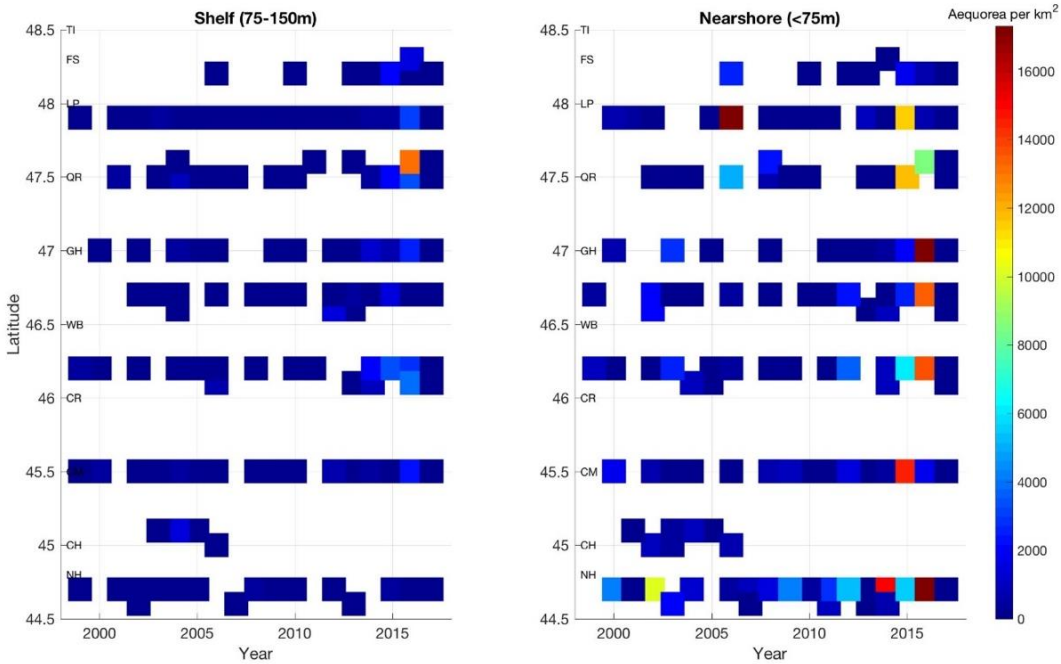


Figure 2.2 *Aequorea* abundance 1999-2017 over the sampled latitudes. A) shelf stations (75-150 m depth), B) nearshore stations (<75 m depth). Nine transects were sampled each year in June ranging from Father and Son in the north to Newport in the south. Each square represents the mean of all stations sampled at that latitude during June. *Aequorea* were not common off shore at depths >150 m.

Aequorea were relatively low in abundance most years in the NCC with many sampled stations recording zero catch. Until 2014, average abundance did not exceed 6,000 individuals per square km except for two stations off of Newport, OR in 2002 and one station off of La Push, WA in 2005 (Figure 2B). The mean catch per station of *Aequorea* for all years was 191 individuals per square kilometer while a maximum of 20,772 individuals was caught in 2016, which was the highest abundance year for the time series (Figure 3). On average the highest catches were collected from the near shore region from La Push (>16,000), Grays Harbor (>16,000), Willapa Bay (>14,000), Columbia River (>14,000), Cape Meares (>14,000), and Newport (>16,000) transects. Abundances greater than 6000 km^2 were all collected from the near shore region except

in 2016 when more than 12,000 individuals were collected from the Queets River transect (Figure 2A). Surface water temperatures were cool with lower salinity in 2008-2011 when abundance of *Aequorea* was low. Surface temperatures increased 2012-2016 and the highest catches of *Aequorea* were in 2015 and 2016 (Appendix Figure 1). Surface salininity was highest in 2015 and moderate in 2016 (Figure 3, Appendix Figure 2).

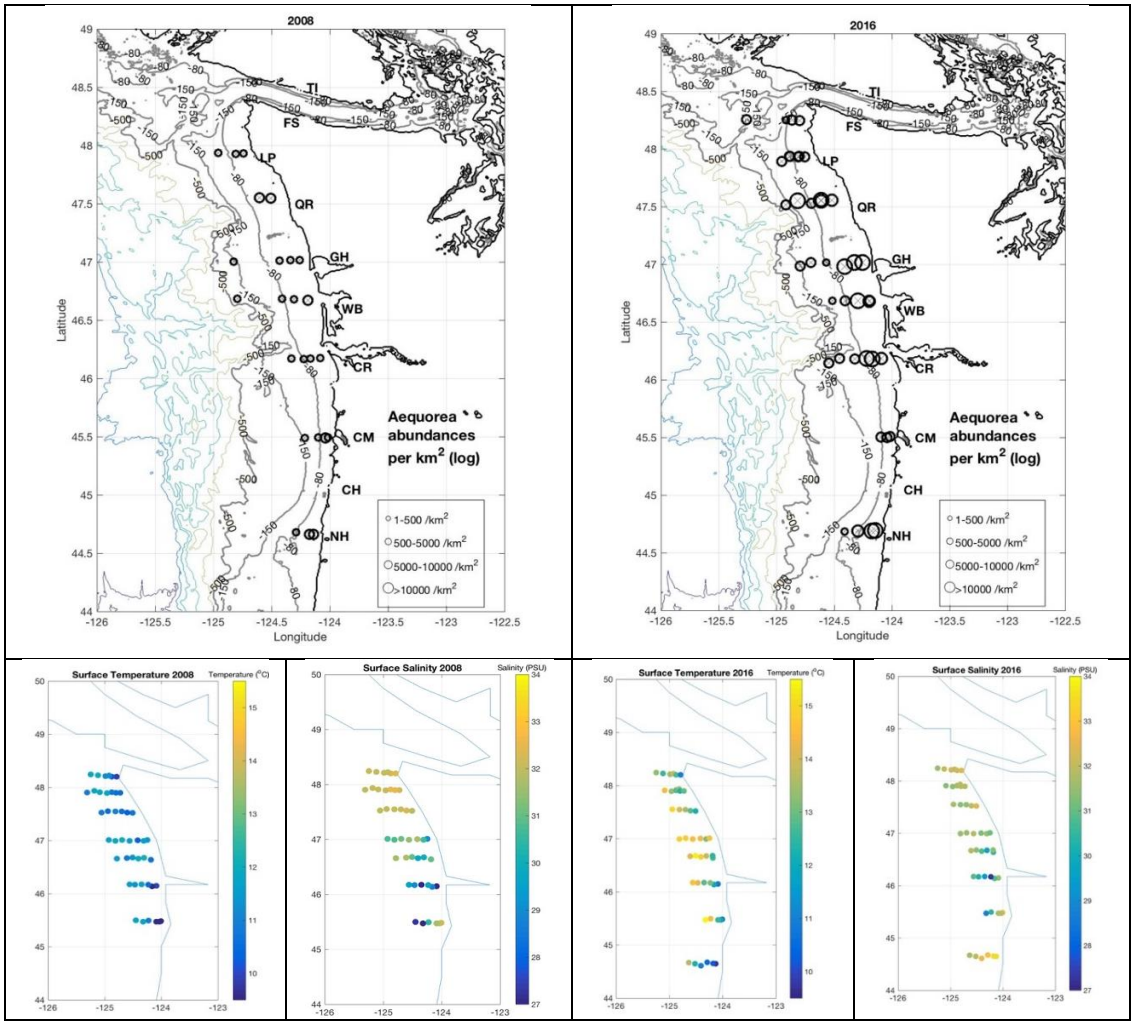


Figure 2.3 Representative plots showing *Aequorea* abundance at each station in A) 2008, a low abundance year and, B) 2016, a high abundance year. The two sub panels below A and B show surface temperature and salinity for 2008 and 2016 respectively.

Aequorea abundance and size (bell diameter) showed different variability over the 18-year time series (Figure 4). Higher abundance years had a lower mean bell diameter

and lower abundance years featured slightly larger jellyfish (Figure 4). For example, 2002, 2005, 2008 and 2013 were fairly low abundance years for *Aequorea*, however mean size was larger and individual sizes were widely distributed (Figure 5).

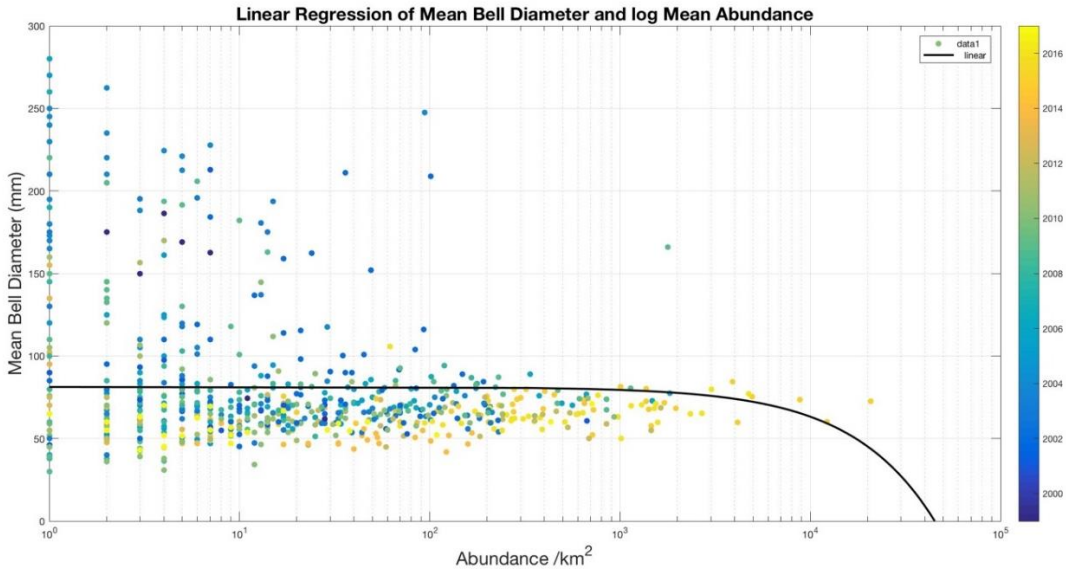


Figure 2.4 Linear regression of mean bell diameter and log mean *Aequorea* abundance. The color bar represents year (1999-2017)

In June, bell diameter was less variable than in September where a range of sizes from 5 to 35 cm were measured. During the 2015 and 2016 high abundance years, bell diameter for all measured individuals ranged from 5-12 cm in June (Figure 5).

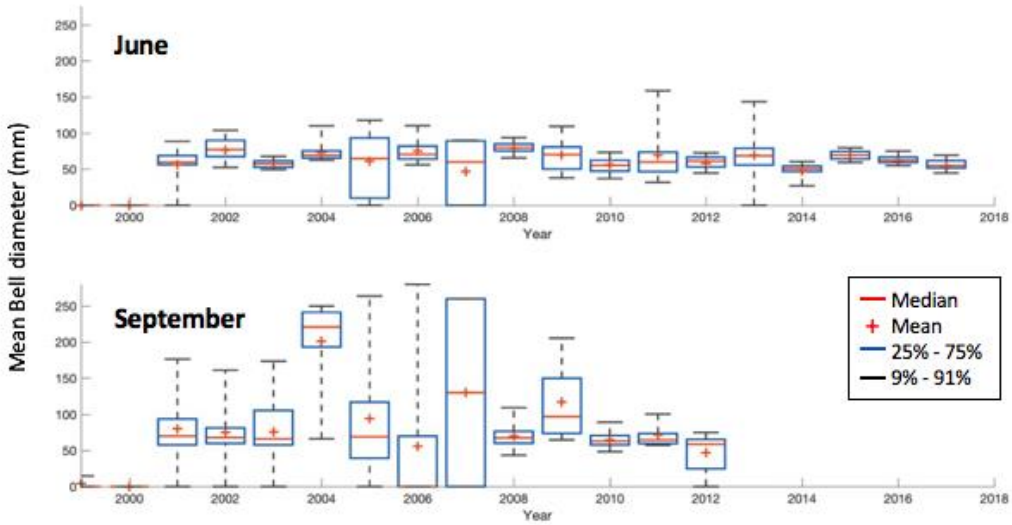


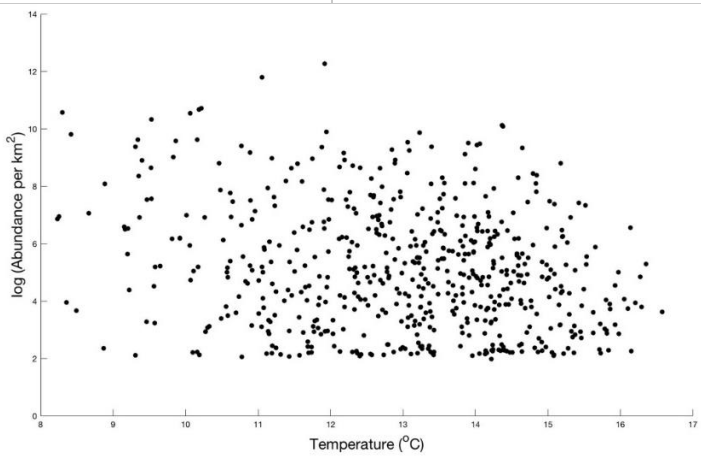
Figure 2.5 *Aequorea* mean bell diameter range for, top panel: June, 1999-2017, and bottom panel: September, 1999-2012.

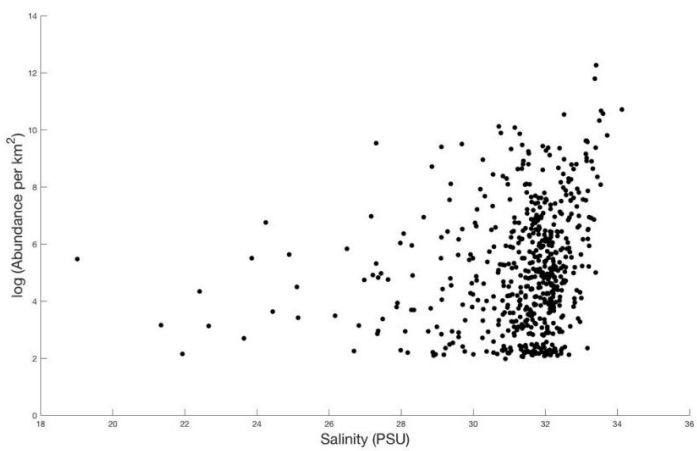
Environmental relationships

Delta-GAM results showed a positive correlation between surface salinity and temperature and a negative relationship with depth and *Aequorea* abundance for the month of June across the 18-year time series (Table 1). Covariates included in the original GAM were: temperature, salinity, chlorophyll a, and station bottom depth. Covariates were then removed one by one if not found to be significant.

Table 2.1 Results from the Delta-GAM model showing significant covariates (*), p-value, and relationship between *Aequorea* abundance and each covariate as positive (increasing +) or negative (decreasing -).

Covariates related to Aequorea abundance/ km^2	**Covariate significance p-value**	**relationship**
Station bottom depth (m) *	p< 0.05	decreasing (-)
Sea surface salinity psu (3 m) **	p=0.001	increasing (+)
Sea surface temperature °C (3 m) ***	p<0.001	increasing (+)
GCV	17845	





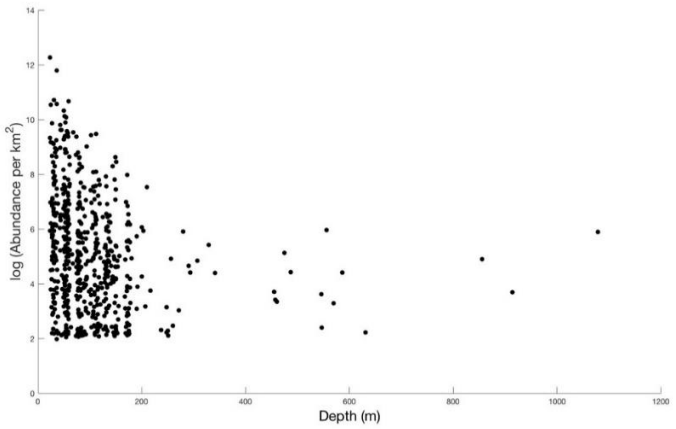


Figure 2.6 *Aequorea* abundance plotted with the three significant covariates: Top panel: SST, middle panel: surface salinity, bottom panel: depth

From 1999-2017 abundance patterns of *Aequorea* closely followed *in situ* environmental variables. For instance, 2007-2011 featured cooler SST and low to moderate catch of *Aequorea* at sampled stations (Appendix Fig. 1) The highest abundances of *Aequorea* for all years in June were found in shallower regions near shore (Figure 2) during weaker upwelling periods and were distributed further off-shore during stronger upwelling (Figure 5). This pattern is particularly evident during the anomalously high abundance years in 2015 and 2016 during a reduced upwelling period.

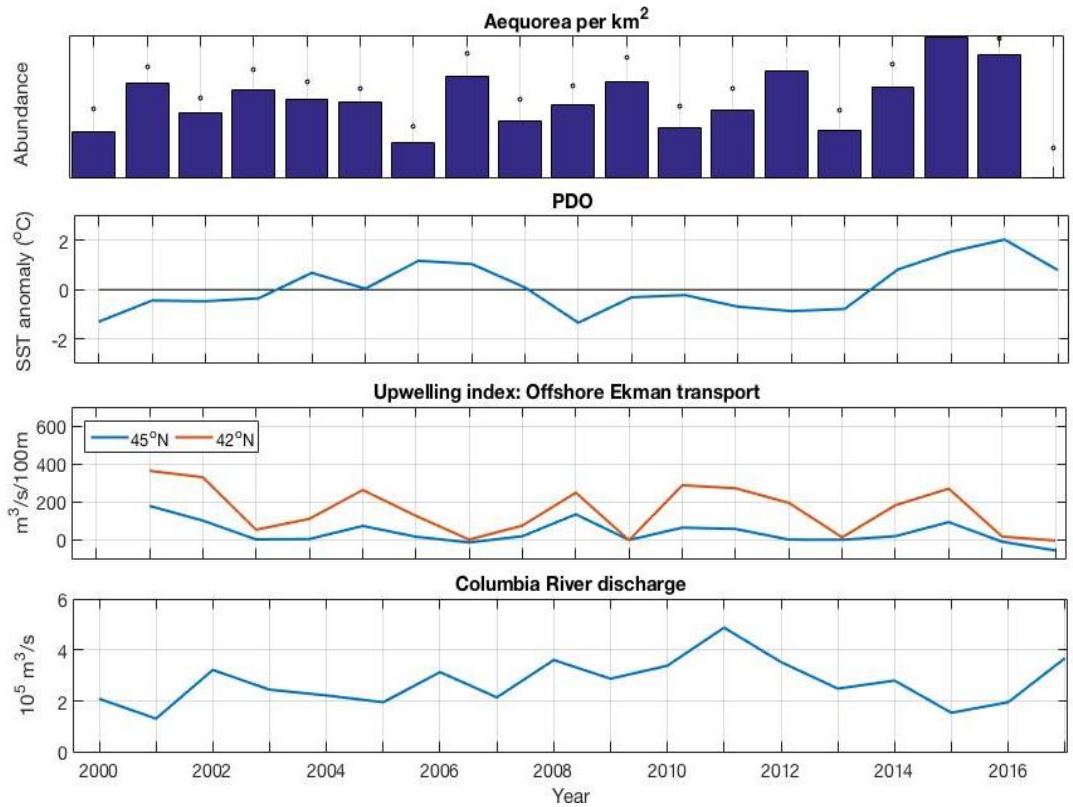


Figure 2.7 log *Aequorea* abundance plotted with large-scale environmental indices showing top panel A: June log *Aequorea* abundance km^2 1999-2017 B: Pacific Decadal Oscillation C: upwelling indices for two latitudes representative of the sampled area, and D: Columbia River discharge.

Discussion

Our analyses showed relationships between population dynamics of *Aequorea*, and environmental conditions on three scales of variability: seasonal, interannual and multi-decadal oscillations (Francis et al. 2012). While it is challenging to assess a direct link between abundance of a particular species and large-scale environmental indices, we may instead focus on local, *in situ* environmental conditions. In the case of *Aequorea* in the NCC, we found a positive correlation between surface temperature and, surface salinity and abundance of medusae (Table 1, Figure 6). Warmer SST periods

corresponded with higher *Aequorea* densities and the highest catches were collected from shallower water depths (<75 m). The strength and timing of upwelling in the NCC is a primary driver of abundance and distribution of zooplankton (Bi et al. 2011; Francis et al. 2012). Shifts from warmer, weaker upwelling periods to cooler, stronger upwelling corresponded to decreases in *Aequorea* populations over the 18-year study period.

Salinity also played an important role in the abundance and distribution of *Aequorea* in the NCC. The amount of discharge from the Columbia River influences salinity throughout the NCC and moderate to high *in situ* salinities associated with lower river discharge were positively correlated with *Aequorea* abundance (Figure 3, Figure 6, Figure 7). In 2015 surface salinity was higher which coincided with lower Columbia River discharge. In 2016 river discharge increased and *in situ* surface salinity decreased. This observed variability in salinity corresponded with variability in abundance of *Aequorea* which peaked in 2015 and 2016, then drastically declined in 2017 (Figure 7, Appendix Figure 2).

The 2015 and 2016 anomalously large abundance of *Aequorea* in the NCC may have been a consequence of another regional oceanographic phenomenon which has had profound effects on the northeast Pacific ecosystem. The warm water mass (the Blob) that formed in 2013 in the northeast Pacific altered marine community structure for several years following its initiation in 2014 (Bond et al. 2015, Kintisch, 2015, DiLorenzo and Mantua 2016, Peterson et al. 2017). Impacts from the Blob ranged from shifts in plankton community composition, harmful algal blooms, species range shifts (Peterson et al. 2017, Auth et al. 2018) and high densities of several types of gelatinous zooplankton including the *Aequorea* peak abundances in 2015 and 2016. These shifts in

community composition have the potential to alter energy pathways to higher trophic level species including fish, marine mammals and seabirds (Peterson et al. 2017, Brodeur et al. 2018). Due to their rapid reproduction and growth capabilities and tolerance of a variety of environmental conditions, particularly a broad temperature range, *Aequorea*, among other gelatinous zooplankters, may be able to thrive through anomalous events altering the physical and biological landscape (Ruzicka et al. 2012, Uye & Brodeur 2017).

Broadly speaking, climate regime shifts are an important driver of phytoplankton and zooplankton assemblages including gelatinous zooplankton. The ability of gelatinous zooplankton such as *Aequorea* to quickly respond and adapt to changing environmental conditions through rapid reproduction, growth and efficient feeding, may allow them to bloom during transition periods which occur on decadal to multidecadal time scales. (Attrill et al. 2007; Lavaniegos & Ohman, 2003, Brodeur et al. 2008). Studies in the Bering Sea (Brodeur et al. 2008) and southern California Current (Lavaniegos et al. 2003) have found an increase in abundance and change in distribution of gelatinous zooplankton (scyphozoan jellyfish and pelagic tunicates) during the transition phase between climate regimes where these species have the potential to impact zooplankton biomass and trophic interactions through feeding and competition for resources (Ruzicka et al. 2008; 2012; Francis et al. 2012). The inverse relationship between the mean size of *Aequorea* and their abundance in a given year suggests that food could be limited in the waters that this species inhabits, although further study would be needed to assess such resource limitation.

Examining relationships between environmental indices and the abundance and distribution of *Aequorea* in the northern California Current in the present study shows a strong influence of shifts in ocean temperatures, strength of upwelling, amount of discharge from the Columbia River on the catches of *Aequorea* in surface trawls. *Aequorea* have a broad cross-shelf distribution, unlike other large gelatinous zooplankton common in near-shore waters of the NCC, and, therefore, are not limited to a particular depth zone. Over the 18-year time series, *Aequorea* were distributed near-shore during reduced upwelling periods or further into the shelf region influenced by increased upwelling. During high abundance periods, *Aequorea* are likely an important predator in the NCC marine food web. This analysis of *Aequorea* related to *in situ* environmental variables has allowed us to better understand how their abundance and distribution patterns can change quickly under a variety of environmental regimes. As observed in 2015 and 2016, during warmer than average SST and moderate salinities, *Aequorea* were able to inhabit a substantially wider area of the coastal zone, solidifying their important role in the NCC pelagic ecosystem.

CHAPTER III

ABUNDANCE, DISTRIBUTION, AND FEEDING ECOLOGY OF *PYROSOMA ATLANTICUM* IN THE NORTHERN CALIFORNIA CURRENT

Introduction

Pyrosomes (Greek for "fire bodies") are holoplanktonic grazers, comprised of individuals called zooids encased in a gelatinous tunic made primarily of cellulose (Godeaux et al. 1998). Pyrosome colony size ranges from less than one centimeter to several meters in length. Pyrosomes belong to the phylum Chordata, subphylum Tunicata, class Thaliacea, which includes salps, doliolids and pyrosomes. Each zooid in a colony is equipped with cilia used for feeding and locomotion, oral and atrial siphons through which water is drawn and ejected, and a mucous sieve used to efficiently capture planktonic microorganisms (Godeaux et al. 1998, Alldredge & Madin 1982).

The few studies that have examined pyrosome diet have indicated that pyrosomes feed primarily on phytoplankton including diatoms, dinoflagellates, prymnesiophytes, and coccolithophores (Culkin & Morris 1970, Drits et al. 1992, Perissinotto et al. 2007). Pyrosomes have high clearance rates of up to 35 l/h (Drits et al. 1992, Perissinotto et al. 2007), which enable them to potentially impact food web interactions by outcompeting other planktonic grazers (Drits et al. 1992). When pyrosomes form dense aggregations otherwise known as "blooms" they are capable of reducing phytoplankton standing stock by >50% in surface waters (Drits et al. 1992). Very little is known about trophic ecology of pyrosomes; it is challenging to conduct feeding experiments with them and due to the small size of their phytoplankton prey, gut content analysis is also challenging.

Therefore, we used fatty acids as biomarkers to better understand pyrosome trophic ecology. Trophic biomarkers including fatty acids (FA) are often used to study food web dynamics of marine organisms to identify feeding habits and trophic position (Pitt et al. 2008, Kelly & Scheibling 2012). Fatty acid (FA) analysis was applied to characterize signatures for different types of phytoplankton assimilated in the tissue of collected pyrosomes. Primary producers have distinct FA markers and therefore can be used to characterize diet and identify trophic connections (Perissonotto et al. 2007, Pitt et al. 2008, Kelly & Scheibling 2012, Tilves et al. 2018). Proportions of FAs and ratios between certain FAs can also help determine dominance of certain phytoplankton in diet (Budge & Parrish 1998, Dalsgaard et al. 2003).

Prior to 2014 pyrosomes were not observed in the NCC, however since 2016, unprecedented aggregations have been observed in coastal waters from Oregon to British Columbia (Brodeur et al. 2018, Sutherland et al. 2018). Pyrosomes are common in tropical and sub-tropical ocean waters (Van Soest 1981), but very little is known about their abundance, distribution, and trophic ecology in mid-latitude systems (Brodeur et al. 2018, Sutherland et al. 2018). It is unclear what initiated the recent range expansion of pyrosomes into the NCC (Brodeur et al. 2018). Above average water temperatures influenced by recent regional environmental conditions from 2013-2017, including the anomalous warm water mass (the Blob; Bond et al. 2015) followed by a strong El Nino (Jacox et al. 2016) may have facilitated pyrosome success in the NCC. Their rapid reproduction and growth capabilities coupled with their efficient feeding behavior may assist in their continued presence in this area (Brodeur et al. 2018, Sutherland et al. 2018).

Due to our limited understanding of pyrosome abundance, distribution, and trophic ecology in the NCC, we cannot yet predict if or how their continued presence may alter food web dynamics through removal of phytoplankton biomass (Brodeur et al. 2018). Our study used generalized additive models (GAMs) to identify relationships between *in situ* environmental variables (temperature, salinity, fluorescence) and the distribution and abundance patterns of pyrosomes in the NCC (42-49ºN) during spring and summer of 2017. We then characterized the identified fatty acid trophic biomarkers as an indicator of pyrosome diet. The identified FA markers from the collected pyrosomes were used to compare spatial and seasonal differences in trophic ecology in the NCC in spring and summer of 2017. This analysis contributes to a better understanding of the potential impacts of pyrosome blooms to the marine food web in an area where they have not previously been studied.

Methods

Field Sampling

Pyrosomes were collected during two research cruises in May and August of 2017. The first cruise was a ten-day NCC ecosystem survey aboard the NOAA ship Bell M. Shimada, May 14-24, 2017 from Bodega Bay, CA (38˚N) to Cape Meares, OR (45.5˚N) (Figure). Sampling included CTD casts for *in situ* environmental conditions (temperature, salinity, oxygen and chlorophyll-a with depth) and net sampling for zooplankton using a vertically-towed ring net (0.5 m diameter and 202 µm mesh) and an obliquely-towed bongo net (0.6 m diameter and 0.5 mm mesh). Nets were equipped with

calibrated flow meters mounted in the net mouth and towed to maximum depth of 100 m or 5 m off of the bottom at shallower stations. Pyrosomes collected in the vertical ring and oblique bongo net tows were counted and measured and a sub-sample of up to five individuals was rinsed with filtered seawater and placed in a -80˚C for subsequent FA analysis.

Pyrosomes were collected on a second research cruise aboard the Shimada August 11-26, 2017 during a NOAA Pacific Hake Fishery Survey from Newport, OR (44.65ºN, 124.5ºW), to the north end of Vancouver Island (50.9ºN, 129.7ºW). Pyrosomes were collected, counted, measured, and preserved for diet analysis from mid-water trawls (Aleutian wing trawl with 875 m^2 mouth opening) and Methot trawl (5 m^2 mouth opening with 1 x 2 mm mesh). Due to the different sampling methods during the two research cruises, pyrosome catch was standardized to the volume sampled (m^3) using (3.14) (Net Diameter)^2 (Distance)/ 4 (General Oceanics Digital Flowmeter).

Fatty Acid Analysis

Immediately after being collected, pyrosomes were measured and stored individually in a -80ºC freezer on board the research vessel and then transferred to a -20ºC freezer in the lab for three months until processing. To prepare samples for lipid extraction, they were first freeze dried, then ground to a powder using a marble mortar and pestle. Material was weighed to 40 mg ± 0.3 and placed in a 10 ml centrifuge tube, then mixed with a chloroform:methanol solution. We used C19 as an internal standard due to its low concentrations in marine samples. After adding the C19 standard, the sample was flushed with nitrogen, sonicated in an ice-water bath, and centrifuged for five minutes at 3000 rpm, 4 ºC. The chloroform/organic layer containing the dissolved lipids

was then transferred to a new 8ml scintillation vial. This process was repeated twice before evaporating the organic layer under nitrogen down to 1.5 ml. One ml of this layer was then removed for transesterification and the remaining 0.5 ml of material was being preserved at -20 ^{o}C for gravimetry (Taipale et al. 2016, Schram et al. 2018).

To begin the transesterification of fatty acids, 1 ml toluene and 2 ml 1% sulfuric acid:methanol solution was added to the lipid extract. Samples were then heated in a water bath for 90 minutes at 90 ^{o}C. After transesterification, samples were left to cool to room temperature before adding 2 ml of hexane and 1.5 ml sodium bicarbonate. The sample was vortexed for 10 seconds and centrifuged for 2 minutes at 1500 rpm at 4 ^{o}C. The upper layer of the newly separated out material (FAME) was transferred to a new tube and evaporated under nitrogen. FAME was re-suspended for a second time by adding 1.5 ml hexane, evaporated to dryness and then transferred to a GC vial for analysis (Taipale et al. 2016, Schram et al. 2018). Fatty acids were processed for analysis through a gas chromatograph mass spectrometer (GC-MS, Model QP2020, Shimadzu; Schram et al. 2018).

Statistical Analysis

The relationship between pyrosome abundance and distribution and environmental variables (temperature, salinity, fluorescence, and dissolved oxygen) was assessed using generalized additive models using the mgcv package in R. Analysis of fatty acid data included a non-metric multidimensional scaling (NMDS) technique to visualize the similarities and differences between FA proportions and spatial factors (latitude, longitude). Spatial differences in FA proportions were tested using a permutational multivariate (PERMANOVA) using latitude as a factor and 999

permutations for each sampled month (May and August). Similarity percentage (SIMPER) analysis was used to identify individual FA contributions to average dissimilarities among the samples (Schram et al. 2018, Tilves et al. 2018). Fatty acid analyses were run in R version 3.3.2 using the Vegan package and graphics were generated in MATLAB.

Results

Abundance, Distribution and Environmental Variables

Pyrosomes collected during the May and August 2017 research cruises in the northern California Current reached densities up to 5 m^3 (Figure 1). Mean pyrosome length in May off of northern California and Oregon was 13.6 cm (6-78 cm) and mean length of pyrosomes collected in August off of Washington and British Columbia was 11.5 cm (range 2-24 cm). Pyrosomes were in higher abundances in May of 2017 and were distributed near shore and in shelf regions. The highest catches of pyrosomes were off of the Rogue River (RR), Heceta Head (HH) and Newpor(NH), OR in May (5 m^3) and off of La Push (LP), WA in August (3 m^3) (Figure 1).

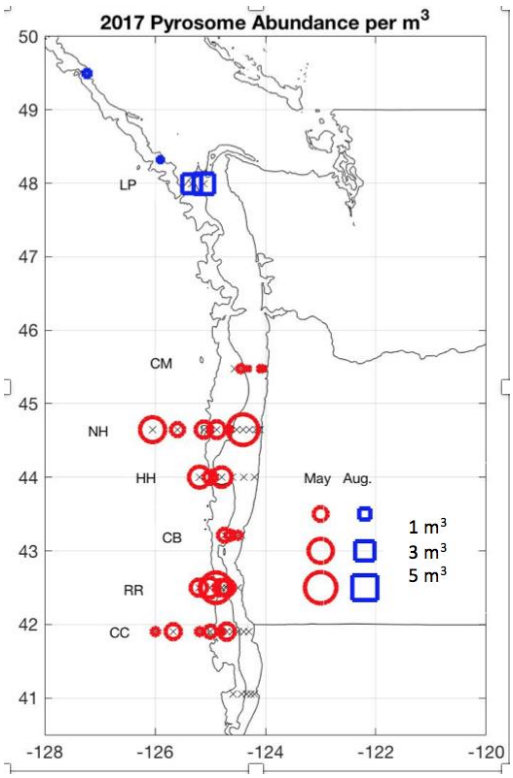


Figure 3.1 Pyrosome abundance (m^3) for May (red circles) and August (blue squares) 2017. Bubble/square size corresponds to abundance of pyrosomes per cubic meter and X indicates zero pyrosome catch.

Results from the generalized additive models showed that sea surface temperature and surface salinity were significant variables ($p<0.05$) related to pyrosome densities in May 2017. Pyrosome aggregations were concentrated at locations with warmer surface water temperatures (12-14°C), moderate salinity (31-33 PSU), and lower fluorescence at 5 m depth (<2 mg/l)) (Table 1 and Figure 2).

Table 3.1 Results from the GAM model showing the relationship between pyrosome abundance and *in situ* environmental variables including SST, surface salinity and fluorescence. The * indicates significance of the covariate along with a p-value < 0.05. Relationships between the covariates and pyrosome abundance are shown as increasing, decreasing, or not significant.

Covariates related to Aequorea abundance/ km^2	Covariate significance p-value	relationship
Sea surface temperature °C (3 m) ***	p<0.001	increasing (+)
Surface salinity (psu) *	p<0.05	increasing (+)
Fluorescence n/s	p>0.05	not significant

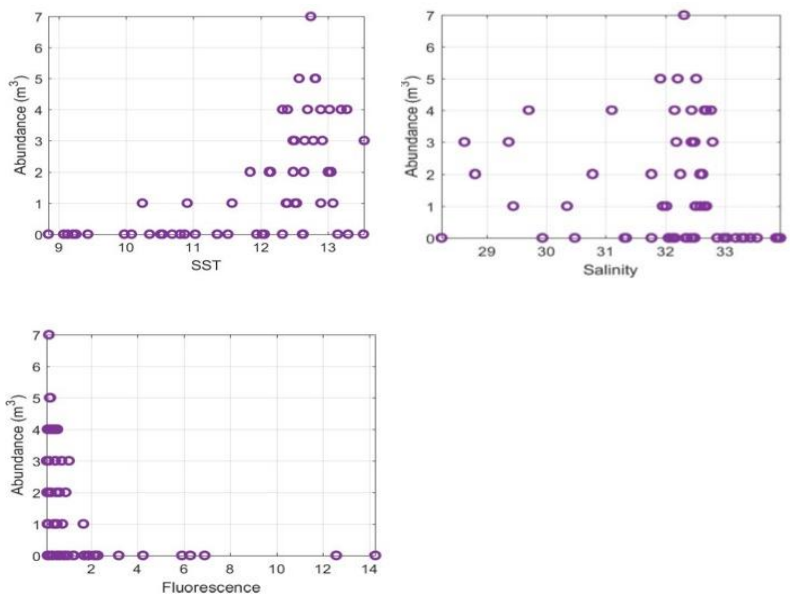


Figure 3.2 May 2017 Pyrosome abundance (m^3) plotted with *in situ* environmental variables collected by CTD casts at 5 m depth. left: sea surface temperature, middle: surface salinity, and right: fluorescence

Fatty Acids

A total of 35 fatty acids were identified in pyrosome samples collected in May and August of 2017 with 14 FA markers contributing to ≥1% of the mean profile. Analysis of fatty acids showed dominant proportions of saturated fatty acids (SAFA): 14:0, 15:0, 16:0 and 18:0, monounsaturated fatty acids (MUFA): 16:1w7c, 18:1w7c,

18:1w9c and 20:1w9c, and polyunsaturated fatty acids (PUFA): 18:2w6c, 18:3w3c,

20:5w3c, 20:3w3, 20:3w6, and 22:6w3 (Table 2).

Table 3.2 Identified FAs that were dominant (≥1% mean profile) in pyrosome samples, type of FA, common name, sample size (n) mean proportion, and standard deviation ordered by the most abundant to least abundant identified FA.

Formula	**Type**	**Name**	**N**	**Mean proportion**	**Standard Deviation**
22:6w3	PUFA	DHA	97	25.3	3.01
16:0	SAFA	Palmitic	97	21.9	5.86
20:5w3	PUFA	EPA	97	13.1	9.23
14:0	SAFA	Myristic	97	8.8	2.73
18:1w9c	MUFA	Oleic	97	6.4	1.84
16:1w7c	MUFA	Palmitoleic	97	5.1	1.35
18:2w6c	PUFA	LIN	97	2.9	0.81
15:0	SAFA		97	2.3	0.64
18:1w7c	MUFA	Vaccenic	97	1.9	0.79
18:0	SAFA	Stearic	97	1.8	0.68
20:3w3	PUFA		97	1.8	0.68
18:3w3	PUFA	ALA	97	1.5	0.54
20:3w6	PUFA		97	1.5	0.54
20:1w9	MUFA		97	1.3	0.58

Multivariate FA proportions were analyzed separately for May and August, 2017. FA proportions were slightly grouped by latitude with the FA 20:5w3 driving separation between proportions at mid and low latitudes (Figure 3).

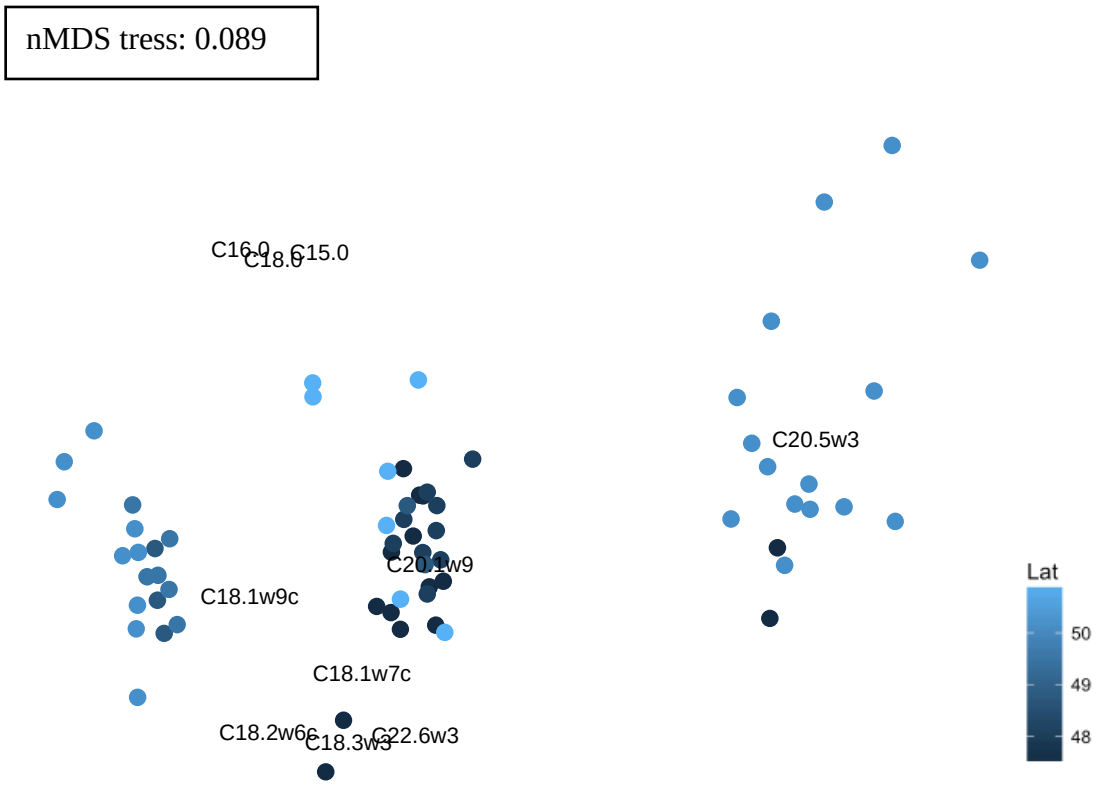


Figure 3.3 Non-metric multidimensional scaling (nMDS) plot showing Euclidean distances between FA proportions (n=99) by space (Latitude) for May 2017. Color represents latitude (42-50 ºN). FAs with mean profiles >1% were included in this analysis.

Multivariate FA proportions did not differ by latitude or longitude for May or August (Figure 3, Table 3). The similarity percentage (SIMPER) analysis showed the top five FA contributions to the average dissimilarities among pyrosomes collected in May (Table 4) and August (Table 5). For both May and August, 20:5w3, 16:0, and 18:1w9c

drove the dissimilarity between FA proportions. In May, 22:6w3 was the second highest contributor to the dissimilarities.

Table 3.3 PERMANOVA results for May and August, 2017 including FA proportions that contributed to >1% of the mean profiles. FA proportions were tested by latitude as a factor.

Month	**df**	**MS**	**Pseudo-F**	**P(perm)**
May	1	230.6	1.34	0.2479
August	1	5.39	0.59	0.54

Table 3.4 SIMPER results for May 2017 includes the top five FA proportion contributions relative to the total FA (mean FA%) and their contribution to the similarity by latitude (Cont %)

FA	**Mean contribution %**	**Cumulative contribution (%)**
C20:5w3	75	45
C22:6w3	24	78
C16:0	29	63
C18:1w9c	13	86
18:1w7c	5	89

Table 3.5 SIMPER results for August 2017 includes the top five FA proportion contributions relative to the total FA (mean FA%) and their contribution to the similarity by latitude (Cont %)

FA	**Mean contribution %**	**Cumulative contribution (%)**
C20:5w3	29	45
C16:0	12	64
C18:1w9c	7	76
18:2w6c	5	84
20:1w9	5	93

Discussion

Pyrosome feeding ecology has not previously been studied in the NCC and in general, pyrosomes have been one of the least studied pelagic tunicates (Perissinotto et al. 2007). *Pyrosoma atlanticum* range has been documented from 50°N-50°S (Van Soest 1981) and high abundances have been observed in the southern California Current (Lavaniegos & Ohman 2003); however, prior to 2014 pyrosomes have not been recorded in the northern California Current off the Pacific Northwest coast (Brodeur et al. 2018). Since 2016, dense aggregations of pyrosomes have been concentrated further north in the NCC (42-48˚N) during the spring and summer leading to short and potentially long term changes to the pelagic marine ecosystem (Brodeur et al. 2018, Sutherland et al. 2018). Although distribution of pyrosomes was patchy in the NCC throughout the spring and summer of 2017 (Brodeur et al. 2018), mean abundance per cubic meter was similar for

the two sampled months (Fig. 1). These abundance patterns also show pyrosomes in similar densities at the beginning of spring and the end of summer over a broad latitudinal range.

The highest abundances of pyrosomes were in areas with warmer sea surface temperatures between 12 and 15 °C, which were above average for NCC shelf waters during the summer (Fig. 3, Table 1). This northward expansion of pyrosomes may be, in part, influenced by the warm water anomaly termed "the Blob" in the northeast Pacific from 2013-2015 followed by a strong El Niño/Southern Oscillation (ENSO) in 2016 (Bond et al. 2015; De Lorenzo and Mantua 2016; Jacox et al. 2016). During this time, sea surface temperatures were 2.5 °C warmer than the average with reduced nutrients and reduced phytoplankton productivity (Peterson et al. 2017). In addition to a relationship between pyrosomes and temperature, results from generalized additive model analysis of *in situ* environmental variables and pyrosome abundance showed higher pyrosomes abundance in moderate to high salinities (Table 1, Figure 2) In August of 2017, pyrosome aggregations were patchier and concentrated further off shore than the aggregations observed in May at more southern latitudes. Results do not indicate a significant relationship between pyrosome abundance and fluorescence measured near the surface (5 m depth) (Table 1, Figure 2) which supports the hypothesis that high abundance and near shore distribution may correspond to temperature and salinity more than food availability.

Due to their efficient grazing on phytoplankton (Perissinotto et al. 2007), pyrosomes have the potential to impact phytoplankton assemblages where they form dense aggregations (Drits et al. 1992). Pyrosomes are not only highly efficient filter feeders but are also able to filter a variety of planktonic microorganisms from diatoms

and dinoflagellates larger than 10 µm (Perissinotto et al. 2007) to diatoms and coccolithophores of 3-5 µm (Drits et al. 1992) and potentially have similarities to other pelagic tunicates able to filter pico-phytoplankton and bacteria-plankton at the submicron scale (Sutherland et al. 2010, Conley et al. 2018). This broad prey-size range may allow them to thrive in relatively low productivity zones which occur during reduced upwelling periods. Weaker upwelling periods may favor pyrosomes in the NCC due to warmer waters and lower nutrients which are similar to tropical regions where pyrosomes have typically been concentrated.

Pyrosomes have some of the highest measured clearance rates of any zooplankton grazer (Perissinotto et al. 2007, Conley et al. 2018), yet little is known about their diet composition, particularly in the NCC where they have not previously been observed. Fatty acid analysis of *Pyrosoma atlanticum* in the south Indian Ocean pointed to a phytoplankton based diet of diatoms as indicated by FA profiles: (20:5n-3), flagellates (22:6n-3), prymnesiophytes and coccolothophores (18:1n-9), and chlorophytes (18:3n-3) (Perissinotto et al. 2007). FA profiles of *P. atlanticum* in the Southern Ocean found signatures for 18:2n-6, a biomarker for chlorophytes or cyanobacteria (Richoux 2011). Results from the above mentioned previous studies are comparable to our fatty acid analysis from May and August 2017 in the NCC (Table 2) with the highest proportions of FAs belonging to biomarkers for phytoplankton including diatoms (20:5n-3), dinoflagellates (22:6n-3, 20:5n-3) and bacteria (branched FA +18:1n-7) (Perissinotto et al. 2007, Pitt et al. 2008, Kelly & Scheibling, 2012, Tilves et al. 2018). The dominant FA proportions in pyrosome samples here were the essential FAs-- EPA (20:5w3), and DHA (22:6w3) -- which were also among the top contributors to the dissimilarities between

samples. Although there were slight differences between FA proportions by latitude, they were not found to be statistically significant suggesting that pyrosomes were exhibiting similar feeding habits in spring and later summer and over a broad latitudinal range.

The northward expansion of pyrosomes into the NCC may not be a temporary phenomenon and could lead to long term changes to the marine pelagic food web (Sutherland et al. 2018). Our FA analysis suggests that pyrosomes feed on a broad range of planktonic microorganisms and that the highest proportions were markers for essential FAs including EPA and DHA. Their dense aggregations and high clearance rates may allow them to impact phytoplankton assemblages altering energy transfer. More research into pyrosome feeding ecology is needed to better understand their trophic niche and implications for the pelagic food web should they remain in temperate ocean regions. As pyrosomes continue to be a dominant presence in the NCC additional research into the environmental drivers and their range expansion will add clarity to their role in the pelagic ecosystem.

CHAPTER IV
GENERAL CONCLUSIONS

Gelatinous zooplankton are an important component of the marine pelagic food web and due to their rapid reproduction, growth, and efficient feeding capabilities are known to form dense aggregations during which they are capable of altering ecosystem dynamics. This research focused on population dynamics and variability of two gelatinous zooplankters (*Aequorea* and *Pyrosoma atlanticum*) in the northern California Current to better understand their relationship to environmental conditions and their role in the NCC pelagic ecosystem. Our time-series analysis using generalized additive models of *Aequorea,* abundance and distribution related to environmental variables (1999 to 2017) showed a close relationship with *in situ* environmental conditions with a positive correlation to sea surface temperature and salinity. Larger scale environmental drivers including the Pacific Decadal Oscillation, discharge from the Columbia River and upwelling strength influenced *Aequorea* abundance, which was anomalously high in 2015 and 2016 in the NCC. *Aequorea* were found to be highly responsive to local scale environmental fluctuations and able to thrive in a range of temperatures and salinities enabling them to quickly adapt to changing conditions. In 2017, *Aequorea* abundance drastically decreased and colonial pelagic tunicate, *Pyrosoma atlanticum,* expanded their range northward into coastal waters off of Oregon, Washington, and British Columbia. Unprecedented abundances of pyrosomes occurred in the northern California Current following the dissipation of the warm water anomaly ("the Blob") followed by a strong ENSO that started in 2016. We explored the *in situ* environmental conditions where pyrosomes formed dense aggregations and found a positive correlation with sea surface

temperature. Pyrosomes feed on planktonic microorganisms and using fatty acid analysis we identified markers for a variety of phytoplankton containing essential fatty acids, EPA and DHA. The highest pyrosome concentrations were found in warmer waters in the NCC and due to their efficient feeding behavior and broad phytoplankton diet may be able to thrive in lower nutrient conditions. These two ecologically distinct gelatinous zooplankters have both been conspicuous components of the NCC pelagic ecosystem in recent years and may increase their influence if current environmental trends continue.

APPENDICES

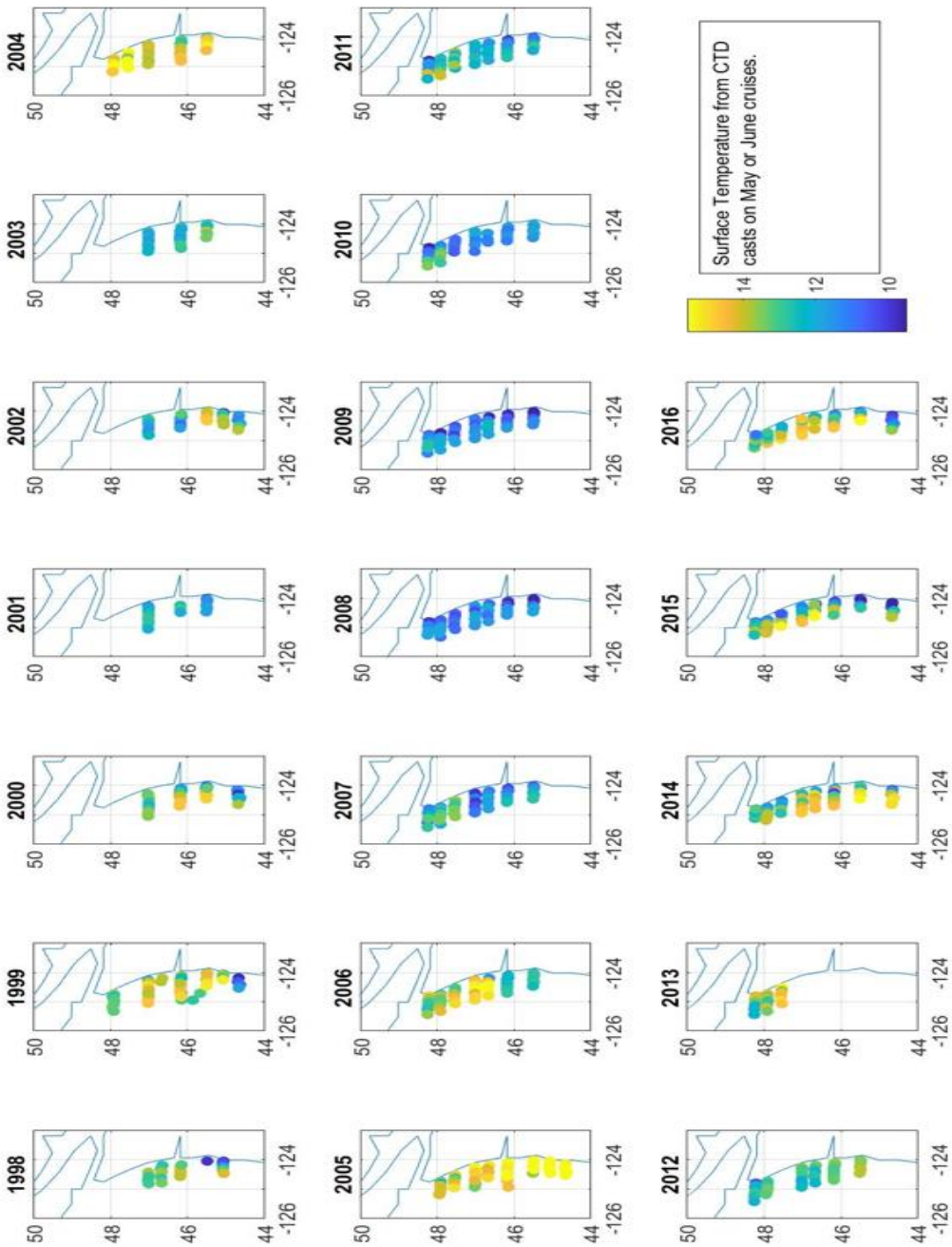


Figure 1: Sea surface temperatures (3 m depth) shown for May/June for all of the sampled years (1999-2017).

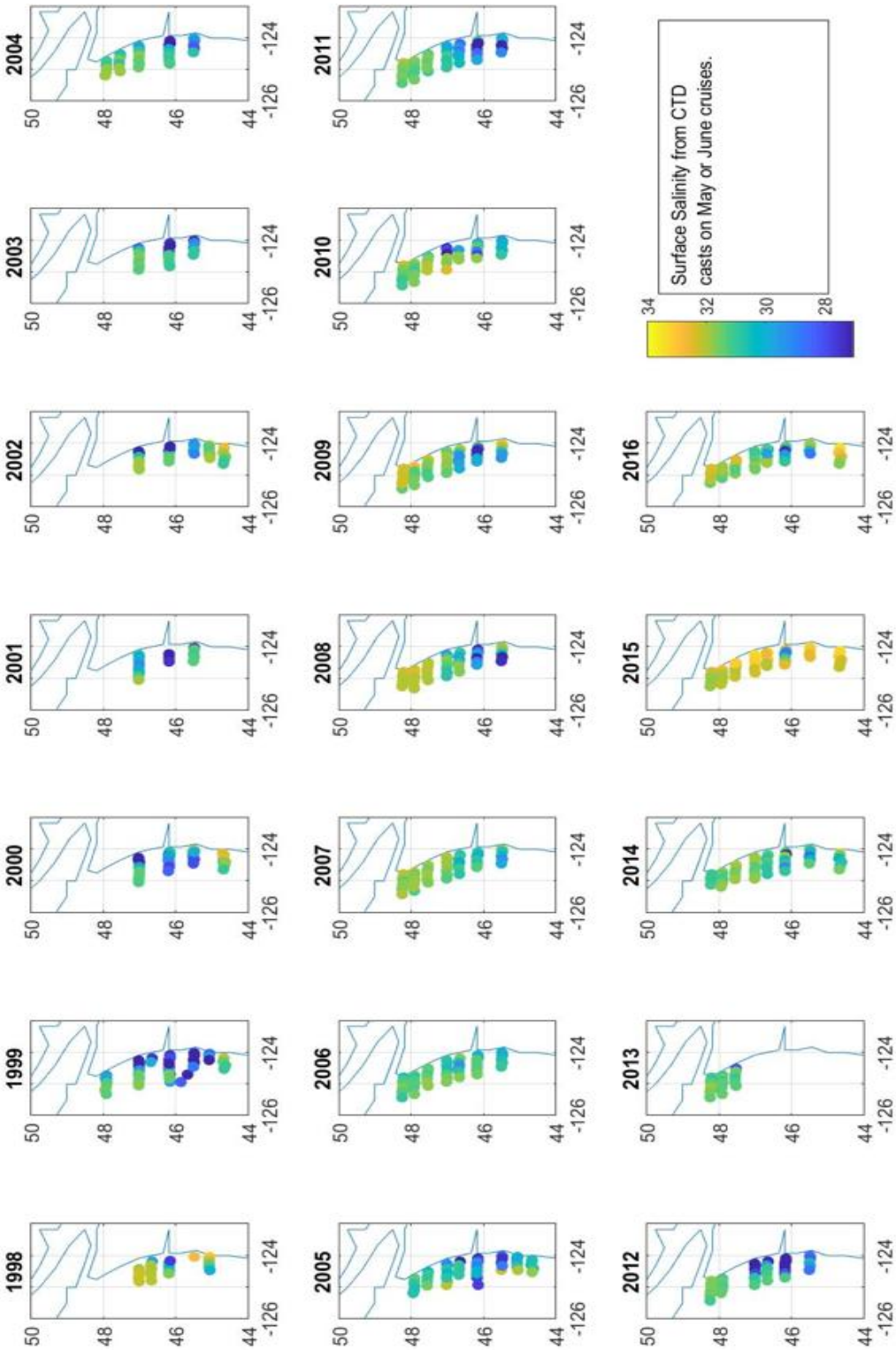


Figure 2: Surface salinities (3 m depth) shown for May/June for all of the sampled years (1999-2017).

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