DISTRIBUTION OF PELAGIC THALIACEANS, *THETYS VAGINA* AND *PYROSOMA ATLANTICUM*, DURING A PERIOD OF MASS OCCURRENCE WITHIN THE CALIFORNIA CURRENT

REBECCA R. MILLER
Cooperative Institute for Marine Ecosystems and Climate
University of California, Santa Cruz
1156 High Street
Santa Cruz, CA 95060
Rebecca.Miller@noaa.gov

JARROD A. SANTORA
Department of Applied Mathematics
University of California, Santa Cruz
1156 High Street
Santa Cruz, CA 95060

TOBY D. AUTH
Pacific States Marine Fisheries Commission
2030 SE Marine Science Drive
Newport, OR 97365

KEITH M. SAKUMA, BRIAN K. WELLS, AND JOHN C. FIELD
Fisheries Ecology Division
Southwest Fisheries Science Center
National Marine Fisheries Service
National Oceanic and Atmospheric Administration
110 McAllister Way
Santa Cruz, CA 95060

RICHARD D. BRODEUR
Fisheries Ecology Division
Northwest Fisheries Science Center
National Marine Fisheries Service
National Oceanic and Atmospheric Administration
2030 SE Marine Science Drive
Newport, OR 97365

ABSTRACT

The spatial distribution, abundance, and size variability of two pelagic tunicate species, *Thetys vagina* and *Pyrosoma atlanticum*, were examined from midwater trawl surveys to assess the historical context and geographical aspects of a major mass occurrence event throughout the California Current Large Marine Ecosystem during 2012–19. Off central California, abundance of both species were significantly greater in 2012–19 compared to 1983–2001, and their recent persistent multiyear abundance peaks were unprecedented. Coastwide abundance and distribution of *T. vagina* during 2013–19 was patchy, with no discernible shifts in distribution or changes in mean length. From 2013–18, abundance and distribution of *P. atlanticum* demonstrated a temporal trend of increasing abundance from south to north, and in northern areas, average *P. atlanticum* colony length increased over time. In 2019, high abundances of *P. atlanticum* occurred south of Monterey Bay, but were not found in the northern California Current. We discuss how in situ and regional-scale environmental drivers may have contributed to this recent multiyear gelatinous mass occurrence, and potential consequences to forage community structure and ecosystem function.

INTRODUCTION

Several notable mass occurrences of gelatinous pelagic tunicates have been documented throughout the Northeast Pacific, including the California Current, since 2011 (Wells et al. 2013; Li et al. 2016; Brodeur et al. 2018; Sutherland et al. 2018). Mass occurrences of pelagic tunicates are similar to other high-profile gelatinous species, including Scyphozoans, in that blooms have significant impacts on marine ecosystem dynamics and human activities, which result in trophic alteration of epipelagic and nearshore food webs (e.g., species diet and interactions), reduction in efficiency of fisheries operations (e.g., damaged fishing nets), and clogging cooling water intakes of coastal hydropower facilities (Brodeur et al. 2018; Brodeur et al. 2019; Iguchi and Kidokoro 2006; Gorman 2017; Eng 2012; Purcell et al. 2007; Graham et al. 2014; Uye and Brodeur 2017). While the population dynamics, spatial ecology, and environmental drivers of pelagic tunicate mass occurrences are not well understood, their rapid population increases are often attributed to anomalous ocean conditions that favor feeding and successful reproduction (Lavaniegos and Ohman 2003; Licandro et al. 2006; Lucas and Dawson 2014). Likewise, it is unclear how pelagic tunicates expand and contract within and beyond their range, or whether extensive population occurrences are a signal of increasing climate trends and variability.

There are numerous species of important, and often understudied, pelagic tunicates of the class Thaliacea, which include salps (family Salpidae) and pyrosomes (e.g., *Pyrosoma atlanticum*). Thaliacean bodies are typically larger than other zooplankton, but are generally lower in carbon relative to their mass, are often transparent, and buoyant to minimize predation risk and energetic expenditures; consequently they tend to have low caloric value relative to body size when compared to crustaceans (Alldredge and Madin 1982; Henschke et al. 2016a). Complex life-history attributes include alternating asexual (solitary forms), sexual (aggregative forms) and overlapping generations for salps; and zooid colonial growth (asexual) and budding (sexual) for pyrosomes (Bone1998; Henschke et al. 2016a). These reproductive strategies enable pelagic thaliacean populations to persist in the water column at low densities with minimal reproduction during periods of low food supply, yet undergo exponential population growth and develop spectacular mass occurrences during optimal environmental conditions (Silver 1975; Perissinotto et al. 2007; Loeb and Santora 2012; Henschke et al. 2016a). During periods of mass occurrence, thaliaceans can represent a substantial fraction of zooplankton biomass and organic carbon which impacts energy flow and productivity in marine ecosystems (Silver 1975; Lavaniegos and Ohman 2003; Henschke et al. 2016a), including high filter-feeding rates on very small (10 µ micron) phytoplankton and microzooplankton (Conley et al. 2018) and carbon contributions to deep-sea benthos in the form of fecal pellets and carcasses (Henschke et al. 2013; Smith et al. 2014; Archer 2018).

In the California Current Large Marine Ecosystem (CCLME), the occurrence and long-term variability of pelagic tunicates have been characterized using collections made by the California Cooperative Oceanic Fisheries Investigations (CalCOFI) program (e.g., Berner 1967; Blackburn 1979). From CalCOFI observations, Lavaniegos and Ohman (2003) found that despite representing a substantial volume of the zooplankton volume, thaliaceans represented a more modest, but highly variable, average fraction of total carbon; 5% off southern California, 13% off central California (Lavaniegos and Ohman 2003). Most of this carbon was attributed to salps, as pyrosomes are known to have a more subtropical distribution (their work documented both *P. atlanticum* and *P. aherniosum*) and were less frequently observed in southern and central California waters. In fact, no pyrosomes were documented in half of the years reported in Lavaniegos and Ohman (2003), with a few of the remaining years (5 to 10 years, depending on the region) having either trace or modest numbers. Most years of high pyrosome abundance included anomalously warm events, such as the 1957–59 El Niño, the 1983 El Niño, and the unusual warm/low productivity event in 2005 in central California (Lavaniegos and Ohman 2007). Furthermore, when previous abundance peaks of pyrosomes occurred they lasted for only a year or two, suggesting that environmental conditions were not favorable for sustained multiyear population blooms and expansions. Aside from Brodeur et al. (2018) and Sunderland et al. (2018), who documented recent *P. atlanticum* occurrence in the North Pacific, previous reports that mention thaliaceans off California, Oregon, or Washington do not explicitly document *P. atlanticum* abundance.

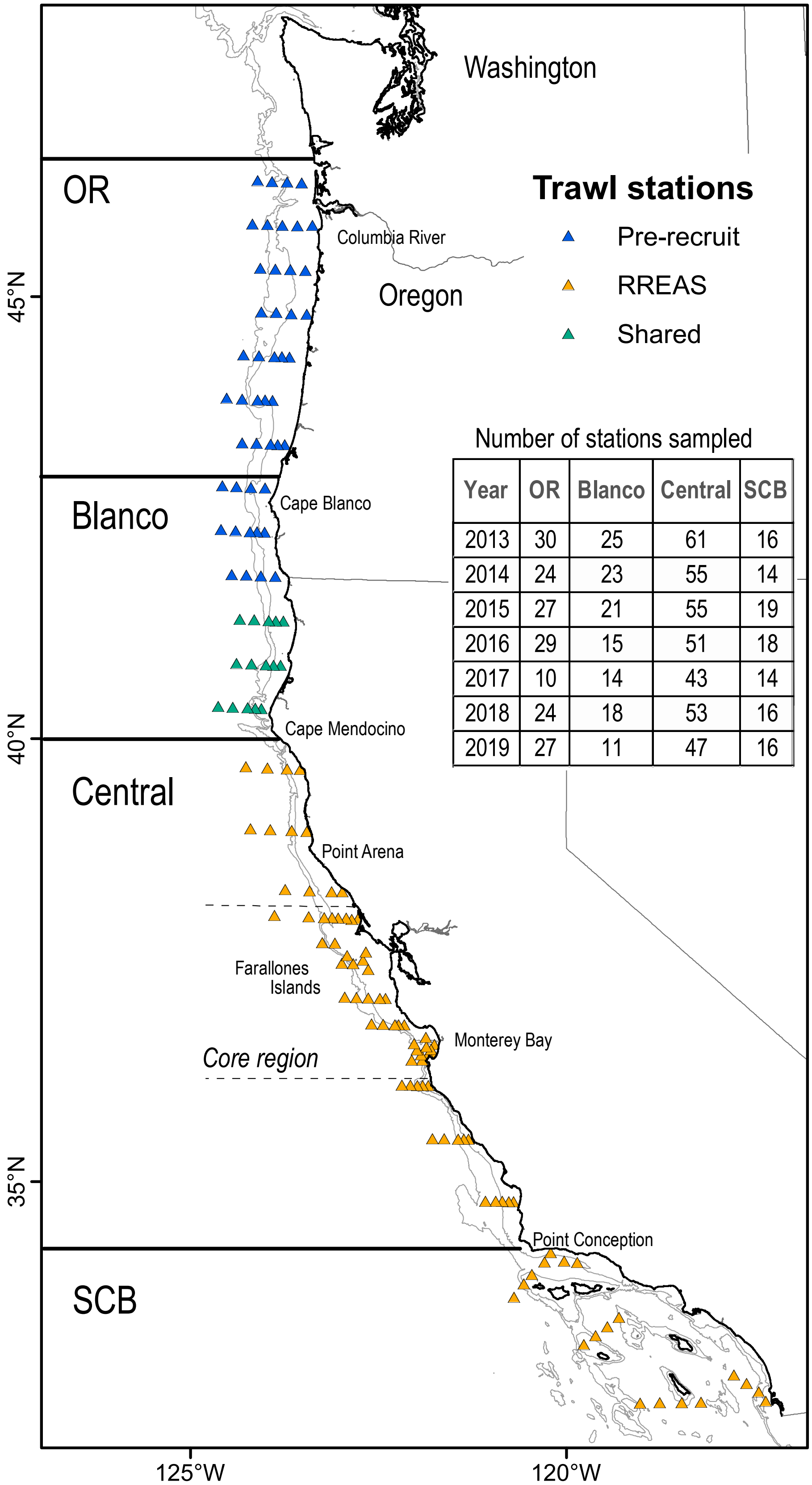
Lavaniegos and Ohman (2003, 2007) evaluated time series of ten frequently occurring salp species (order Salpida) in CalCOFI collections and found indications of shifts in species composition between cool- and warm-water species, and greater overall abundance in central and southern California during cool years or time periods. During 1961–64, Hubbard and Pearcy (1971) conducted a study off Oregon and documented six commonly occurring salp species, also noting shifts between the one warm year (e.g., 1963) and other cooler years. Hubbard and Pearcy (1971) encountered *Thetys vagina* in the spring of 1963, noting this species tended to be a cosmopolitan but typically warm-water species. More recently, Peterson and Keister (2002) documented high densities of *Salpa fusiformis* off Oregon in April of 1999. Li et al. (2016) also documented unusually high abundance levels of several northern salp species, including *Salpa aspera* in the Gulf of Alaska during 2011, an event that may have contributed to the massive salp occurrence that was encountered off central and southern California in 2012 (Wells et al. 2013; Smith et al. 2014; Sakuma et al. 2016), for which *Salpa aspera* appears to have been one of the most abundant species (SIO Pelagic Invertebrates Collection Database, accessed Oct. 2019, https://oceaninformatics.ucsd.edu/zoodb/secure/login.php).

We investigate the spatiotemporal patterns of a recent mass occurrence of *Thetys vagina* and *Pyrosoma atlanticum* (hereafter referred to as *Thetys* and *Pyrosoma*) throughout the CCLME using data from a midwater trawl survey conducted in late spring. These species are among the largest pelagic tunicates that occur in the CCLME, such that all but the smallest individuals (<9.5 mm) can be sampled with a midwater trawl (Sakuma et al. 2016). Our study examines the distribution, abundance, and size variability of these species before, during, and after the unprecedented large marine heat wave in the eastern North Pacific Ocean of 2014–16 (Bond et al. 2015; Di Lorenzo and Mantua 2016; Jacox et al. 2018). To evaluate their spatio-temporal abundance trends, we enumerated catches in central California from 1983–2001, and coastwide from 2013–19, allowing us to put in context the relative abundance and distribution of the recent mass occurrence to previous abundance levels. We derive a length-to-weight relationship in order to convert recent estimates of abundance and length composition (length information was not collected on these species prior to 2012) to biomass, and examined *Thetys* and *Pyrosoma* length by year and region to evaluate trends in size over space and time. We then discuss the ecosystem and food-web implications of the bloom patterns and offer possible explanations of oceanic transport mechanisms that may have allowed the *Thetys* and *Pyrosoma* mass occurrence to expand and contract throughout the entire CCLME.

METHODS

Study area

The CCLME is a temperate eastern boundary upwelling ecosystem that is influenced by subarctic and subtropical source water variability (Hickey 1979; King



Year	OR	Blanco	Central	SCB
2013	30	25	61	16
2014	24	23	55	14
2015	27	21	55	19
2016	29	15	51	18
2017	10	14	43	14
2018	24	18	53	16
2019	27	11	47	16

Figure 1. Fixed stations and regions sampled by the RREAS and pre-recruit juvenile rockfish surveys. Depth contours are 200 and 600 m. Table indicates the number of stations sampled for each year. Stations between the dashed line are located in the core region.

et al. 2011). Although the CCLME is highly dynamic, the structure and variability of the pelagic food-web and species assemblages are fairly well understood in terms of biogeography and coastal geomorphology. During spring and summer, southward transport of the California Current increases and physical interactions with coastal promontories influences coastal upwelling, mesoscale ocean circulation, and retention patterns (Checkley and Barth 2009). The primary geographic promontories associated with strong upwelling centers and biogeographic breaks in oceanographic conditions are Cape Blanco, Cape Mendocino, and Point Conception (Checkley and Barth 2009; Fenberg et al. 2015; Gottscho 2016; Friedman et al. 2018), with additional smaller promontories such as Point Reyes and Point Arena in central California affecting regional oceanographic dynamics (fig. 1). These capes and points are associated with upwelling jets and influence the southward and offshore movement of coastal surface waters. The area between Capes Blanco and Mendocino generally exhibits the greatest variability in offshore transport and turbulence. North of Cape Blanco the continental shelf widens and the coast is oriented straight north-south, the dominant direction of wind, such that upwelling is more laminar. South of Cape Mendocino the coast is oriented northeast-southwest and the shelf is narrower, with an increased incidence of coastal prominences resulting in the development of several upwelling centers that also influence meandering upwelling jets. South of Point Conception, the California Current interacts with complex bathymetry (e.g., deep basins and banks) and is characterized by ephemeral areas of upwelling and relaxation. We apply these biogeographic breaks within the CCLME for estimating regional spatiotemporal indicators of *Thetys* and *Pyrosoma* abundance, distribution, and size.

Ecosystem surveys

Micronekton catch data were derived from the combined efforts of the National Oceanic and Atmospheric Administration (NOAA) Rockfish Recruitment and Ecosystem Assessment Survey (RREAS) operated by the Southwest Fisheries Science Center (SWFSC) for California waters, and the pre-recruit survey operated by the Northwest Fisheries Science Center (NWFSC) in waters off Oregon and Washington. The surveys occur annually in May–July during the season of ocean upwelling and increased southward transport. Since 1983, the RREAS has conducted midwater trawls quantifying micronekton species assemblages and regional hydrographic conditions (Ralston et al. 2015; Sakuma et al. 2016; Santora et al. 2017). The RREAS originally sampled the central California coast (Monterey to Point Reyes; Region C fig. 1) and expanded in 2004 to cover the entire California coast. The pre-recruit survey, initiated in 2011 off of Oregon and Washington, has the same objectives and trawl methodology as the RREAS (Brodeur et al. 2019a), and data have been pooled for evaluating spatial distribution and abundance patterns of juvenile rockfish (Field et al. 2017) and epipelagic micronekton forage communities (Friedman et al. 2018). The combination of these surveys provides full spatial coverage of nearly all of the US waters of the entire CCLME (excluding the coastal areas off of Northwest Washington State) for the 2013–19 time period (fig. 1).

Trawls were conducted at fixed sample stations (fig. 1) using a modified Cobb midwater trawl with a target headrope depth of 30 m and a tow speed of ~2 knots. Most RREAS stations are sampled 1–3 times per year (Sakuma et al. 2016), while the pre-recruit stations are sampled once per year (Brodeur et al. 2019). Trawls are typically 15 min in duration and conducted at night to reduce net avoidance by visually-dependent agile organisms and allow for the capture of organisms that exhibit Type I diel vertical migration (i.e., up at night, down during the day). For the RREAS, in instances where pre-trawl visual observations indicate large numbers of jellyfish or other gelatinous zooplankton a 5-minute trawl is conducted and the catch are expanded based on an expansion factor developed from an analysis of coupled 5- and 15-minute trawls (N. Grunloh and K. Sakuma unpublished data). Under very high abundance levels of gelatinous zooplankton, stations are abandoned entirely to avoid significant damage to the sampling gear. Until 2012, either abandoning or reducing trawl durations was done only in response to high abundance levels of scyphozoans (e.g., the Pacific sea nettle, *Chrysaora fuscescens*, and the moon jellyfish, *Aurelia* spp.). However, in 2012 the extraordinarily high number of salps throughout the survey area resulted in several trawls that substantially damaged trawl nets, and a high proportion of the 2012 trawls were shortened to 5 minutes in order to minimize gear damage throughout the survey. Salps and *Pyrosoma* had previously been enumerated from the start of the survey in 1983, with *Thetys* distinguished from all other Salpidae (which were not identified to the species level), and with improved and standardized subsampling methods standardized beginning in 1990 (Ralston et al. 2015; Sakuma et al. 2016). Due to competing priorities and time constraints, enumeration of salps and *Pyrosoma* was halted in 2002, however, the increased abundance of salps in 2012 led to a decision to return to the enumeration of salps and *Pyrosoma* as part of the survey catch analysis.

The number of *Thetys* and *Pyrosoma* captured in trawls are expressed as a standardized catch per unit effort (CPUE), with standardized trawl being the unit of effort. Within the long-term central California study area (core area), the 1983–2001 and 2012–19 sampling periods provided a total of 1,714 trawls averaged by 698

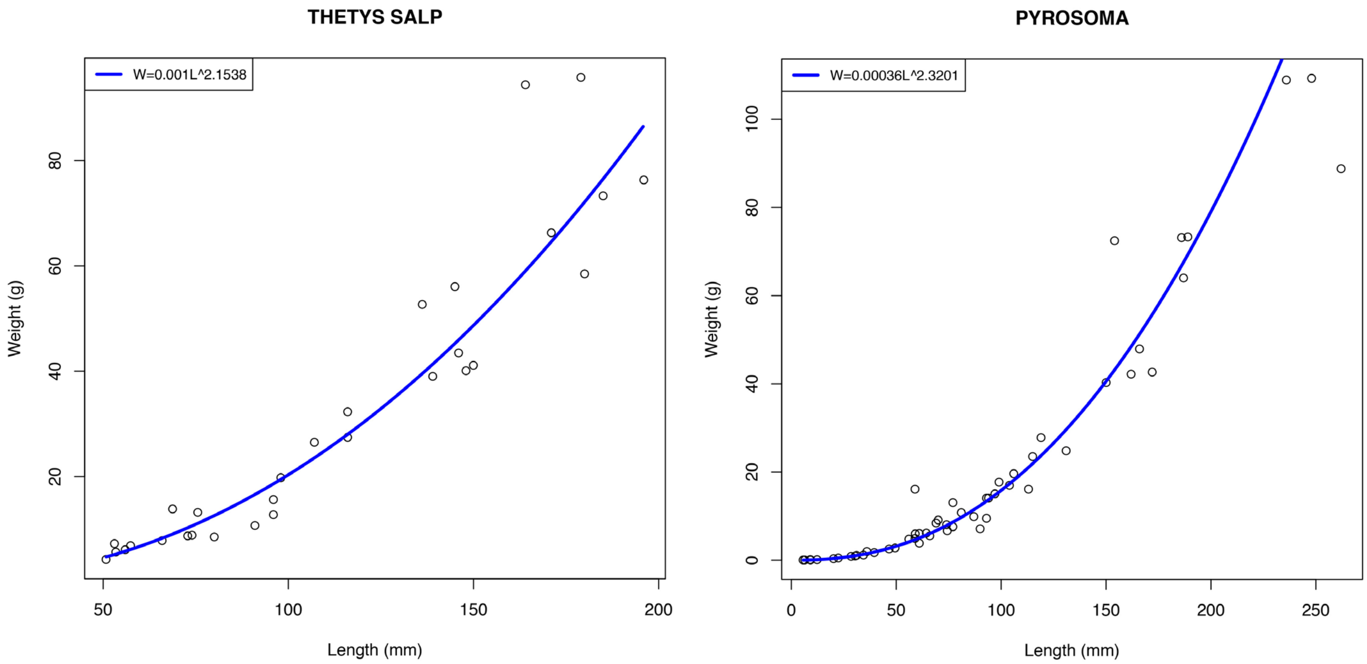


Figure 2. Length-to-weight relationships for *Thetys vagina* and *Pyrosoma atlanticum*.

station-year observations. For the coastwide study, the catches and lengths of *Thetys* and *Pyrosoma* were evaluated for 2013–19 (with 2013 the first year of complete coastwide coverage) using a total of 1,145 trawls averaged by 776 station-year observations. Catches for trawls aborted due to the high prevalence of *Pyrosoma* (2 trawls in 2017) were included by assigning the maximum catch recorded in a trawl for the respective taxa.

Length to biomass conversions of *Thetys vagina* and *Pyrosoma atlanticum*

Estimates of *Thetys* and *Pyrosoma* biomass are presented because length frequency and colony counts are highly variable whereas biomass is comparable among survey regions. For each trawl, length measurements (mm) were taken for a random subset of up to 30 *Thetys* and *Pyrosoma*. Both of these gelatinous species have a sufficiently rigid body structure to allow for reliable length measurements. For length analyses, stations that were sampled once during the year and had a species count of only one *Thetys* individual or *Pyrosoma* colony were removed. Combined, both surveys measured lengths of 6,790 *Thetys* (ranging 8–315 mm) and 13,170 *Pyrosoma* (ranging 3–540 mm), resulting in a total of 419 and 559 positive station-year observations, respectively. We derived a length-to-weight conversion from 30 *Thetys* samples (lengths = 51–196 mm, wet weights = 4.2–95.8 g) and 55 *Pyrosoma* samples (lengths = 5.6–262 mm, wet weights = 0.1–109.3 g) during the 2016 and 2019 survey. We applied the following allometric growth length-to-weight equation to determine relationships: *Thetys*, Weight = 0.001Length^2.1538, and *Pyrosoma*, Weight = 0.00036Length^ 2.3201 (fig. 2). Relative biomass was calculated by multiplying the average catch (CPUE) by the average weight for each taxa by haul (in g wet weight).

Distribution of *Thetys vagina* and *Pyrosoma atlanticum*

Catch data for *Thetys* and *Pyrosoma* were assessed for spatial variability and presence of regional maxima (i.e., hot spots) for the core region (1983–2001; 2012–19), and coastwide (2013–19). Catches (core area) and standardized relative biomass estimates (coastwide) were spatially interpolated using kriging with inverse distance weighting (Geostatistical Analyst toolbox in ArcMap 10.3; ESRI 2015). For kriging, a spatial neighborhood of five stations was chosen due to the approximate number of stations per survey transect (fig. 1), and interpolated surfaces were buffered at approximately 40 km from each station. For each year, we calculated the mean latitude of the coastwide biomass and denote the station with the maximum catch. Off central California, mean catches for the early years of the survey (1983–2001) were compared to the later survey years (2012–19) using a paired samples t-test. For the coastwide analysis, we calculated Moran's *I* to assess the relative spatial intensity (i.e., degree of spatial clustering of accumulations), of *Thetys* and *Pyrosoma* per year (Santora et al. 2011; Wells et al. 2017). To assess interannual regional variability, CPUE and length data were evaluated using ANOVA, and a post-hoc Tukey's HSD was used to determine mean differences within each biogeographic region by year (R Core, 2018).

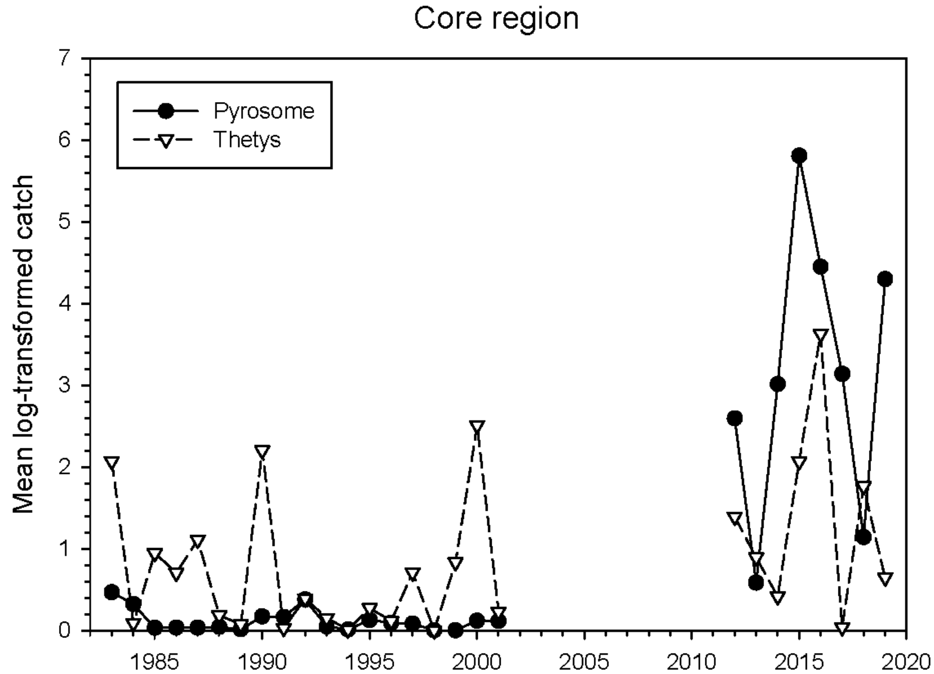


Figure 3. Time series of the annual mean log-transformed catch, ln(catch+1), for *Pyrosoma atlanticum* and *Thetys vagina* within the core region for the years 1983–2001 and 2012–19.

RESULTS

Temporal variability off central California

The time series of annual mean catches (CPUE) from 1983–2019 within the core region showed a moderate increase of *Thetys* during the 2012–19 time period, while *Pyrosoma* catches in 2012–19 increased by several orders of magnitude (fig. 3). *Thetys* abundance was variable from 1983–2001, with large peaks in 1983, 1990, 2000, and moderate multiyear peak during 1985–87. The average catch of *Thetys* during 1983–2001 compared to 2012–19 was significantly greater (0.608 ± 0.31 SD and 1.31 ± 0.70 SD, respectively; $p < 0.0001$; fig 3). Particularly noteworthy is the significant difference, by several orders of magnitude, of *Pyrosoma* catches during the 1983–2001 and 2012–19 time periods (0.098 ± 0.07 SD and 2.94 ± 1.37 SD, respectively; t-test $p < 0.0001$; fig. 3). Although *Pyrosoma* catches had low abundances during 1983–2001, they were present in 17 of 19 years, with zero catches 1998 and 1999. Abundance peaks of *Pyrosoma* occurred in 2012, 2014–16, and in 2019; the sustained multiyear peaks in abundance. Comparison of the spatial mean abundance during each time period indicates a greater spatial intensity of catches of both species (fig. 4). Despite the magnitude and variability of catches during the different time periods, both *Thetys* and *Pyrosoma* catches were greater offshore, with lower abundance at inshore stations near Point Reyes, Gulf of Farallones, and southern Monterey Bay (fig. 4). During the later time period (2012–19) the offshore station at 37.6˚N had the regional maximum catches for both *Thetys* and *Pyrosoma* (fig. 4).

Interannual spatial variability within the CCLME

During 2013–19, relative biomass estimates of *Thetys* exhibited enhanced mesoscale variability throughout the CCLME (fig. 5), with the highest catch rates (peaking at 58,729 grams wet weight per haul) from central Oregon through northern-central California (44˚–38˚N) in 2013. The catch data indicate reduced biomass coastwide in 2014, increasing but patchy coastwide biomass in 2015, and during 2016 the greatest biomass was focused in central California (between Cape Mendocino and Point Conception; peaking at 37,330 grams wet weight per haul; fig 5). *Thetys* biomass was lower in 2017 and 2018, except for in southern California in 2018 (fig 6). *Thetys* biomass in 2019 was reduced in all regions relative to 2018, but biomass was only significantly lower in the southern California region (Tukeys *p*-value < 0.001) (fig. 6). Stations with maximum *Thetys* biomass were located in central California for four of the seven years evaluated. *Thetys* maximum biomass in 2015 and 2016 occurred offshore at 38.5˚N, while in 2014 and 2017 the maximum biomass was offshore at 40.5˚N. Moran's *I* analysis of *Thetys* coastwide biomass indicate significant and

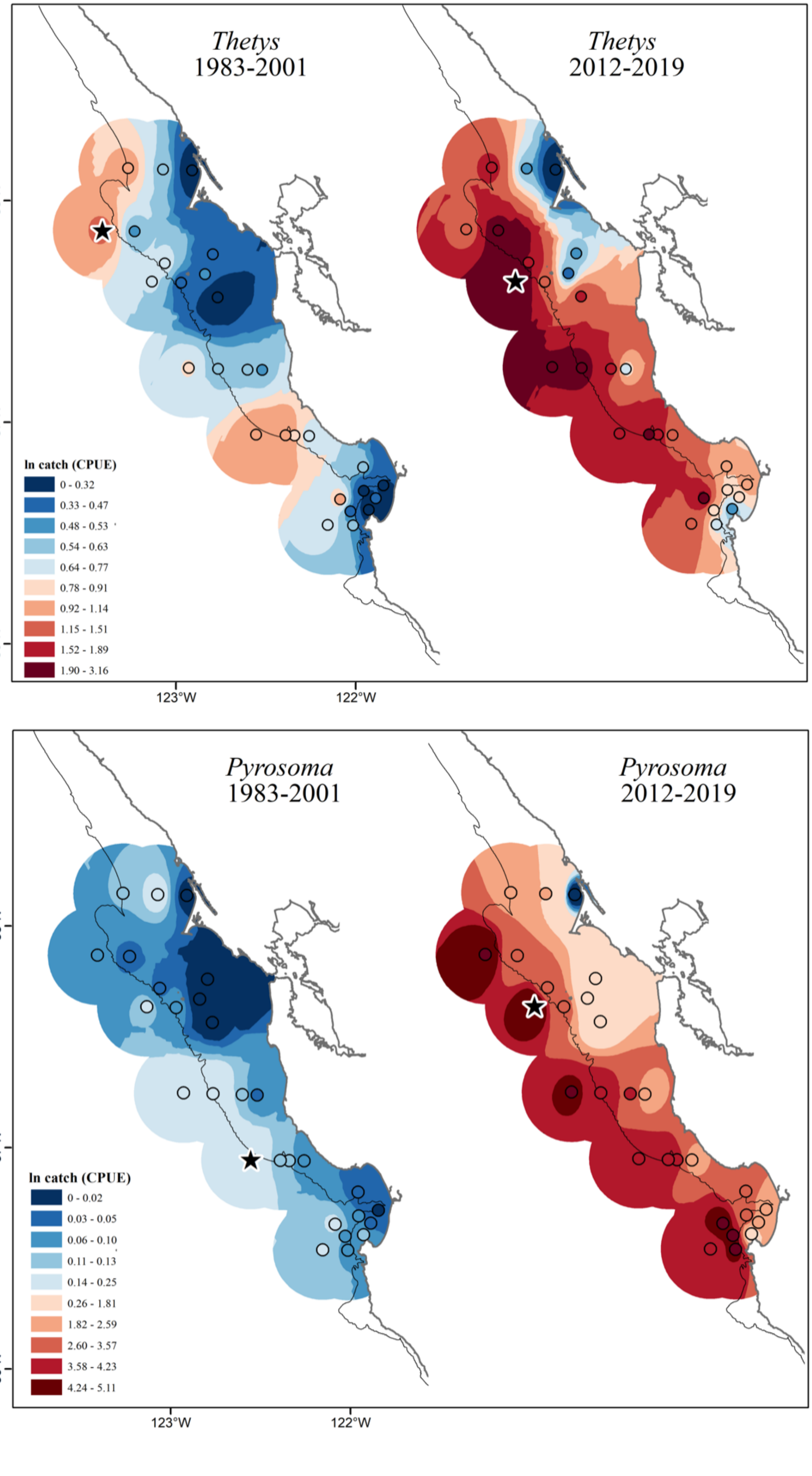


Figure 4. Top panel shows core region spatial mean catches (CPUE) of *Thetys vagina* for two time periods (1983–2001; 2012–19). Bottom panel shows core region spatial mean catches (CPUE) of *Pyrosoma atlanticum* for two time periods (1983–2001; 2012–19). The star represents the station with the maximum catch. The 200 m depth contour is shown. Classification is based on 10% quantiles.

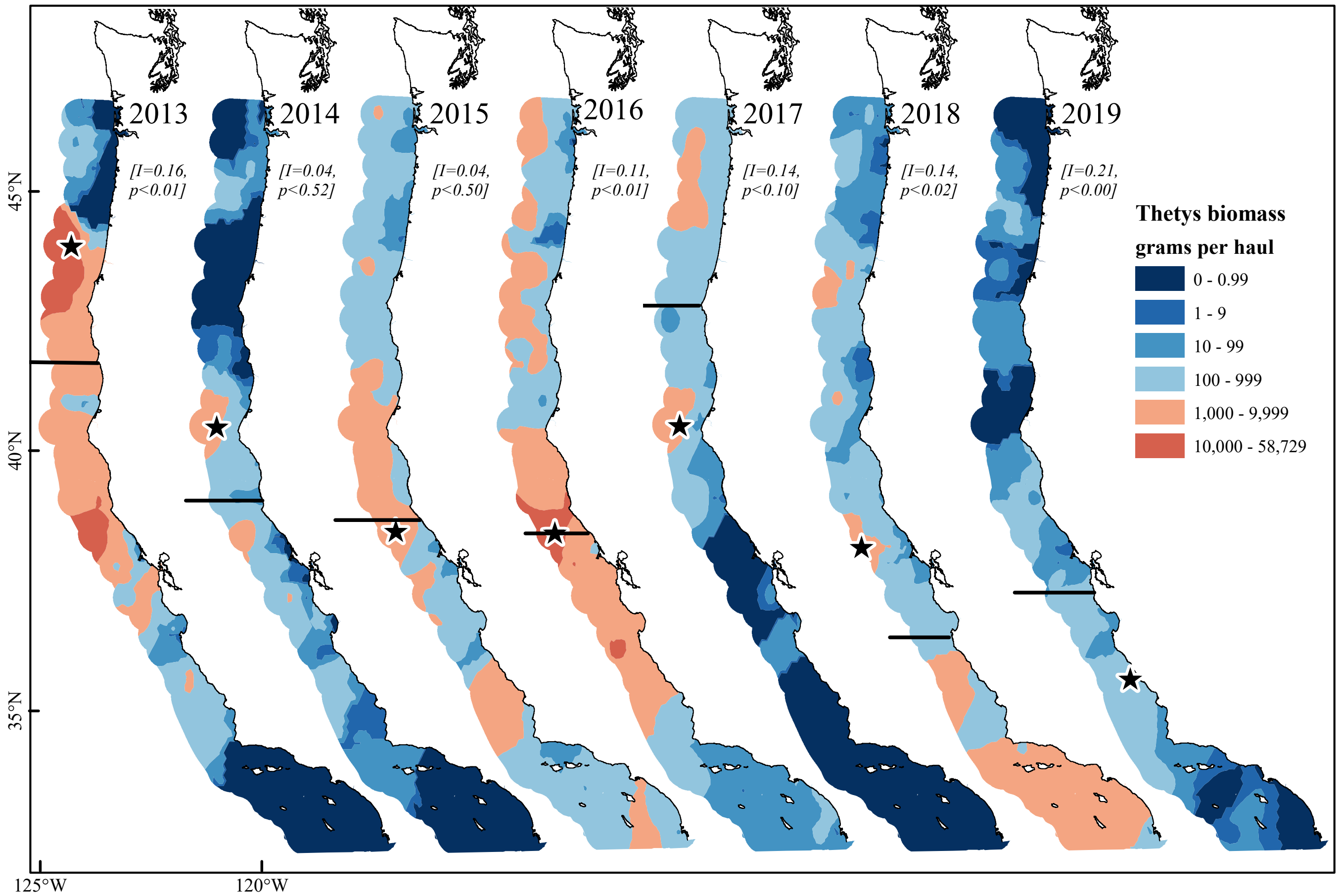


Figure 5. *Thetys vagina* biomass (grams of wet weight per haul) during the May–June period in the California Current Large Marine Ecosystem in 2013–19. The solid line represents the latitude at which the coastwide biomass mean occurred for each year. The star represents the station with the maximum catch. The Moran's *I* and *p*-value are presented for each year, where Moran's *I* value of 0–1 suggests spatial clustering, 0 spatial randomness, –1–0 suggests spatial dispersion.

greater spatial intensity (or clustering), in 2013, 2016, 2018, and 2019 (fig. 5). During those years, the mean latitudinal biomass showed a sequentially increasing pattern from north to south. Moran's *I* values during 2014, 2015, and 2017 indicated less spatial intensity and consistent with a randomly distributed pattern (fig. 5). *Thetys* median lengths were between 100–150 mm and were consistent among regions and years (fig. 7). In the Oregon region, *Thetys* median lengths decreased from 135 mm in 2013 to 114 mm in 2018, but the trend over time was not significant ($p = 0.66$). Lengths for *Thetys* from southern California, central California and Blanco regions had no discernible trend; however, median lengths from the central California region were significantly larger ($p < 0.001$) in 2016 and 2019 when compared to the preceding years.

Pyrosoma relative biomass trends demonstrated a distinct temporal trend of increasing abundance within the CCLME from south to the north during 2013–18, while in 2019 abundance was vastly reduced in northern regions and predominately located in the central region (37°–35°N); (fig.6, fig. 8). *Pyrosoma* biomass in 2013–14 had a patchy, southern distribution, and were significantly less abundant ($p < 0.0001$) in the central region, when compared to 2015. *Pyrosoma* biomass during the 2015–16 marine heatwave were centered near Monterey Bay in 2015 (mean latitude 36.7°N), while in 2016 the mean latitude was centered in the Cape Blanco region (41.3°N) with biomass abundant in both the central region and the Oregon offshore stations. In 2017 and 2018 *Pyrosoma* biomass was significantly greater ($p < 0.0001$) in the Oregon and Blanco regions, reaching peak relative abundance levels in the waters off of Washington, Oregon, and Northern California (fig. 6, fig. 8). By 2019 only one small pyrosome (19 mm) was found in the Oregon region, while *Pyrosoma* biomass was greatest in the central region and notably the median biomass was slightly larger in this region than it was in 2015 (fig. 6). The stations with *Pyrosoma* maximum catches were located in the Oregon region immediately after the marine heat wave (catches peaking at 73,179 grams wet weight per haul in 2016, 1,655,032 in 2017 and 927,988 in 2018, respectively). The highest catch rates for pyrosomes for both 2015 and 2019 were off-

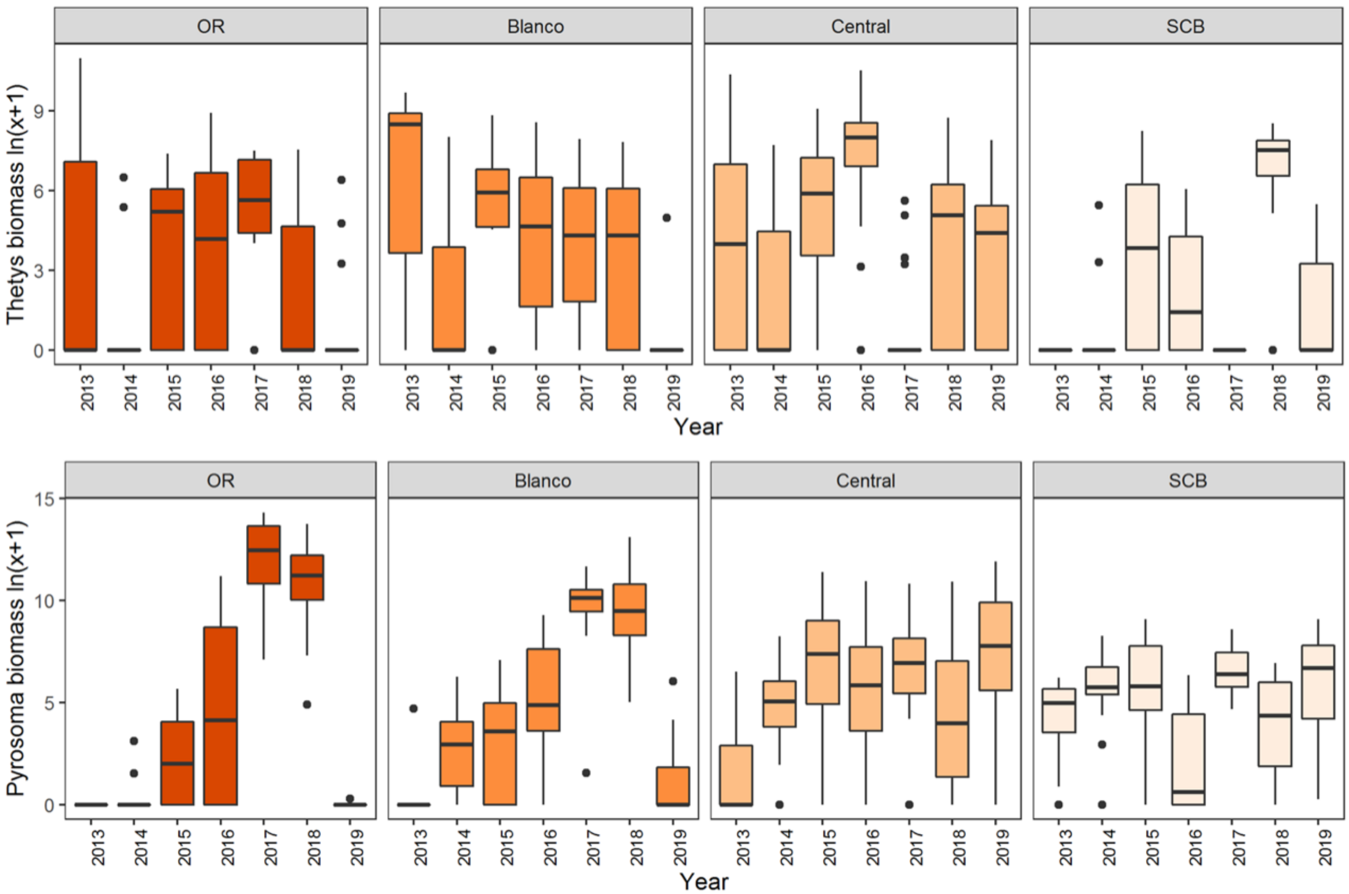


Figure 6. Boxplots of *Thetys vagina* and *Pyrosoma atlanticum* biomass by region and year in the California Current Large Marine Ecosystem during the May–June period. Boxplots show the median, interquartile range (Q25, Q75), whiskers show highest or lowest value, dots represent extreme values.

shore waters of central California (35.7˚N). Throughout this time period of increasing abundance there was also an increase in the spatial autocorrelation, or clustering, of *Pyrosoma* which were significantly clustered during and after the marine heat wave from 2015–19, with the highest Moran's *I* value observed in 2019 (0.32: $p < 0.0001$).

Coincident with the positive abundance trends were increasing colony size in northern regions over time and decreasing colony sizes in the SCB region (fig 7). In the SCB region *Pyrosoma* median lengths trended smaller from 2013–17, from 67 mm in 2013 to 19 mm with a low variance ($p < 0.012$) in 2017; while in 2018–19 median lengths were larger (50 and 69 mm, respectively). Off central California, median *Pyrosoma* lengths were similar (53, 35, 45, and 38 mm) during the period from 2013 to 2016, while from 2017–19, lengths increased to 111,79 and 112 mm, respectively ($p < 0.0001$). In the Blanco region, *Pyrosoma* lengths significantly increased from a median of 49 mm in 2014 to 138 mm in 2018 ($p < 0.0001$), while in 2019 median lengths were slightly smaller (113 mm). Off Oregon, *Pyrosoma* colony median lengths increased by a factor of three, from 40 to 125 mm ($p < 0.03$) from 2014 to 2017.

An unusual, rarely encountered *Pyrosoma* species in the RREAS survey, was caught in 2019 off of Davenport, California, (lat 37.0˚ N) with a station bottom depth of 128 m. It was identified as *Pyrosomella verticillata*, based on the keys in vanSoest 1981 and Bone 1998 (L. Sala, Scripps Institution of Oceanography, pers. comm.). *Pyrosomella verticillata* is known to occur in the warm Indo-West Pacific waters (vanSoest 1981), however in 2008 a colony was found in the southwest Atlantic Ocean (Carvalho and Bonecker 2008) indicating the potential for greater oceanic distribution.

DISCUSSION

Our study described the spatial and temporal aspects of the extraordinarily large mass occurrence of two pelagic thaliacean taxa, *T. vagina* and *P. atlanticum* throughout the CCLME. As observed in our long-term monitoring area off central California, both species had significantly greater catches during 2012–19 compared to the 1983–2001 time period. Although *T. vagina* displayed 3 strong abundance peaks during 1983–2001, they were largely ephemeral, but their abundance persisted and increased in frequency during 2012–19. On the other

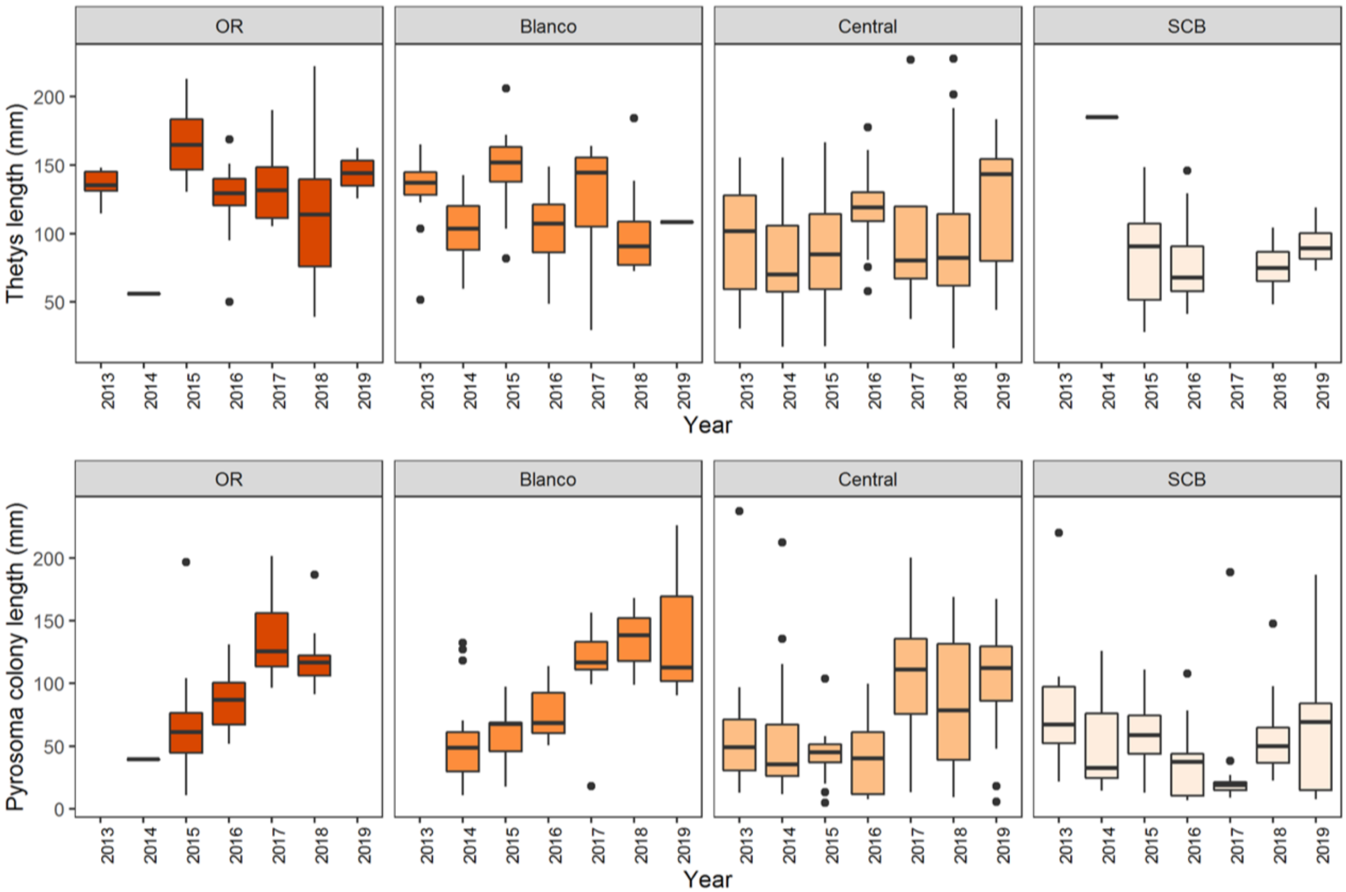


Figure 7. Boxplots of *Thetys vagina* and *Pyrosoma atlanticum* lengths (mm) in the California Current Large Marine Ecosystem by region and year during the May–June period. Boxplots show the median, interquartile range (Q25, Q75), whiskers show highest or lowest value, dots represent extreme values.

hand, *P. atlanticum* displayed no peaks until 2012 and were then persistent for 8 years. Although oceanographic variables were not formally evaluated in this study, these strong interdecadal differences suggest that ocean conditions played some role in facilitating the recent multiyear persistent blooms of these species. Ocean and climate conditions within the central-northern California Current during 1983–2001 were characterized by several strong ENSO events and largely considered a positive (warm) phase of the Pacific Decadal Oscillation, which generally leads to above average ocean temperatures in the California Current and Northeastern Pacific ocean (Peterson and Schwing 2003; Checkley and Barth 2009). Ocean conditions during 2012–19 were variable, having a mixture of both strong upwelling conditions and sustained warming events (Wells et al. 2013; Bond et al. 2015; Di Lorenzo and Mantua 2016; Thompson et al. 2018), suggesting that temperature alone is likely not responsible for driving mass occurrence. Given the passive movement and nature of these organisms, it seems more likely that anomalous ocean current transport, combined with food availability (e.g., phytoplankton species and particle size), may have supported and sustained the persistent multiyear blooms (Lavaniegos and Ohman 2003; Henschke et al. 2016).

Our study provides novel insight on the extent of the sustained mass occurrence event across the extent of a large marine ecosystem. Coastwide catch patterns from 2013–19 generally demonstrate a patchy distribution for *Thetys* and an increase in northward distribution, abundance, and significant clustering for *Pyrosoma*. There were notable latitudinal clines in size observed for *Pyrosoma* over space and time, with no such patterns in size observed for *Thetys*. Oceanographic conditions varied substantially within the California Current during 2013–19, ranging from one of the strongest upwelling years on record (2013), a multiyear marine heat wave (2014–16), a strong El Niño (2016), and a return to near average upwelling conditions (2017–19), but with pronounced differences in sea temperature and upwelling between northern and southern regions (Wells et al. 2013; Thompson et al. 2018). The northward and onshore expansion of biomass and size variability of *Pyrosoma* may be in response to the large marine heatwave of 2015–16 (Brodeur et al. 2019a). Importantly, other species of salps appeared in unprecedented

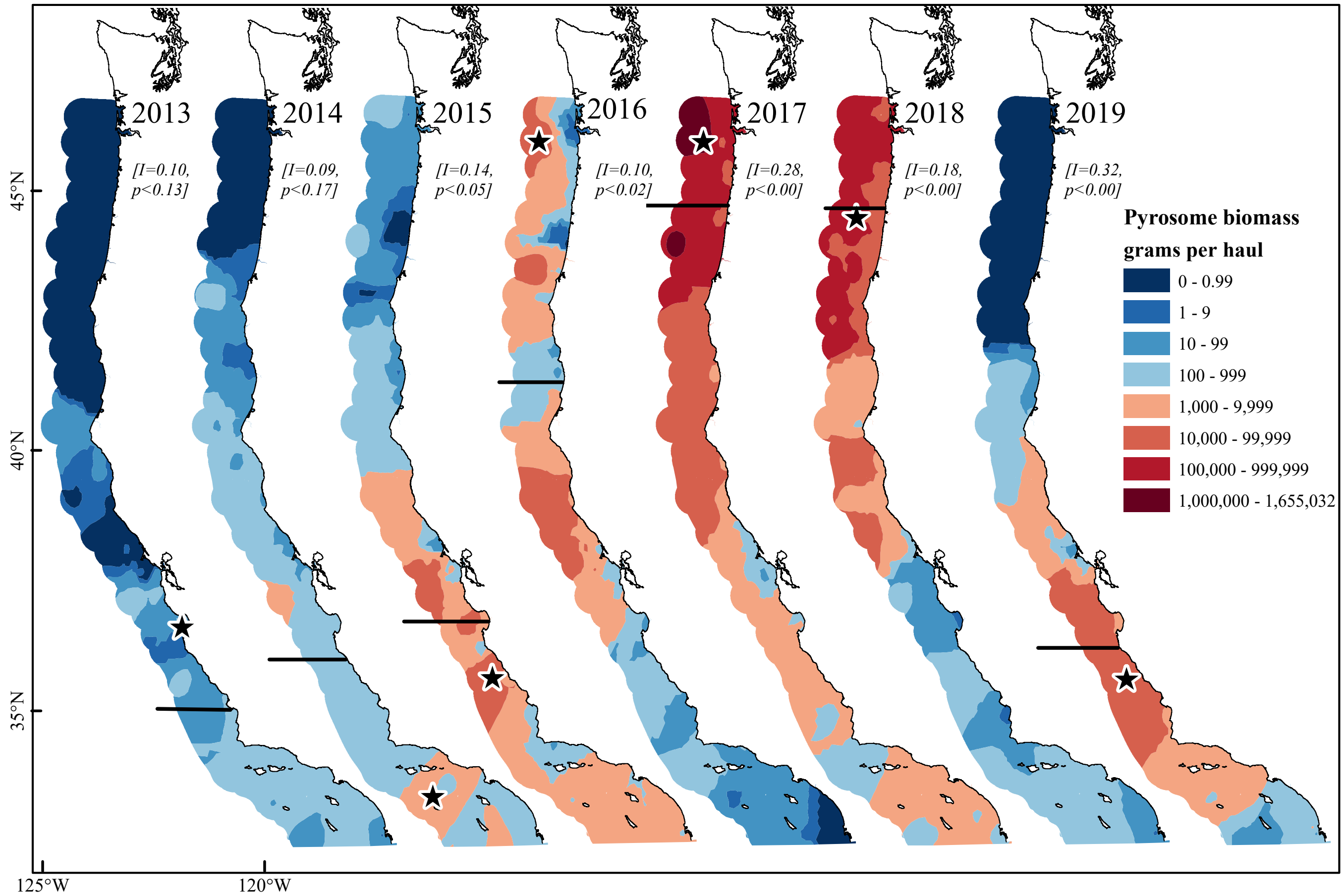


Figure 8. *Pyrosoma atlanticum* biomass (grams of wet weight per haul) during the May–June period in the California Current Large Marine Ecosystem from 2013–19. The solid line represents the latitude at which the coastwide biomass mean occurred for each year. The star represents the station with the maximum catch. The biomass hotspot indicates a chronological south to north progression. The Moran's *I* and *p*-value are presented for each year, where Moran's *I* value of 0–1 suggests spatial clustering, 0 spatial randomness, –1–0 suggests spatial dispersion.

numbers throughout the northeast Pacific Ocean since 2011 (Wells et al. 2013; Smith et al. 2014; Li et al. 2016; Thompson et al. 2018), therefore the mass occurrence of pelagic thaliaceans were clearly not limited to these two taxa alone throughout this time period.

The persistent multiyear high abundance of several taxa of gelatinous zooplankton within the CCLME during this seven year period is unusual. There is limited information on what conditions promote mass occurrence of pelagic tunicates in the CCLME, which tend to exhibit episodic population peaks between longer time periods of lower abundance. Other pelagic tunicate blooms around the world have episodic duration and timing over days (Deibel 1985), months (Boero et al. 2013), or years (Lavaniegos and Ohman 2007; Loeb and Santora 2012), and such blooms could be indicators of the prevailing oceanographic conditions. Although both *Thetys* and *Pyrosoma* blooms appear to have preceded the 2014–16 marine heat wave in the Northeast Pacific Ocean, which was one of the strongest and most prolonged events on record (Hobday et al. 2018), the question of what effect the marine heat wave may have had in enhancing or extending the ongoing mass occurrence is worthy of consideration. For example, it is likely that some of the salps described in the 2012 bloom off California (Wells et al. 2013) originated from the 2011 mass occurrence described in the Gulf of Alaska (Li et al 2016). Similarly, the tremendous abundance and apparently historically unprecedented spatial expansion of *Pyrosoma* were largely concurrent with the onset of the large marine heat wave, which could have facilitated the northward expansion of these organisms. By 2017, Brodeur et al. (2018) reported *Pyrosoma* in anomalously high abundance throughout the Northeast Pacific, including the west coast of Vancouver Island and into the northern Gulf of Alaska. *Pyrosoma* are thought to be associated with advection of offshore warm water into coastal waters (Brodeur et al. 2018; 2019, Sutherland et al. 2018). Due to the consistency of our sampling, we were able to track this northward expansion first into northern California and eventually up to the northern end of our sampling area (i.e., southern Washington), with concurrent decreases in populations off central and southern California.

We provide an assessment of size-related life-history characteristics for *Thetys* and *Pyrosoma* throughout the CCLME (from 32° to 46°N). While *Thetys* lengths were generally similar in space and time throughout the CCLME, their lengths were significantly larger within the central California region in 2016. This was towards the end of the marine heat wave which had the highest *Thetys* catches within central California, possibly indicating favorable ocean conditions suited for *Thetys* reproduction and growth. *Pyrosoma* sizes off southern California became progressively smaller from 2013–17, perhaps indicating that ocean conditions were ideal for reproductive sexual budding and seeding in these areas. On the other hand, north of central California, *Pyrosoma* lengths increased during the 2015–18 mass occurrence, possibly indicating that sufficient food resources allowed for zooid colonial growth (asexual). For example, although *Pyrosoma* lengths in the northern California Current were of literature-based estimates of sexual reproductive size (e.g., >40 mm; van Soest 1981), the variance of the lengths in 2016–18 were not below 40 mm, possibly indicating younger, newly seeded *Pyrosoma* were not as prevalent. While it is unknown what the life span of *Pyrosoma* colonies are or whether colony size is related to age, Henshke et al. (2019) reported that food availability contributes to the sustained growth and development of *Pyrosoma* mass occurrences. These species have particular filter feeding efficiencies, and although phytoplankton size and composition is not available with this data set, the species composition and size structure of phytoplankton and zooplankton communities could be influencing the population dynamics of these species.

Other unknowns are whether the catch, lengths, and lifecycle stage of these taxa differ throughout the water column, and specifically whether trawl sampling at night (target depth layer 30 m) was optimal for collecting these taxa. *Pyrosoma* are known to undertake large diel vertical migrations of up to 1,000 m (Henschke et al. 2019), with the depth and timing of migration related to colony size (Andersen and Sardou 1994). Daytime video observations off Oregon show that *Pyrosoma* was most abundant at a depth of between 25 and 35 m during the day but this species is known to migrate closer to the surface at night (Sutherland et al. 2018; Blondheim et al. unpublished data). Although the survey trawls fished near the surface during the short recovery period, we believe that the majority of catches were made at the target depth layer, and the trawls may have missed a substantial part of the biomass (and other size classes) of both *Thetys* and *Pyrosoma* at other depth layers. While this analysis is the largest spatial scale of *Thetys* catches on the US West Coast that we are aware of, the lifecycle stage of *Thetys* were not identified as solitary or aggregate forms. Not distinguishing between the reproduction forms could be a contributing factor as to why no discernible patterns were found for *Thetys* biomass and lengths.

An important next step in quantifying the determinants of coastwide variability and potential interactions of thaliaceans within the forage assemblage is to identify the connection between source water variability and their occurrence and distribution (Schroeder et al. 2019). There is some regional work to provide a foundation for this endeavor. Lavaniegos and Ohman (2007) showed that the decline in thaliaceans inferred from CalCOFI observations was associated with an increase in water column density stratification, supporting the need to look more closely at source waters and transport trends to resolve abundance and seeding/distribution patterns relative to oceanographic drivers. To further support the oceanographic connectivity between the southern and central California sectors of the CCLME, Lavaniegos and Ohman (2007) noted that a large fraction of the interannual variability of zooplankton is shared between sectors. However, the CalCOFI data for most years cannot be used for trends in fine scale distribution or patchiness for either central or southern California, as station-specific zooplankton are pooled into a single large grouping, enumerated and aggregated (Lavaniegos and Ohman 2003).

Given the magnitude of the recent thaliacean mass occurrence compared to past abundance trends, it is likely that during the 2012–19 time period, thaliaceans represented a far greater percentage of total productivity and standing carbon than the 5%–8% that was previously estimated by Lavaniegos and Ohman (2007) for the southern and central sectors of the CCLME. For example, *Thetys vagina* is poorly sampled in typical plankton sampling gear; the species was identified only twice (1955 and 1964) in the CalCOFI time series through 2003, despite being encountered at relatively high abundances during the years 1983, 1990, and 1999 within midwater trawls reported in this study. Other previous studies of *Thetys vagina* occurrences have been based on data collected from larger sampling devices, such as other midwater trawl (10 meter diameter otter trawls) surveys (Iguchi and Kidokoro 2006) or larger (1 m^2) plankton net surveys (Henschke et al. 2016b). Although our results are informative regarding the relative abundance and spatial distribution patterns of *Thetys* and *Pyrosoma* from 2013–19 throughout the CCLME, some type of analysis or calibration to enable robust estimates of abundance per unit area (e.g., cubic meters sampled or square meters of water column) will be necessary to evaluate the potential impact of these mass occurrences quantitatively, and to compare our abundance estimates to those available from other time series. Such estimates could not be developed in this analysis, for despite the fact that there are estimates of net opening and area swept by our gear, it is highly unlikely that these low motility pelagic tunicates are fully selected by the total mouth opening of the trawl. Rather, the selectivity of the gear is likely to vary substantially with the size of the target organism, as net mesh sizes are fairly large (15.2 cm, or 6 inches) at the net opening, and are reduced to 6.7 cm (3 inches) and 3.8 cm (1.5 inches) as the net tapers to the fine (0.95 cm, 3/8 inch) cod-end liner. Thus, as with many other micronekton, the selectivity of the target species will vary by size, presumably to a much greater extent for the highly variable (by size) *Pyrosoma* colonies relative to *Thetys*, which generally have a more limited size range. Consequently, future efforts to estimate the absolute (rather than relative) biomass of thaliaceans over time and space using trawl survey data will require careful evaluation of selectivity and catchability patterns, which may require calibration with survey gear that is more typically used for sampling gelatinous zooplankton (Kwong et al. 2018).

Ecosystem implications of the gelatinous pelagic tunicate mass occurrence

Pelagic tunicate mass occurrence are known to alter macro-zooplankton communities and functioning of marine food webs (Alldredge and Madin 1982, Drits et al. 1992; Perissinotto et al. 2007). *Pyrosoma* are aggregate filter feeders with each zooid rapidly consuming pico- and microplankton. Areas with high *Pyrosoma* biomass have been demonstrated to cause the depletion of chlorophyll-*a* standing stocks (Drits et al. 1992; Perissinotto et al. 2007, Décima et al. 2019). However, these studies were generally conducted in oceanic, low productivity regions, therefore the impact of *Pyrosoma* grazing in highly productive regions like the California Current is not well known. Similarly, there is limited information on feeding in *Thetys* populations. Based on a small sample size of individuals collected in the Japan Sea, Iguchi and Kidokoro (2006) determined that *Thetys* feed mainly on small phytoplankton and tintinnids, but also consumed a small number of copepods. Overall, large salp blooms have been shown to have negative effects on lower trophic level productivity in many ecosystems (Alldredge and Madin 1982; Perissinotto and Pakhomov 1998; Henschke et al. 2016b).

Due to their large individual size and relatively low energy content, persistent thaliacean mass occurrence may have major implications for mid- and higher-trophic level predators in marine food webs, as these gelatinous organisms may not be appropriate prey items for mobile predators that require high lipid or high caloric values (e.g., salmon, seabirds, and marine mammals). However, they may be suitable for many other predators, such as leatherback turtles (*Dermochelys coriacea*; Hays et al. 2009; Jones et al. 2012) and many species of rockfish (*Sebastes* spp.; Adams 1987; Lee and Sampson 2009; Chiu 2018). For example, both Adams (1987) and Lee and Sampson (2009) found that widow rockfish (*S. entomelas*) off California and Oregon preyed heavily on salps, which represented from 30% to >90% of diet volume in those studies depending on year and season. Lee and Sampson (2009) found that yellowtail rockfish (*S. flavidus*) also preyed heavily on gelatinous zooplankton off Oregon, and Chiu (2018) found the same for yellowtail rockfish in central California during 2013 and 2014. The Chiu (2018) study was the only study known to the authors to include substantial rockfish predation on *Pyrosoma* as well as salps, which comprised >5% of the diet by number and nearly 8% by weight, as might be expected given the relative rarity of *Pyrosoma* prior to the recent mass occurrence. Several small pelagic fishes such as northern anchovies (*Engraulis mordax*), Pacific sardines (*Sardinops sagax*), and Pacific herring (*Clupea pallasi*) consumed a mainly gelatinous diet during the recent marine heat wave, relative to their normal diet of mostly crustaceans during cooler year (Brodeur et al. 2019b). Zuercher and Galloway (2019) demonstrated that pelagic tunicates and other offshore macrozooplankton represent important energetic subsidies to nearshore kelp forests. Given these findings, it seems likely that thaliaceans represent a fairly important source of forage for many rockfish and other predators during periods of high abundance.

A substantial fraction of the carbon associated with thaliacean mass occurrence is likely to be exported to other food webs to be used by non-pelagic, benthic predators (Lebrato and Jones 2009; Archer et al. 2018; Brodeur et al. 2018). Specifically, Smith et al. (2014) showed that the 2012 salp mass occurrence, and subsequent die-off in Monterey Bay was an unprecedented event with respect to carbon export to deep water benthic habitats. It has also been noted that that the fecal pellets and carcasses of larger salps (such as *Thetys*) and *Pyrosoma* tend to sink considerably faster than those of smaller species or individuals (Smith et al. 2014; Henschke et al. 2016a; Henschke et al. 2016b). Pelagic tunicates also provide shelter for species during certain life stages, including juvenile medusa fish (*Icichthys lockington*), juvenile small-eye squaretail (*Tetragonurus cuvieri*), hyperiid amphipods (*Phronima*), and tuberculate octopus (*Ocythoe tuberculata*) (Love 2011, and as observed on RREAS survey). Thus, the role of these gelatinous organisms with respect to both their position in the food web, in the overall carbon cycle and community structure warrants continued investigation into both the oceanographic drivers and consequences of their distribution and population dynamics through effective monitoring efforts. Given the projections of increased warming and expectations of larger and more sustained marine heat waves in the California Current and the global ocean in general (Joh and Di Lorenzo 2017; Frölicher and Laufkötter 2018), we may anticipate that these mass occurrences may continue and perhaps intensify in the coming decades, with unknown consequences.

ACKNOWLEDGEMENTS

We would like to thank the captains, crew, and participating scientists on all of the research vessels (e.g., RV *Bell M. Shimada*, RV *Reuben Lasker*, RV *Ocean Starr*) used for the juvenile rockfish surveys. We especially thank I. Iglesias who wrote the r code for the allometric growth length-to-weight relationship curve, and L. Sala who identified *Pyrosomella verticillata*. V. J. Loeb, J. Bizzarro, M. Monk, and 2 anonymous reviewers provided helpful comments and insight in improving the quality of this manuscript.

LITERATURE CITED

Adams, P. B. 1987. Diet of widow rockfish (*Sebastes entomelas*) in northern California. *In*: Lenarz, W. H., and D. R. Gunderson (Eds.) Widow rockfish: proceedings of a workshop. NOAA Technical Report, NMFS 48, pp. 37–41.

Alldredge, A. L., and L. P. Madin. 1982. Pelagic tunicates: unique herbivores in the marine plankton. BioScience. 32(8):655–663.

Andersen, V., and J. Sardou. 1994. *Pyrosoma atlanticum* (Tunicata, Thaliacea): diel migration and vertical distribution as a function of colony size. J. Plankton Res. 16:337–349.

Archer, S. K., A. S. Kahn, S. P. Leys, T. Norgard, F. Girard, C. Du Preez, and A. Dunham. 2018. Pyrosome consumption by benthic organisms during blooms in the NE Pacific and Gulf of Mexico. Ecology. 99:981–984.

Berner, L. O. 1967. Distributional atlas of Thaliacea in the California Current Region. Calif. Coop. Ocean. Fish. Invest. Rep. Atlas 8.

Blackburn, M. 1979. Thaliacea of the California Current region: relations to temperature chlorophyll, currents and upwelling. Calif. Coop. Ocean. Fish. Invest. Rep. 20:184–194.

Boero, F., G. Belmonte, R. Bracale, S. Fraschetti, S. Piraino, and S. Zampardi. 2013. A salp bloom (Tunicata, Thaliacea) along the Apulian coast and in the Otranto Channel between March–May 2013. F1000Research, 2:181.

Bond, N. A., M. F. Cronin, H. Freeland, and N. Mantua 2015. Causes and impacts of the 2014 warm anomaly in the NE Pacific, Geophys. Res. Lett. 42:3414–3420, doi:10.1002/2015GL063306.

Bone, Q. 1998. The Biology of Pelagic Tunicates. Oxford Univ. Press, Oxford.

Brodeur, R., I. Perry, J. Boldt, L. Flostrand, M. Galbraith, J. King, J. Murphy, K. Sakuma, and A. Thompson. 2018. An unusual gelatinous plankton event in the NE Pacific: The Great Pyrosome Bloom of 2017. PICES Press. 26(1):22–27.

Brodeur, R. D., T. D. Auth, and A. J. Phillips. 2019a. Major shifts in pelagic community structure in an upwelling ecosystem related to an unprecedented marine heatwave. Front. Mar. Sci. 6:212, doi:10.3389/fmars.2019.00212.

Brodeur, R.D., M.E. Hunsicker, A. Hann, and T.W. Miller. 2019b. Effects of warming ocean conditions on feeding ecology of small pelagic fishes in a coastal upwelling ecosystem: a shift to gelatinous food sources. Mar. Ecol. Prog. Ser. 617–618:149–163.

Carvalho, P. F., and S. L. Bonecker. 2008. Tunicata, Thaliacea, Pyrosomatidae, *Pyrosomella verticillata* (Neumann, 1909): first record from the Southwest Atlantic Ocean. Check List 4(3):272–274.

Checkley, D. M., and J. A. Barth. 2009. Patterns and processes in the California Current system. Prog. Oceanogr. 83:49–64.

Chiu, J., 2018. Diets and stable isotope signatures of yellowtail rockfish (*Sebastes flavidus*) in Central California. Masters of Science Thesis, Moss Landing Marine Laboratory, San Jose State University.

Conley, K. R., F. Lombard, and K. R. Sutherland. 2018. Mammoth grazers on the ocean's minuteness: a review of selective feeding using mucous meshes. Proc. R. Soc. B. 285:20180056, doi:org/10.1098/rspb.2018.0056.

Décima, M., M. R. Stukel, L. López-López, and M. R. Landry. 2019. The unique ecological role of pyrosomes in the Eastern Tropical Pacific. Limnol. Oceanogr. 64:728–743.

Deibel, D. 1985. Dolioids Blooms of the pelagic tunicate, *Dolioletta gegenbauri*: Are they associated with Gulf Stream frontal eddies? J. of Marine Res., 43(1) 211–236.

Di Lorenzo, E., and N. Mantua. 2016. Multi-year persistence of the 2014/15 North Pacific marine heatwave. Nat. Clim. Chang. 6:1042–1047, doi:10.1038/nclimate3082.

Drits, A. V., E. G. Arashkevich, and T. N. Semenova. 1992. *Pyrosoma atlanticum* (Tunicata, Thaliacea): grazing impact on phytoplankton standing stock and role in organic carbon flux. J. Plankton Res. 14:799–809.

Eng, James. "Diablo Canyon Nuclear Plant in California Knocked Offline by Jellyfish-Like Creature Called Salp." *NBC News*. April 27, 2012. http://usnews.nbcnews.com/_news/2012/04/27/11432974-diablo-canyon-nuclear-plant-in-california-knocked-offline-by-jellyfish-like-creature-called-salp?lite. Accessed September 23, 2019.

ESRI. 2015. ArcGIS 10.3 Environmental Systems Research Institute. Redlands, Calif.

Field, J. C., E. J. Dick, N. Grunloh, X. He, K. Sakuma, and S. Ralston. 2018. Coastwide Pre-Recruit Indices from SWFSC and NWFSC/PWCC Midwater trawl Surveys (2001–16). Appendix B in He, X. and J.C. Field. Stock assessment update: Status of bocaccio, *Sebastes paucispinis*, in the Conception, Monterey and Eureka INPFC areas for 2017. Pacific Fishery Management Council, Portland, Oregon. 224 p. https://www.pcouncil.org/groundfish/stock-assessments/by-species/bocaccio-rockfish/.

Friedman, W. R., J. A. Santora, I. D. Schroeder, D. D. Huff, R. D. Brodeur, J. C. Field, and B. K. Wells. 2018. Environmental and geographic relationships among salmon forage assemblages along the continental shelf of the California Current. Mar. Ecol. Prog. Ser. 596:181–198.

Frölicher, T. L., and C. Laufkötter. 2018. Emerging risks from marine heat waves. *Nature Communications* 9, Article number: 650.

Gorman, Steve. "Jellied sea creatures confound scientists, fisherman on U.S. Pacific Coast." Reuters. June 27, 2017. https://www.reuters.com/article/us-environment-pyrosomes/jellied-sea-creatures-confound-scientists-fishermen-on-u-s-pacific-coast-idUSKBN19I145. Accessed September 23, 2019.

Gottscho, A. D. 2016. Zoogeography of the San Andreas Fault system: Great Pacific Fracture Zones correspond with spatially concordant phylogeographic boundaries in western North America. Biol Rev, 91: 235–254. doi:10.1111/brv.12167.

Graham, W. M., S. Gelcich, K. L. Robinson, C. M. Duarte, L. Brotz, J. E. Purcell, L. P. Madin, H. Mianzan, K. R. Sutherland, S. Uye, K. A. Pitt, C. H. Lucas, M. Bogeberg, R. D. Brodeur, and R. H. Condon. 2014. Linking human well-being and jellyfish: ecosystem services, impacts and societal responses. Front Ecol. Environ. 12:515–523.

Hays, G. C., M. R. Farquhar, P. Luschi, S. L. Teo, and R. M. Thys. 2009. Vertical niche overlap by two ocean giants with similar diets: Ocean sunfish and leatherback turtles. J. Exp. Mar. Biol. Ecol. 370(1–2):134–143.

Henschke N., D. A. Bowden, J. D. Everett, S. P. Holmes, R. J. Kloser, R. W. Lee, and I. M. Suthers. 2013. Salp-falls in the Tasman Sea: a major food input to deep-sea benthos. Mar Ecol Prog Ser 491:165–175. https://doi.org/10.3354/meps10450.

Henschke, N., J. D. Everett, A. J. Richardson, and I. M. Suthers. 2016a. Rethinking the role of salps in the ocean. Trends Ecol. Evol. 31(9):720–733.

Henschke, N., J. D. Everett, and I. M. Suthers. 2016b. An observation of two oceanic salp swarms in the Tasman Sea: *Thetys vagina* and *Cyclosalpa affinis*. Mar. Biodiv., Rec., 9(1), 21.

Henschke, N., E. A. Pakhomov, L. E. Kwong, J. D. Everett, L. Laiolo, A. R. Coghlan, and I. M. Suthers. 2019. Large vertical migrations of *Pyrosoma atlanticum* play an important role in active carbon transport. J. Geophys. Res: Biogeosci, 124, 1056–1070. https://doi.org/10.1029/2018JG004918

Hickey, B. M. 1979. The California Current system—hypotheses and facts. Progress in Oceanography, 8(4), pp.191–279.

Hobday, A. J., E. C. J. Oliver, A. Sen Gupta, J. A. Benthuysen, M. T. Burrows, M. G. Donat, N. J. Holbrook, P. J. Moore, M. S. Thomsen, T. Wernberg, and D. A. Smale. 2018. Categorizing and naming marine heatwaves. Oceanography. 31:162–173.

Hubbard Jr., L.T., and W. G. Pearcy. 1971. Geographic distribution and relative abundance of Salpidae off the Oregon coast. J. Fish. Res. Board Can. 28(12):1831–1836.

Iguchi, N. and H Kidokoro. 2006. Horizontal distribution of *Thetys vagina* Tilesius (Tunicata, Thaliacea) in the Japan Sea during spring 2004. Journal of Plankton Research, 28(6), pp.537–541.

Jacox, M. G., M. A. Alexander, N. J. Mantua, J. D. Scott, G. Hervieux, R. S. Webb, and F. E. Werner. 2018. Forcing of multiyear extreme ocean temperatures that impact California Current living marine resources in 2016. Bull. Am. Meteorol. Soc. 99:S27–S33.

Joh, Y., and E. Di Lorenzo. 2017. Increasing coupling between NPGO and PDO leads to prolonged marine heatwaves in the Northeast Pacific. Geophys. Res. Lett. 44:11,663–11,671, doi:10.1002/2017GL075930.

Jones, T. T., B. L. Bostrom, M. D. Hastings, K. S. Van Houtan, D. Pauly, and D. R. Jones. 2012. Resource requirements of the Pacific leatherback turtle population. PLoS One. 7(10):e45447.

King, J. R., V. N. Agostini, C. J. Harvey, G. A. McFarlane, M. G. G. Foreman, J. E. Overland, E. Di Lorenzo, N. A. Bond, and K. Y. Aydin. 2011. Climate forcing and the California Current ecosystem. ICES J. Mar. Sci. 68:1199–1216.

Kwong, L. E., E. A. Pakhomov, A. V. Suntsov, M. P. Seki, R. D. Brodeur, L. G. Pakhomova, and R. Domokos. 2018. An intercomparison of the taxonomic and size composition of tropical micronekton based upon several sampling gears. Deep-Sea Res. I 135:34–45.

Lavaniegos, B. E., and M. D. Ohman. 2003. Long-term changes in pelagic tunicates of the California Current. Deep-Sea Res. II. 50(14–16):2473–2498.

Lavaniegos, B. E., and M. D. Ohman. 2007. Coherence of long-term variations of zooplankton in two sectors of the California Current System. Prog. Oceanogr. 75(1):42–69.

Lebrato, M., and D. O. B. Jones. 2009. Mass deposition event of *Pyrosoma atlanticum* carcasses off Ivory Coast (West Africa). Limnol. Oceanogr. 45:1197–1209.

Lee, Y. W., and D. B. Sampson. 2009. Dietary variations in three co-occurring rockfish species off the Pacific Northwest during anomalous oceanographic events in 1998 and 1999. Fish. Bull. 107(4):510–522.

Li, K., A. J. Doubleday, M. D. Galbraith, and R. R. Hopcroft. 2016. High abundance of salps in the coastal Gulf of Alaska during 2011: A first record of bloom occurrence for the northern Gulf. Deep-Sea Res. Part II. 132:136–145.

Licandro, P., F. Ibañez, and M. Etienne. 2006. Long-term fluctuations (1974–99) of the salps *Thalia democratica* and *Salpa fusiformis* in the northwestern Mediterranean Sea: Relationships with hydroclimatic variability. Limnol. Oceanogr. 51(4):1832–1848.

Loeb, V. J., and J. A. Santora. 2012. Population dynamics of *Salpa thompsoni* near the Antarctic Peninsula: Growth rates and interannual variations in reproductive activity (1993–2009). Proces. Oceanogr. 96:93–107.

Love, M. S. 2011. Certainly more than you want to know about the fishes of the Pacific Coast. Santa Barbara. Really Big Press.

Lucas, C. H., and M. D. Dawson. 2014. What are jellyfishes and Thaliaceans and why do they bloom? In: Pitt, K.A., and Lucas, C.H. (Eds.) Chapter 2, Jellyfish Blooms. Springer, Dordrecht, Netherlands, pp. 9–44, doi:10.1007/978-94-007-7015-7_2.

Perissinotto, R., and E. A. Pakhomov. 1998. The trophic role of the tuniate *Salpa thompsoni* in the Antarctic marine ecosystem. J. Mar. Syst. 17:361–374.

Perissinotto, R., P. Mayzaud, P. D. Nichols, and J. P. Labat. 2007. Grazing by *Pyrosoma atlanticum* (Tunicata Thaliacea) in the south Indian Ocean. Mar. Ecol. Prog. Ser. 330:1–11.

Peterson, W. T., and J. E. Keister. 2002. The effect of a large cape on distribution patterns of coastal and oceanic copepods off Oregon and northern California during the 1998–99 El Niño-La Niña. Prog. Oceanogr. 53(2–4):389–411.

Peterson, W. T., and F. B. Schwing. 2003. A new climate regime in northeast Pacific ecosystems. *Geophysical research letters*, 30(17).

Purcell, J. E., S.-I. Uye, and W.-T. Lo, 2007. Anthropogenic causes of jellyfish blooms and their direct consequences for humans: a review. Mar. Ecol. Prog. Ser. 350: 153–174.

R Core Team. 2018. R: a language and environment for statistical computing [online]. *In* R Foundation for Statistical Computing, Vienna, Austria.

Ralston, S., J. C. Field, and K. M. Sakuma. 2015. Long-term variation in a central California pelagic forage assemblage. J. Mar. Syst. 146:26–37.

Sakuma, K.M., J. C. Field, N. J. Mantua, S. Ralston, B. B. Marinovic, and C. N. Carrion. 2016. Anomalous epipelagic micronekton assemblage patterns in the neritic waters of the California Current in Spring 2015 during a period of extreme ocean conditions. Calif. Coop. Ocean. Fish. Invest. Rep. 57:163–183.

Santora, J. A., S. Ralston, and W. J. Sydeman. 2011. Spatial organization of krill and seabirds in the central California Current. ICES J. Mar. Sci., 68(7), 1391–1402.

Santora, J. A., J. C. Field, I. D. Schroeder, K. M. Sakuma, B. K. Wells, and W. J. Sydeman. 2012. Spatial ecology of krill, micronekton and top predators in the central California Current: Implications for defining ecologically important areas. Prog. Oceanogr. 106:154–174.

Santora J. A., E. L. Hazen, I. D. Schroeder, S. J. Bograd, K. A. Sakuma, and J. C. Field. 2017. Impacts of ocean climate variability of pelagic forage species in an upwelling ecosystem. Mar Ecol Prog Ser. 580:205–220.

Schroeder, I. D., J. A. Santora, S. J. Bograd, E. L. Hazen, K. M. Sakuma, A. M. Moore, C. A. Edwards, B. K. Wells, and J. C. Field. 2019. Source water variability as a driver of rockfish recruitment in the California Current Ecosystem: implications for climate change and fisheries management. Can. J. Fish. Aquat. Sci. 76(6):950–960.

Silver, M.W. 1975. The habitat of *Salpa fusiformis* in the California Current as defined by indicator assemblages 1. Limnol. Oceanogr. 20(2):230–237.

SIO Pelagic Invertebrates Collection. CalCOFI Database. Accessed October 2019. San Diego. https://oceaninformatics.ucsd.edu/zoodb/secure/login.php.

Smith Jr., K.L., A. D. Sherman, C. L. Huffard, P. R. McGill, R. Henthorn, S. Von Thun, H. A. Ruhl, M. Kahru, and M. D. Ohman. 2014. Large salp bloom export from the upper ocean and benthic community response in the abyssal northeast Pacific: day to week resolution. Limnol. Oceanogr. 59(3):745–757.

Sutherland, K. R., H. L. Sorensen, O. N. Blondheim, R. D. Brodeur, and A. W. Galloway. 2018. Range expansion of tropical pyrosomes in the northeast Pacific Ocean. Ecology. 99(10):2397–2399.

Thompson, A. R., I. D. Schroeder, S. J. Bograd, E. L. Hazen, A. Leising, B. K. Wells, J. L. Largier, J. L. Fisher, K. Jacobson, S. Zeman, E. P. Bjorkstedt, R. R. Robertson, F. P. Chavez, M. Kahru, R. Goericke, S. McClatchie, C. E. Peabody, T. R. Baumgartner, B. E. Lavaniegos, J. Gomez-Vales, R. D. Brodeur, E. A. Daly, C. A. Morgan, T. D. Auth, B. J. Burke, J. Field, K. Sakuma, E. D. Weber, W. Watson, J. Coates, R. Schoenbaum, L. Rogers-Bennett, R. M. Suryan, J. Dolliver, S. Loredo, J. E. Zamon, S. R. Schneider, R. T. Golightly, P. Warzybok, J. Jahncke, J. A. Santora, S. A. Thompson, W. Sydeman, and S. R. Melin. 2018. State of the California Current 2017–18: Still not quite normal in the north and getting interesting in the south. Cali. Coop. Ocean. Fish. Invest. Reports 59:1–66.

Uye, S. I., and R. D. Brodeur, (Eds.). 2017. Report of Working Group 26 on jellyfish blooms around the North Pacific Rim: Causes and consequences. PICES Sci. Rep. 51:1–221.

van Soest, R. W. M. 1981. A monograph of the order Pyrosomatida (Tunicata, Thaliacea). Journal of Plankton Research, 3(4), 603–631.

Wells, B. K., I. D. Schroeder, J. A. Santora, E. L. Hazen, S. J. Bograd, E. P. Bjorkstedt, V. J. Loeb, S. McClatchie, E. D. Weber, W. Watson, A. R. Thompson, W. T. Peterson, R. D. Brodeur, J. Harding, J. Field, K. Sakuma, S. Hayes, N. Mantua, W. J. Sydeman, M. Losekoot, S. A. Thompson, J. Largier, S. Y. Kim, F. P. Chavez, C. Barceló, P. Warzybok, R. Bradley, J. Jahncke, R. Georicke, G. S. Campbell, J. A. Hildebrand, S. R. Melin, R. L. DeLong, J. Gomez-Valdes, B. Lavaniegos, G. Gaiola-Castro, R. T. Golightly, S. R. Schneider, N. Lo, R. M. Suryan, A. J. Gladics, C. A. Horton, J. Fisher, C. Morgan, J. Peterson, E. A. Daly, T. D. Auth, and J. Abell. 2013. State of the California Current 2012–13: No such thing as an 'average' year. California Cooperative Oceanic Fisheries Investigations Reports. 54:37–71.

Wells, B. K., J. A. Santora, M. J. Henderson, P. Warzybok, J. Jahncke, R. W. Bradley, D. D. Huff, I. D. Schroeder, P. Nelson, J. C. Field, and D. G. Ainley 2017. Environmental conditions and prey-switching by a seabird predator impact juvenile salmon survival. J Mar Sys. 174:54–63.

Zuercher, R., and A. W. Galloway. 2019. Coastal marine ecosystem connectivity: pelagic ocean to kelp forest subsidies. Ecosphere. 10(2):e02602.