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High abundance of salps in the coastal Gulf of Alaska during 2011: A first record of bloom occurrence for the northern Gulf

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ABSTRACT

Atypical high abundances of two salp species occurred in the coastal Gulf of Alaska during 2011. *Salpa aspera* dominated numerically in aggregate form during spring, and became uncommon during summer, while *Cyclosalpa bakeri* increased from low during spring to high abundance during summer. Both species were absent, or nearly so, by fall. *C. bakeri* abundance was positively correlated to surface temperature in spring and summer, and both species abundances were negatively correlated to chlorophyll *a*. The proportion of aggregate forms of both species was higher than that of solitary forms during spring and summer. The length–frequency of *S. aspera* aggregate individuals ranged primarily from 10 to 50 mm, and solitary forms reached 130 mm, while *C. bakeri* aggregates were 10–25 mm, with solitary forms up to 75 mm. Estimated biomass of *S. aspera* was $0.35 \pm 0.64 \text{ mg C m}^{-3}$ in southeastern Alaska during spring then decreased to $0.03 \pm 0.12 \text{ mg C m}^{-3}$ during summer. Estimated biomass of *C. bakeri* was $0.03 \pm 0.06 \text{ mg C m}^{-3}$ over the entire sampling domain during spring, then rose to $0.15 \pm 0.25 \text{ mg C m}^{-3}$ during summer. The volume of water filtered daily by *S. aspera* was estimated to be up to 17% of the 200 m water column at some stations during spring, but only up to ~3.5% during summer. Substantially higher grazing impact was possible if animals were largely confined to the surface mixed layer (typically 20–30 m thick). The average volume filtrated was higher during spring for *S. aspera*, but for *C. bakeri* it was higher during summer. We propose that the combined effect of the northward transport of seed populations, their rapid biomass increase through asexual reproduction, and the high clearance rate of salps contributed to atypically low chlorophyll *a* in the Gulf of Alaska during spring and summer of 2011. This unusual event impacted ecosystem function during 2011, and might be expected to increase in frequency as the Gulf continues to respond to climate variations.

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1. Introduction

Salps are gelatinous planktonic tunicates with a life history alternating between sexual (aggregate) and asexual (solitary) stages (Godeaux et al., 1998). They are usually scarce within the zooplankton, but sometimes form dense swarms (so called "salp blooms", $> 1 \text{ ind. m}^{-3}$) under favorable conditions (Andersen, 1998). Salps have some of the highest clearance rates of any zooplankton – up to several liters $\text{h}^{-1} \text{ salp}^{-1}$ – with particularly high feeding efficiency on small phytoplankton and bacteria (Alldredge and Madin, 1982; Madin and Purcell, 1992; Madin and Deibel, 1998), although larger cells can also be consumed by many species (e.g. Vargas and Madin, 2004). During intense blooms or swarms

when abundances can exceed 100 s m^{-3} , they can consume over 100% of the daily primary production (Huntley et al., 1989; Madin et al., 1997; Hereu et al., 2006).

The combination of high feeding rates (Madin and Deibel, 1998), asexual budding in their life cycle (Alldredge and Madin, 1982), and rapid growth rates (Heron, 1972; Heron and Benham, 1984) enables salps to increase their population sizes explosively when conditions are favorable. Salp swarms have been reported for several species, notably for *Salpa fusiformis*, *S. thompsoni*, *S. aspera*, *S. maxima*, *Thetys vagina*, *Iasis zonaria*, *Thalia democratica*, and *Cyclosalpa bakeri*. Such swarms have been recorded in many regions of the world's oceans, including the western Mediterranean Sea (Ménard et al., 1994), northwestern Spain (Huskin et al., 2003), the Bermuda region (Madin et al., 1996; Stone and Steinberg, 2014), and the slope waters off the eastern US (Wiebe et al., 1979; Deibel, 1985; Paffenhöfer et al., 1995; Madin et al., 2006; Deibel and Paffenhöfer, 2009). Salp blooms are also common in the

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Pacific Ocean, such as off southeast Australia (Heron and Benham, 1984; Zeldis et al., 1995) and near Japan (Tsuda and Nemoto, 1992; Iguchi and Kidokoro, 2006). High abundances are common for some salps at high latitudes, especially in the Southern Ocean (Atkinson et al., 2004; Loeb and Santora, 2012) and the subarctic Pacific (Purcell and Madin, 1991; Madin and Purcell, 1992; Madin et al., 1997).

The mechanisms controlling the frequency and distribution of salp blooms are not fully understood, except in a few specific cases. In general, the reported dense swarms have occurred mainly in shelf-break areas or oceanic oligotrophic regions. The oligotrophic Bermuda region has long been considered a “sporadic hot-spot” for salp swarms (Madin et al., 1996), where long-term fluctuations of salp abundance and biomass are influenced by mesoscale eddies and climate oscillations (Stone and Steinberg, 2014). In the oligotrophic western Mediterranean strong stratification reduced the probability of high abundances of salps, while strong winds facilitated the development of blooms (Ménard et al., 1994). Reduced abundance of salps in the California Current was also attributed to long-term increases in thermal stratification that weakened eddy kinetics and thereby reduced transport of seed populations into the current (Lavanegos and Ohman, 2003, 2007). *Thalia* populations near the southeastern Australia shelf-margin appeared anti-correlated with non-salp zooplankton and related to the availability of preferred food (Henschke et al., 2014), suggesting factors that enhance food in an oligotrophic habitat are important.

Similarly, other shelf-break regions seem to be “hot spots” for the occurrence and development of salp blooms. Deibel (1985) reported that blooms of thaliaceans colonized the mixing waters of the northeast US Gulf Stream through their rapid response to physical and phytoplankton dynamics, as later confirmed by Paffenhöfer et al. (1995). Maximum abundances of salps were found at the shelf-break front by a poleward saline intrusion containing abundant small phytoplankton off northeast Spain (Huskin et al., 2003). Near Japan, salp blooms have occurred where warm waters interact with subarctic fronts (Tsuda and Nemoto, 1992; Iguchi and Kidokoro, 2006). An understanding of the mechanisms influencing salps in shelf and slope waters requires consideration of mesoscale processes, food availability and potential seed populations. It is notable that while salps, specifically *C. bakeri*, have been studied at Ocean Station P in the Subarctic Pacific (Purcell and Madin, 1991; Madin and Purcell, 1992; Madin et al., 1997), published work has been confined to waters of the central gyre rather than the shelf-break habitat that may also favor population blooms.

In contrast to 15 years of zooplankton sampling in the northern GOA with salps rarely observed (i.e. a few individuals in < 0.1% of the samples examined), during the spring and summer of 2011 we encountered high occurrences and abundances of salps during broad-scale surveys conducted as part of the Gulf of Alaska Integrated Ecosystem Research Program (GOAIERP). With 2011 producing atypical observations at multiple trophic levels (e.g. Strom et al., this issue), it is

difficult to know if this usual occurrence of salps was driven by the same forces, or itself a significant factor in disrupting the normal phytoplankton–crustacean–zooplankton–fish trophic pathway (Huntley et al., 1989; Paffenhöfer et al., 1995; Atkinson et al., 2004). The objective of this study was to examine the species composition, abundance and size/stage of salps encountered during the seasonal surveys and to understand how the occurrence and development of a salp bloom might have been influenced by physical and biological conditions in the GOA.

2. Materials and methods

2.1. Study site

The continental shelf of the Gulf of Alaska (GOA) is a highly productive marine system and sustains a number of important fisheries resources (Weingartner et al., 2002). Variability in meteorology, bathymetry, currents, and eddies, as well as Ekman transport, contributes to the GOA's extremely productive waters across its continental shelf and slope (Wickett, 1967; Okkonen et al., 2003; Stabeno et al., 2004; Ladd et al., 2005). The Alaska Current and Alaskan Stream are vigorous circulation features that provide alongshore pathways for planktonic organisms (Weingartner et al., 2002; Batten and Crawford, 2005; Batten and Freeland, 2007). Cross-shelf exchange processes are important for zooplankton distribution with the surface-layer transport more seaward in summer and more shoreward in winter (Mackas and Coyle, 2005). Since 1970 water column temperatures have risen more than 0.8 °C and vertical density stratification has also increased in the northern GOA (Royer and Grosch, 2006). Copepods, euphausiids and larvaceans typically dominate the abundance and biomass of filter-feeding zooplankton in the GOA (Coyle and Pinchuk, 2005; Liu and Hopcroft, 2008; Pinchuk et al., 2008; Doubleday and Hopcroft, 2015), and are important prey for various larval fishes.

2.2. Sampling

Broad-scale surveys in the continental shelf of GOA were undertaken during April/May, July/August and September/October of 2011, representing the oceanographic spring, summer and fall seasons, respectively (Table 1). Based on the topography and the sampling locations, the study area was divided into three domains: (1) the eastern GOA, along Baranof Island with a narrow shelf; (2) the central GOA, from Yakutat Bay to Kayak Island; (3) the western GOA, from Kenai Peninsula to Kodiak Island with a broad shelf (Fig. 1). Sampling occurred continuously, without regard to time of day. The number of stations examined varied between cruises (Table 1). The central region in particular was only sampled well during spring, so our focus was primarily to compare the eastern and western regions.

Table 1
Details of oceanographic cruises in the coastal Gulf of Alaska during 2011: sampling date range (mm/dd), number of stations sampled, stations examined, and stations containing salps.

| Region | Season | Cruise | Sampling date | Stations sampled | Stations examined | Stations with salps |
|---------|--------|-------------|---------------|------------------|-------------------|---------------------|
| Eastern | Spring | TN263/1TT11 | 05/03–05/10 | 58 | 33 | 26 |
| | Summer | 1NWE11 | 07/03–07/17 | 51 | 29 | 20 |
| | Fall | 3NWE11 | 09/08–09/22 | 37 | 26 | 0 |
| Central | Spring | TN263/1TT11 | 05/10–05/16 | 45 | 44 | 36 |
| | Summer | 2NWE11 | 08/02–08/04 | 6 | 6 | 5 |
| | Fall | 3NWE11 | 9/07–09/22 | 4 | 4 | 3 |
| Western | Spring | TXS11 | 04/28–05/05 | 47 | 47 | 19 |
| | Summer | 2NWE11 | 08/05–08/21 | 47 | 25 | 18 |
| | Fall | 4NWE11 | 09/26–10/08 | 37 | 22 | 0 |

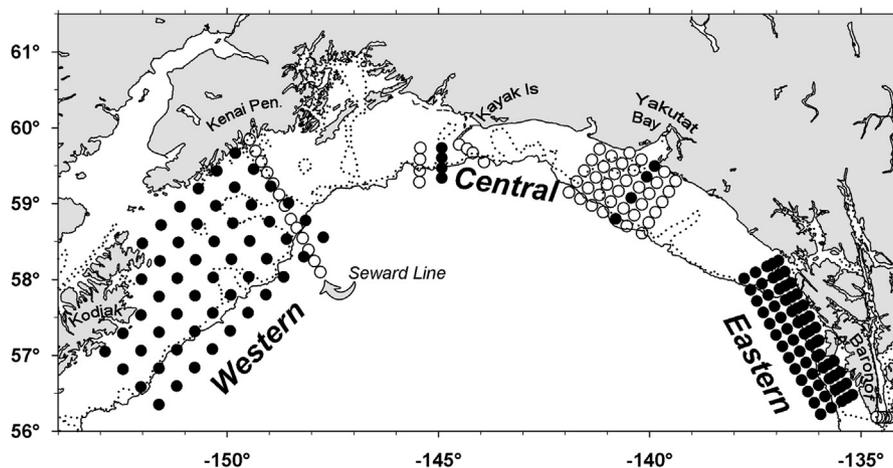


Fig. 1. Sampling stations in the eastern, central and western regions of the coastal Gulf of Alaska during 2011. The 200 m contour is shown as a dotted line, the 500 m contour as a solid line.

On each cruise, a Seabird SBE 9/11 or SBE 25 CTD profiled the water column to determine temperature and salinity, with a rosette of 5-L Niskin bottles used for water sampling (Stabeno et al., this issue; plus unpublished). Water samples for the measurement of chlorophyll *a* (Chl-*a*) concentrations were collected every 10 m from 50 m to the surface, filtered at low pressure onto GF/F filters, and stored frozen for post-cruise fluorometric analysis (Parsons et al., 1984). During the spring cruises, chlorophyll was size-fractionated through 20 μm pore-size polycarbonate filters to determine biomass partitioning above and below 20 μm at all stations, then extracted immediately (see Strom et al., this issue for details). There was no chlorophyll size-fractionation during summer and fall, except along the Seward Line.

The zooplankton samples examined for salps were collected with a Bongo net (60 cm mouth diameter, 505 μm mesh) towed obliquely from just above the bottom (or to a maximum of 200 m depth) to the surface while underway at ~ 2 knots. The nets were equipped with calibrated General Oceanics flowmeters to determine the volume of water filtered in each tow. All samples were preserved in a 10% formalin-seawater solution for later analysis.

2.3. Processing

A subset of more than 50% of the stations sampled were examined for salps for each spring and summer cruise (Table 1). For the fall cruises, no salps were found with the exception of 3 stations in the central region (Table 1). Using the preserved samples, the aggregate and solitary forms of salp species were counted, identified and measured separately (Table 1). Body length of each specimen was measured as the distance from the anterior to posterior apertures. Carbon weight was estimated from body-length using species-specific regression equations (*C. bakeri* – Madin and Purcell, 1992; *S. aspera* – Madin and Deibel, 1998, their Table 5.3). Species-specific filtration rates were available for *C. bakerii* (as two different equations in Madin and Purcell, 1992), however for *S. aspera* filtration rates were only available for congeneric species (*S. fusiformis* – Andersen, 1985; *S. maxima* and *S. cylindrica* – Madin and Cetta, 1984; *S. maxima* – Harbison and Gilmer, 1976; *S. thompsoni* – Huntley et al., 1989). For *S. aspera*, we employed only the upper filtration rate equations for *S. maxima* and *S. thompsoni*. In all cases we applied each equation to both body forms, creating a range of the values predicted by each. Although the total length of salps preserved in formaldehyde has been shown to decrease over time, we did not correct salp length, so the carbon biomass estimates should be considered conservative. Salp abundance is expressed as number of individuals

per 100 m^3 , and carbon biomass as mg C m^{-3} . Length–frequency distributions were based on the total number of measured individuals for spring and summer cruises.

2.4. Data analyses

A Kruskal–Wallis ANOVA was used to examine physical and biological parameters, followed by Dunn's multiple comparison test, with a significance level of $P < 0.05$. An independent-samples *T*-test was conducted to examine significant differences between the ≥ 20 and < 20 - μm size fractions of Chl-*a* concentration in spring. Salp abundances were log-transformed and compared to environmental variables (surface sea temperature, salinity, and Chl-*a*) using a Pearson correlation test.

3. Results

3.1. Environmental conditions

The eastern GOA region was characterized by relatively higher temperature and lower salinity in comparison to the western region, with the exception of salinity during summer (Fig. 2). Chl-*a* in the eastern region was significantly lower than that of the western region during spring ($P < 0.05$) and summer ($P < 0.001$) (Fig. 2). The ≥ 20 - μm and < 20 - μm Chl-*a* concentrations differed significantly in spring ($P < 0.001$), with the smaller size-fraction representing more than 90% of total Chl-*a* in the eastern region, 60% in the central, but only 32% in the western region.

3.2. Species composition and stages

Two species of salps were identified: *S. aspera* and *C. bakeri*. Both species occurred in spring and summer, with salps present in 60–90% of stations examined, then disappeared in both the eastern and western regions during fall (Table 1). Both life forms (aggregate and solitary) were encountered. The aggregate form generally dominated both species in spring and summer, contributing $> 90\%$ of their abundance (Table 2). Although *C. bakeri* were present in the central region during the fall cruise, its solitary form dominated at that time (Table 2), which suggested that it was not actively reproducing.

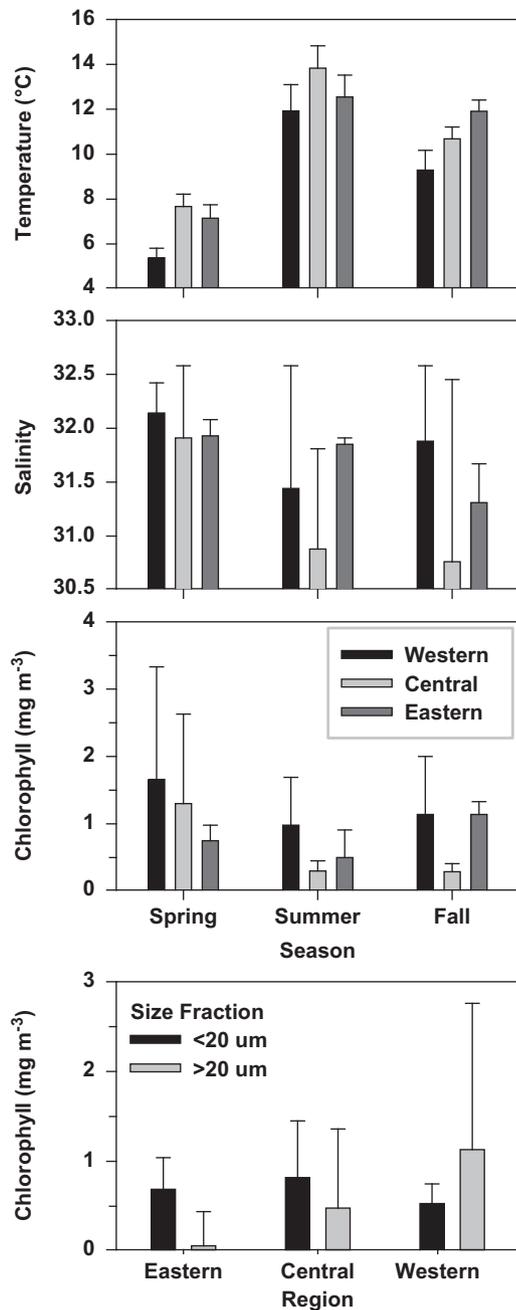


Fig. 2. Surface temperature, salinity and chlorophyll-*a* concentration by season, and size-fractionated chlorophyll-*a* concentration by region for the coastal Gulf of Alaska during 2011. Values are mean \pm SD.

3.3. Length–frequency distribution

Length–frequency distributions of the two body forms of each species varied between spring and summer (Fig. 3). The lengths of *S. aspera* aggregates were broadly distributed from ~5 to 75 mm during spring with 88% of individuals within the range of 10–60 mm, while the fewer individuals collected during summer were generally between 30 and 50 mm. In spring, some small aggregate individuals were found in chains in the eastern region, but in general chains were fragmented by sampling or preservation. The size range of *S. aspera* solitary forms was broad, from 10 to 130 mm. The lengths of *C. bakeri* aggregate forms ranged mainly from 10 to 25 mm; individuals within this range accounted for 80% and 75% of total individuals during spring and summer, respectively. For the *C. bakeri* solitary form more than 70% of the individuals during the spring had lengths

in the 30–70 mm range, while the summer length range was between 10 and 50 mm.

3.4. Abundance and biomass

During spring, mean total salp abundance (\pm SD) was 12.4 ± 17.1 ind.100 m⁻³, ranging from 0 to 70 ind.100 m⁻³. Mean abundance was 14.2 ± 24.9 ind.100 m⁻³ during summer with a maximum observation of 121 ind.100 m⁻³, approaching the accepted definition of salp bloom concentrations. During fall, salps were found only in the central region where abundance was low, 0.2 ± 0.6 ind.100 m⁻³. During spring, salp abundance was higher in the eastern region than in the western region ($P < 0.001$), while during summer it was higher in the western than that in the eastern (Fig. 4), although not significantly. Salps were more abundant in the slope waters than in the shelf waters during spring ($P < 0.001$), but not during summer ($P = 0.309$) or fall ($P = 0.961$). The carbon biomass of the two species varied during spring and summer, although high variability in individual sizes precluded statistical differentiation. The average biomass of *S. aspera* was 0.35 ± 0.64 mg C m⁻³ during spring and 0.03 ± 0.12 mg C m⁻³ during summer, with higher values in the eastern region during spring. For *C. bakeri*, average biomass during spring was 0.03 ± 0.06 mg C m⁻³, but increased during summer to 0.15 ± 0.25 mg C m⁻³. Its highest biomass was found in the central and western regions during summer. *S. aspera* biomass was higher in the slope waters, while *C. bakeri* was somewhat higher on the shelf during summer.

The abundance distribution of *S. aspera* differed from that of *C. bakeri* during spring and summer (Fig. 5). *S. aspera* dominated with 79% of total salp abundance during spring, but with distribution mainly confined to the eastern and central regions, at which time it dominated the zooplankton community biomass (as displacement volume). Its abundance decreased to only sporadic occurrence in the eastern and western regions during summer. Although *C. bakeri* was distributed widely during spring it increased to higher abundance during summer, accounting for 96% of the total. During fall *C. bakeri* occurred only in the central region and with low abundance. The relationship between the abundance of *S. aspera* and Chl *a* concentration was negative during spring (≥ 20 μm Chl *a*), and negative for *C. bakeri* during summer. There was a significant positive relationship between *C. bakeri* abundance and temperature (Table 3).

3.5. Estimation of clearance and filtration rates

The estimated values for clearance rate and volume of water filtered showed broad ranges based on equations from different sources, with equations from Madin and Cetta (1984) giving the highest rate, and those of Huntley et al. (1989) conducted at 1 °C giving the lowest estimates (Figs. 6 and 7). The clearance rates of *S. aspera* individuals varied widely due to the broad size range of individuals within the population, but in many cases they were estimated to be several liters per hour. Large solitary individuals appeared capable of filtering 10–100 s of liters per day (Fig. 6). *C. bakeri* had lower filtration rates than *S. aspera*, typically 0.1–1.0 L h⁻¹ (Fig. 6), partly as a consequence of its generally smaller body size relative to *S. aspera*. The estimated volume of water filtered at each station by *S. aspera* differed seasonally, with higher values during spring (typically 1–100 L d⁻¹ = 0.1–10% of water volume d⁻¹) than summer (typically < 1 L d⁻¹), while *C. bakeri* filtration increased from < 1 L d⁻¹ during spring to 0.1–8 L d⁻¹ during summer (Fig. 7). High filtration rates for *S. aspera* occurred primarily in the eastern and central regions during spring, while high filtration rates for *C. bakeri* occurred mainly in the central and western regions during summer.

Table 2

The percentage of sexual (aggregate) and asexual (solitary) life forms of *Salpa aspera* and *Cyclosalpa bakeri* encountered during oceanographic sampling in the Gulf of Alaska during 2011.

| Region | Season | <i>Salpa aspera</i> | | | <i>Cyclosalpa bakeri</i> | | |
|---------|--------|---------------------|---------------|--------------|--------------------------|---------------|--------------|
| | | Number | Aggregate (%) | Solitary (%) | Number | Aggregate (%) | Solitary (%) |
| Eastern | Spring | 1728 | 95.9 | 4.1 | 266 | 96.6 | 3.4 |
| | Summer | 62 | 98.4 | 1.6 | 274 | 89.0 | 11.0 |
| | Fall | 0 | 0 | 0 | 0 | 0 | 0 |
| Central | Spring | 1803 | 97.4 | 2.6 | 610 | 97.9 | 2.1 |
| | Summer | 0 | 0 | 0 | 507 | 90.9 | 9.1 |
| | Fall | 0 | 0 | 0 | 20 | 25.0 | 75.0 |
| Western | Spring | 174 | 93.7 | 6.3 | 179 | 97.8 | 2.2 |
| | Summer | 45 | 100 | 0 | 1012 | 91.8 | 8.2 |
| | Fall | 0 | 0 | 0 | 0 | 0 | 0 |

Aggregate: aggregate form; Solitary: solitary form.

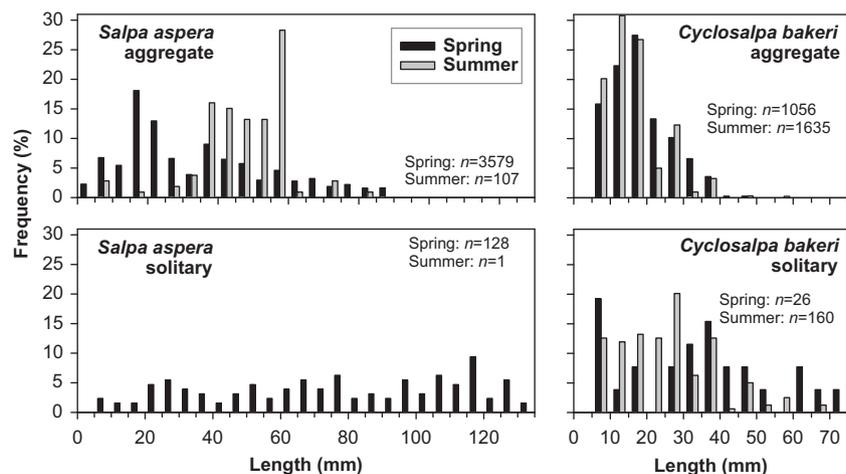


Fig. 3. Length frequency distribution of *Salpa aspera* and *Cyclosalpa bakeri* for aggregate and solitary forms in the Gulf of Alaska during 2011.

4. Discussion

4.1. Salps in the northern North Pacific

This study is the first examination of salps in the continental shelf and slope waters of the GOA, showing their seasonal dispersion from southeastern Alaska and subsequent decline in the fall. The near absence of salps in the 18-year Seward Line time series (Hopcroft and Coyle, unpublished) highlights the unusual nature of the salp occurrence during 2011 in the northern GOA. By global standards however, and compared to elsewhere in the North Pacific, the abundance observed during this study's "bloom" was low. In warm waters of Japan at 40°N, abundances of up to 40 ind. m⁻³ (4000 ind.100 m⁻³) have been reported (Tsuda and Nemoto, 1992), with high biomass also common off southern California (Lavaniegos and Ohman, 2003). Abundances of 10,000 ind.100 m⁻³ have been reported in the Central GOA Gyre at Ocean Station P at temperatures similar to those observed during this study's summer (Madin et al., 1997). Perhaps the most useful comparison comes from the Vancouver Island continental margin (e.g. Mackas et al., 2004, 2007, plus unpublished data), where samples have been collected in the upper 250 m by 230 μm mesh nets at 12–40 stations 4–5 times annually since 1990 (~4000 distinct samples). There, *S. aspera* periodically blooms to abundances as high as 3000 ind.100 m⁻³, and *C. bakeri* has approached 600 ind.100 m⁻³ (Fig. 8), with blooms most frequent during summer and fall. Despite our lower peak abundances, it is notable

that the Vancouver Island average abundances are similar to those of this study.

Our abundance and filtration estimates are based on the assumption that salps are homogeneously distributed throughout the water column. Stratification, phytoplankton biomass and primary productivity all occur in a relatively thin mixed layer (~30 m deep) in the Gulf of Alaska (e.g. Strom et al., 2007, this issue; Coyle et al., 2012), with even the subsurface chlorophyll maximum typically above 50 m. Thus, if salps were concentrated in the upper 30–50 m where most chlorophyll occurs (as observed by Tsuda and Nemoto, 1992), then abundances and filtration rates in the upper mixed layer could be from 4 to 10 times higher than our current estimates suggest. Unfortunately we cannot address this question because our stratified sampling was restricted to the Seward Line in spring and fall when salp abundance was low in that area.

Within our study we found distinct differences in the temporal and spatial distributions of *S. aspera* and *C. bakeri* that appeared to be related to environmental conditions. Given our perception of the unusual nature of the bloom, three main items of interest emerged: (1) the origin of the salp bloom, i.e. the source population; (2) the conditions that favored their widespread occurrence in 2011; and (3) the potential ecosystem impacts of the bloom.

4.2. Source population

Salpa aspera has a wide distribution from about 45°N to 45°S in all three oceans (van Soest, 1998). In some ecosystems, it has been shown to perform diel vertical migration (DVM) of at least 800 m

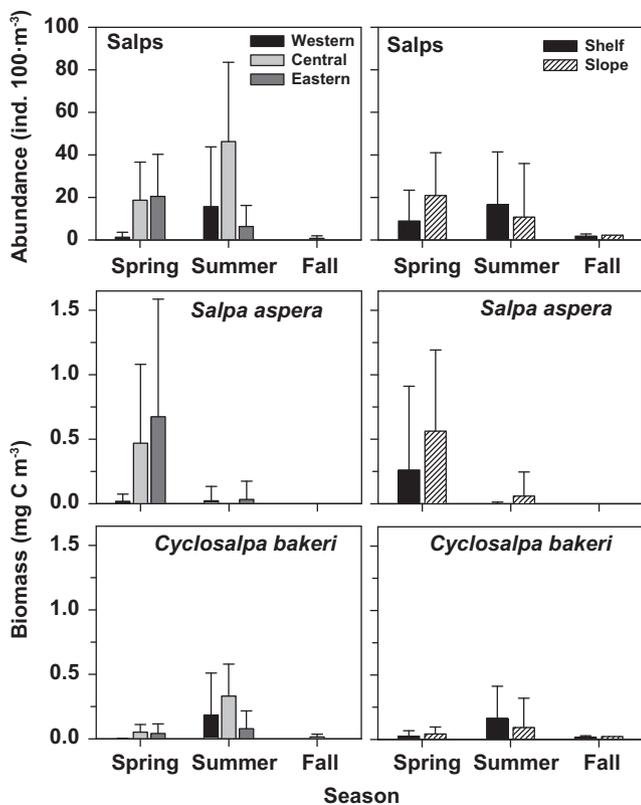


Fig. 4. Seasonal variations of salp abundance (ind.100 m⁻³) within regions and habitats of the Gulf of Alaska during 2011. Values are mean \pm SD.

(Wiebe et al., 1979; Madin et al., 2006), although the occurrence of DVM in our study could not be established due to our sampling methodology. *C. bakeri* is very common in northeastern parts of the Pacific (Purcell and Madin, 1991; Madin and Purcell, 1992; Madin et al., 1997; Lavaniegos and Ohman, 2003, 2007; Hereu et al., 2006), but *C. bakeri* DVM has only been reported over depths of 60 m (Purcell and Madin, 1991). The two genera probably respond differently to environment conditions (as suggested by Fig. 8). *C. bakeri* is occasionally abundant in the subarctic Pacific (Purcell and Madin, 1991; Madin and Purcell, 1992). In the California Current where it is more common fluctuations in *C. bakeri* abundance appear related to climate, with it being present during cool phases

Table 3

Relationships between log abundances of *Salpa aspera* and *Cyclosalpa bakeri* and environmental variables in the Gulf of Alaska during 2011 identified using Pearson correlation.

| Factor | Temperature | Salinity | Chla | |
|----------------------------|-------------|----------|--------------|-------------------|
| | | | < 20 μ m | \geq 20 μ m |
| Spring | | | | |
| <i>S. aspera</i> abundance | n.s. | n.s. | n.s. | 0.305** |
| <i>C. bakeri</i> abundance | 0.424*** | n.s. | n.s. | n.s. |
| Summer | | | | |
| <i>S. aspera</i> abundance | n.s. | n.s. | n.s. | |
| <i>C. bakeri</i> abundance | 0.448** | n.s. | -0.313* | |

n.s.—not significant.

* $p < 0.05$.

** $p < 0.01$.

*** $p < 0.001$.

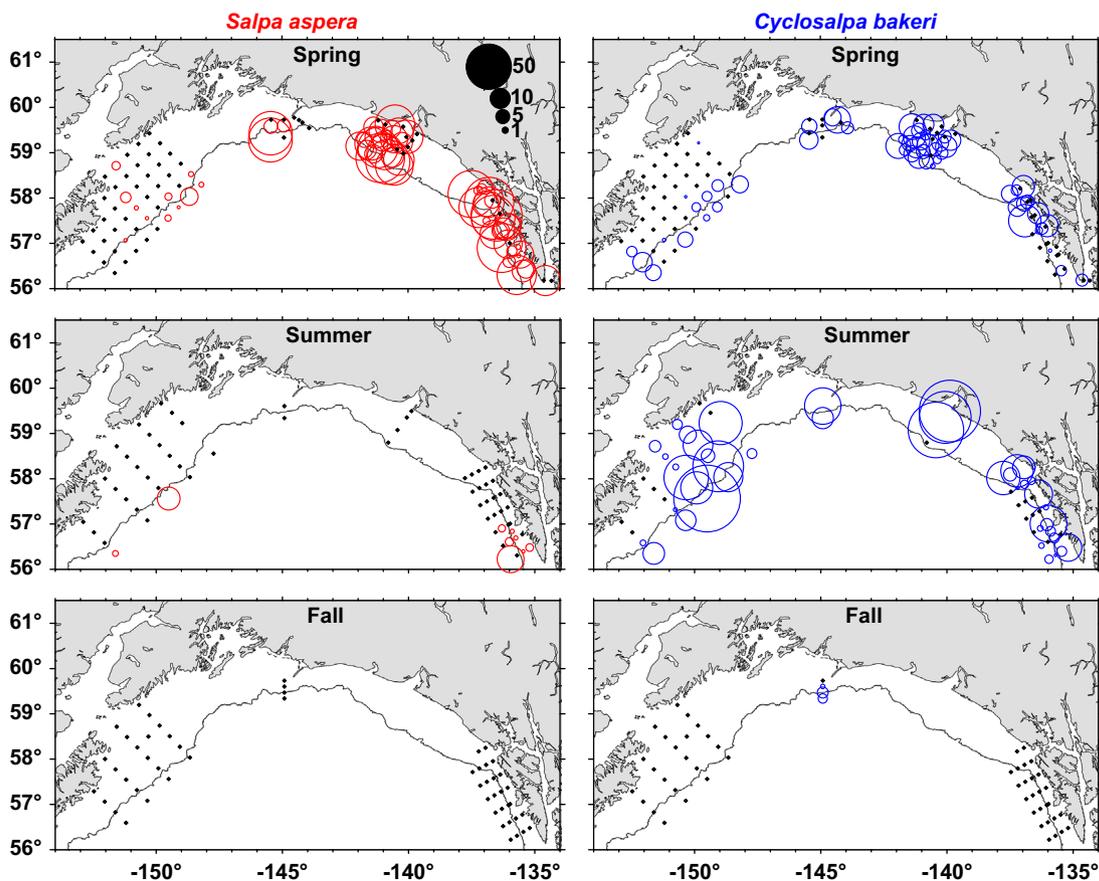


Fig. 5. Abundance distribution of *Salpa aspera* and *Cyclosalpa bakeri* in the Gulf of Alaska during spring, summer and fall of 2011 (ind.100 \cdot m⁻³).

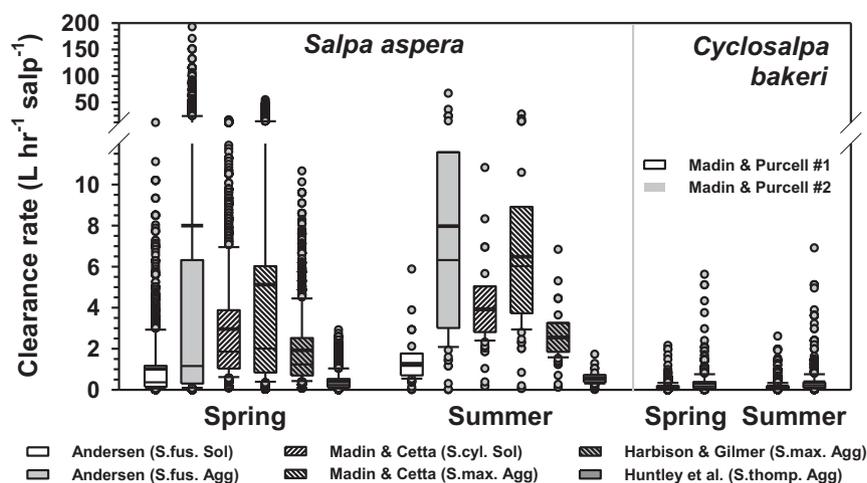


Fig. 6. Estimated filtration rate ($L\ hr^{-1}\ salp^{-1}$) of *Salpa aspera* and *Cyclosalpa bakeri* in the Gulf of Alaska during spring and summer of 2011, based on equations in Andersen (1985), Madin and Cetta (1984), Harbison and Gilmer (1976), Huntley et al. (1989) and Madin and Purcell (1992). The solid line through the box is the sample median, dotted line is the mean, limits of the boxes are the 25th and 75th percentile. Whiskers are the 10th and 90th percentiles and the single points are outliers.

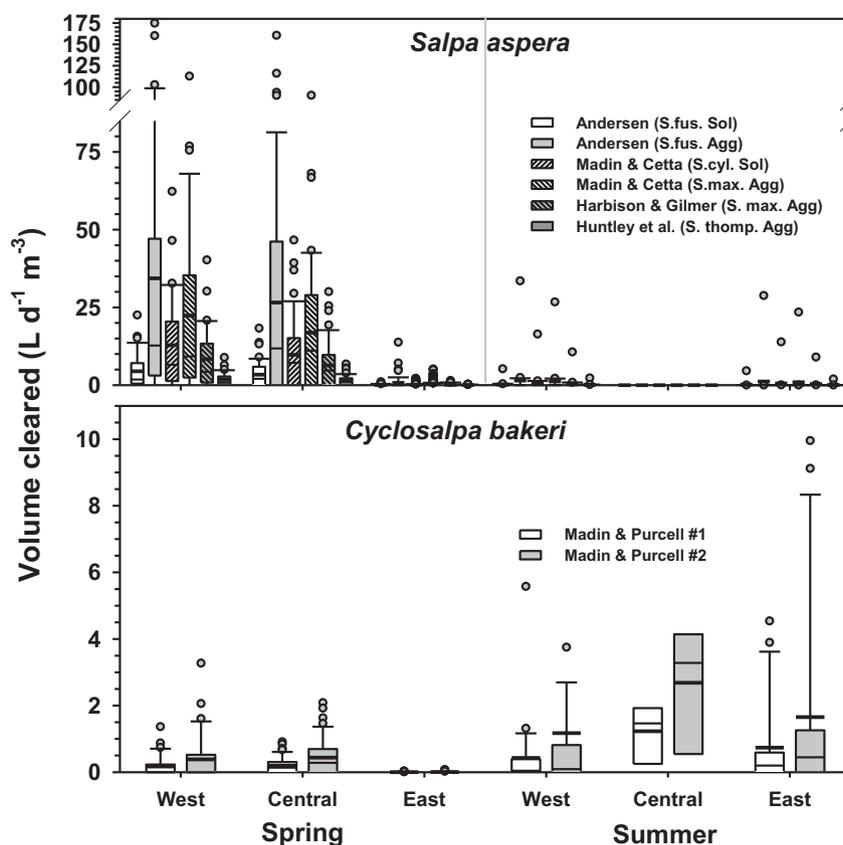


Fig. 7. Estimated volume of water ($L\ d^{-1}\ m^{-3}$) filtered by *Salpa aspera* and *Cyclosalpa bakeri* in the Gulf of Alaska during spring and summer of 2011. The solid line through the box is the sample median, dotted line is the mean, limits of the box are the 25th and 75th percentile. Whiskers are the 10th and 90th percentiles and the single points are the outliers.

and absent during the warm phases (Lavaniegos and Ohman, 2003). Both species have been recorded only rarely in the northern GOA, but have been more commonly observed near the transition zone at the bifurcation of the North Pacific Current to the south (Mackas and Galbraith, 2002; Mackas et al., 2005; Mackas and Coyle, 2005).

The “upstream” conditions for the northern Gulf of Alaska (i.e. conditions in the waters off British Columbia) are routinely monitored by the two major Canadian oceanographic time series: Line P

(from Victoria, British Columbia, to Ocean Station P in the central gyre) and the Vancouver Island continental margin (see above), both of which are sampled several times per year. In the North Pacific Current bifurcation region to the west of Vancouver Island, *S. aspera* and *C. bakeri* were not abundant during 2011 but a moderate peak of *S. aspera* was apparent during 2010 (Fig. 8). *C. bakeri* was present at many stations in 2010 albeit at low abundances. In fall (September/October) of 2010, *S. aspera* and *C. bakeri* were present with an average of $31.6\ ind.100\ m^{-3}$ and $0.7\ ind.100\ m^{-3}$,

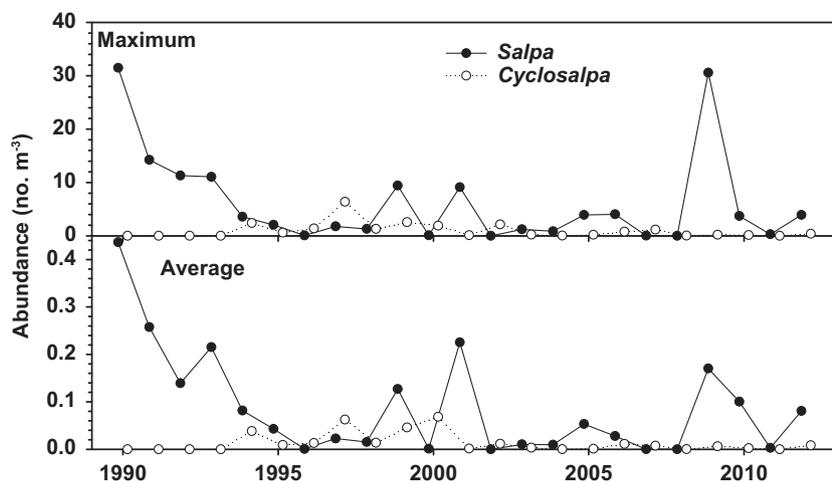


Fig. 8. Annual variation of *Salpa aspera* and *Cyclosalpa bakeri* abundance (ind. 100 m^{-3}) west of Vancouver Island, Canada, 1990–2012. Both mean (lower panel) and maximum (upper panel) abundance presented. Figure is based on ~4000 samples collected by broad-scale surveys over 23 years with 4–5 cruises annually (Galbraith, unpublished).

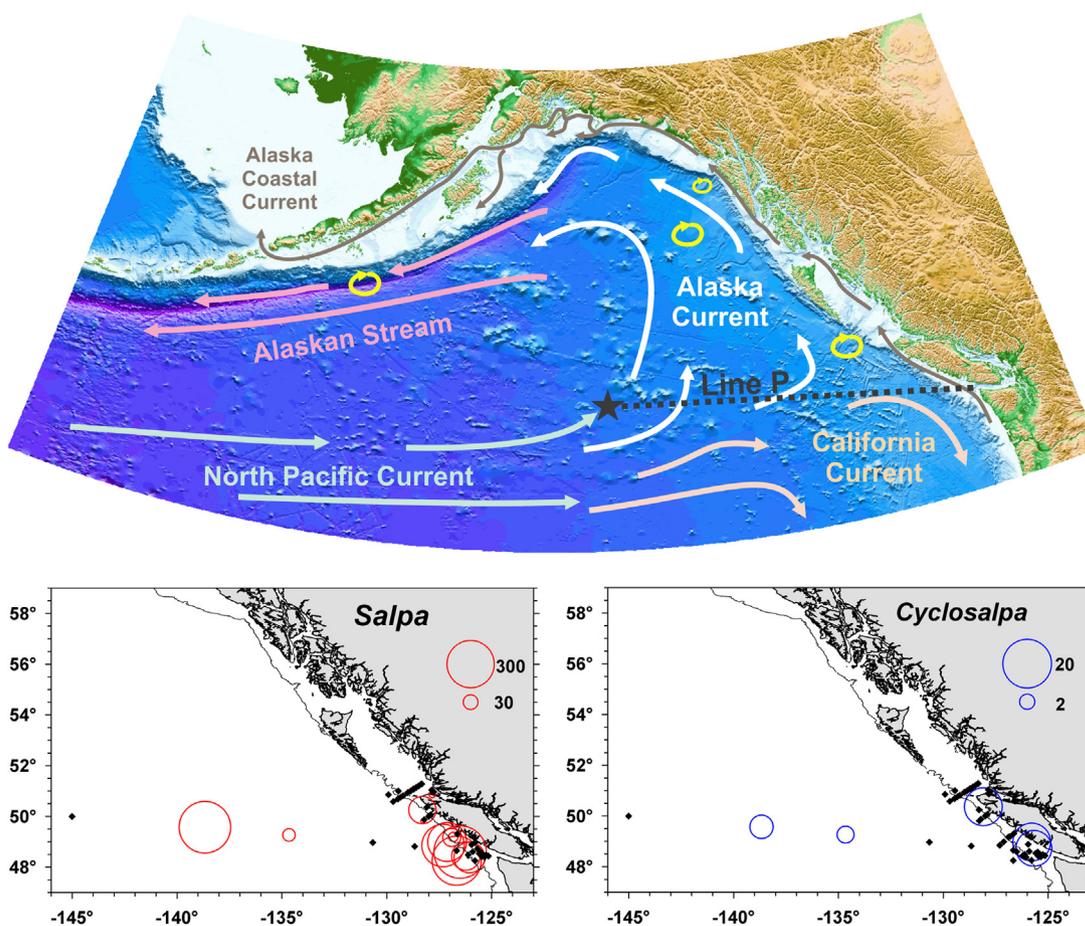


Fig. 9. Schematic of the general circulation of the Gulf of Alaska (after Weingartner et al., 2002) and spatial distribution of salps during fall of 2010 (ind. 100 m^{-3}). Star shows the location of Ocean Station Papa (Station P) in the subarctic Pacific and the dashes represent Canada's sampling Line P.

respectively, and corresponding maxima of 371 and 12 ind. 100 m^{-3} respectively in the waters surrounding Vancouver Island (Fig. 9). Thus, given a suitable transport mechanism, the Vancouver Island shelf could represent a salp source if some retention mechanism maintained salp populations over the winter. The weaker down-welling winds that were observed in the first quarter of 2011 (C. Ladd, NOAA, pers. comm.) may have contributed to such winter retention. In cold waters under non-optimal conditions, Antarctic

salps may have generations times of as long as 9 months (Loeb and Santora, 2012), after which the more typical explosive growth (e.g. Andersen and Nival, 1986) can occur under suitable conditions.

The circulation in the GOA originates from the eastward flowing North Pacific Current (NPC). As the NPC approaches the North American continent, it bifurcates into the southward-flowing California Current and the northward-flowing Alaska Current (Freeland and Cummins, 2005) (Fig. 9). This bifurcation occurs in the

south-eastern GOA and can vary in position annually (Freeland and Cummins, 2005; Freeland, 2006). The plankton community is typically different on either side of the bifurcation movement (Batten and Freeland, 2007), with shifts in the position and intensity of the bifurcation manifested as changes in the abundance of 'northern' and 'southern' copepods in the transition region (e.g. Mackas et al., 2001, 2004). The Alaskan currents respond primarily to the cyclonic wind stress curl over this basin, and represent alongshore pathways for planktonic communities in the GOA (Weingartner et al., 2002). Thereafter, persistent onshore Ekman transport is responsible for the seasonal presence of large oceanic copepods over the shelf (Wickett, 1967; Cooney, 1986; Coyle and Pinchuk, 2005). This surface-layer transport of zooplankton is more shoreward in winter and spring than summer in the northeast Pacific (Mackas and Coyle, 2005). Thus it is reasonable to suggest that under suitable conditions, a seed population of salps could be easily transported around the GOA margin and into the northern GOA. Large eddies that play a significant role in cross-shelf and shelf-break circulation (Okkonen et al., 2003; Ladd et al., 2005) could further enhance the retention and eventual transport of a seed population. However the multi-month transit times of water (Stabeno et al., this issue) and zooplankton (Coyle et al., 2013) around the Gulf of Alaska margin, and the presence of wide size range of both life stages for each species indicate that in situ population increase was also occurring. The closer proximity of the eastern GOA to the source population may help explain why *S. aspera* appeared there first and at higher abundances than the western GOA.

4.3. Possible cause and consequence of salp bloom

The chlorophyll levels in spring and summer 2011 were lower than expected based on previous studies (Childers et al., 2005), with the spring phytoplankton bloom not even apparent from satellites (Strom et al., this issue). Chl-*a* at most stations was $< 1.0 \text{ mg m}^{-3}$, and nearly all the chlorophyll-*a* was in cells $< 20 \mu\text{m}$ in the eastern and central regions in spring (Fig. 2). The abundances of *S. aspera* and *C. bakeri* were negatively related to Chl-*a* during the spring and summer, as has been observed elsewhere for some salp species (Zeldis et al., 1995; Liu et al., 2012). Although extremely efficient filter feeders at low particle concentrations (Alldredge and Madin, 1982), some salps may not be able to modify filtration rates in response to changes in food concentration such that their mucus nets become clogged at high concentrations of particles (Harbison et al., 1986). Dramatic reduction in salp feeding rates have been observed in the Southern Ocean when the Chl-*a* concentration exceeded $1\text{--}1.5 \text{ mg m}^{-3}$ (Perissinotto and Pakhomov, 1998), which they believed lead to the collapse of the salp population. Other surveys have also suggested that low numbers of salps occur when Chl-*a* exceeds 1 mg m^{-3} (Kawaguchi et al., 2004). Alternatively, higher abundances of salps may simply maintain lower concentrations of Chl-*a* through their grazing activities while low abundances of salps do not constrain Chl-*a*. Our data is consistent with either of these scenarios and notably the only regions where Chl-*a* concentrations exceeded 1.0 mg m^{-3} in spring was in the westernmost region where salps were not observed. The low Chl-*a* in spring may have resulted from high salp feeding efficiency in conjunction with other factors (see below) during the surveyed period.

The spring phytoplankton bloom is mainly influenced by wind and solar irradiance in the GOA. The strength of the spring bloom has varied annually in response to wind stress curl over the northern GOA during the previous winter (Fiechter and Moore, 2009). Strom et al. (this issue) showed a general absence of a spring bloom in the GOA during 2011, with small, low-light-adapted cells predominating, and suggested that light limitation might be responsible for suppressing the phytoplankton spring bloom. Such conditions would favor the development of salp populations. The high filtration rates of *S. aspera*

grazing may have subsequently prevented large cells from increasing when light limitation was removed and seasonal stratification began. A continued persistence of salps would rapidly export phytoplankton carbon (Zeldis et al., 1995; Perissinotto and Pakhomov, 1998; Hereu et al., 2006) and the associated macronutrients from the mixed layer euphotic zone. As a consequence, other zooplankton species may have suffered. The abundance of all *Neocalanus* species during spring 2011 was at or below its long-term mean at the Seward Line, with larger numbers of earlier life-stages present, suggesting somewhat delayed rates of growth (Hopcroft, unpublished data). Furthermore, the abundance of small copepods such as *Pseudocalanus* and *Oithona* during spring was well below the long-term average (Hopcroft and Coyle, unpublished). This may have resulted from low food availability or because the nauplii and eggs of smaller copepods were removed through the high filtration rates occurring during salp blooms (Paffenhöfer et al., 1995). Our upper estimates of volume filtered, if applied to copepod removal (either by unselective grazing, or fatal ensnarement of copepods in mucus), are similar to the population growth rates of these smaller species in the GOA (Liu and Hopcroft, 2008). By contributing to the persistence of low chlorophyll on the shelf, *S. aspera* may have created a more suitable habitat for *C. bakeri* that allowed a much smaller seed population of *C. bakeri* to bloom and disperse as summer commenced. Thus, the salp bloom may have had a profound effect on the production, efficiencies and pathways of transfer to higher trophic-levels in the GOA during 2011.

To our knowledge, there is no record of high salp abundances in Alaskan continental shelf waters of the GOA prior to 2011. Although we have some confidence this is the case in the northern GOA, sparse historical sampling in the eastern GOA does not preclude them being somewhat more common there. We propose that given suitable conditions (i.e. low chlorophyll and strong downwelling), a seed population of salps transported from the coastal subarctic Pacific in winter could be transferred alongshore from the eastern to the western shelf of the GOA in spring and summer. The high abundance, rapid feeding efficiency, and active asexual reproduction of salps in spring could exert significant control on the phytoplankton bloom, making conditions favorable to their protracted persistence through the summer. Determining the rarity of the 2011 salp bloom, and the ability to anticipate changes in the frequency of salp blooms, will depend on continued long-term oceanographic observations in the GOA.

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References

- Allredge, A.L., Madin, L.P., 1982. Pelagic tunicates: unique herbivores in the marine plankton. *Bioscience* 32, 655–663.
- Andersen, V., 1985. Filtration and ingestion rates of *Salpa fusiformis* Cuvier (Tunicata:Thaliacea): effects of size, individual weight and algal concentration. *J. Exp. Mar. Biol. Ecol.* 87, 13–29.
- Andersen, V., 1998. Salp and pyrosomid blooms and their importance in biogeochemical cycles. In: Bone, Q. (Ed.), *The Biology of Pelagic Tunicates*. Oxford University Press, Oxford, pp. 125–137.
- Andersen, V., Nival, P., 1986. A model of the population dynamics of salps in coastal waters of the Ligurian Sea. *J. Plankton Res.* 8, 1091–1110.
- Atkinson, A., Siegel, V., Pakhomov, E., Rothery, P., 2004. Long-term decline in krill stock and increase in salps within the Southern Ocean. *Nature* 432, 100–103.

- Batten, S.D., Freeland, H.J., 2007. Plankton population at the bifurcation of the North Pacific Current. *Fish. Oceanogr.* 16, 536–546.
- Batten, S.D., Crawford, W.R., 2005. The influence of coastal origin eddies on oceanic plankton distributions in the eastern Gulf of Alaska. *Deep-Sea Res. II* 52, 991–1009.
- Childers, A.R., Whitlege, T.E., Stockwell, D.A., 2005. Seasonal and interannual variability in the distribution of nutrients and chlorophyll a across the Gulf of Alaska shelf: 1998–2000. *Deep-Sea Res. II* 52, 193–216.
- Cooney, R.T., 1986. The seasonal occurrence of *Neocalanus cristatus*, *Neocalanus plumchrus*, and *Eucalanus bungii* over the shelf of the northern Gulf of Alaska. *Cont. Shelf Res.* 5, 541–553.
- Coyle, K.O., Pinchuk, A.I., 2005. Seasonal cross-shelf distribution of major zooplankton taxa on the northern Gulf of Alaska shelf relative to water mass properties, species depth preference and vertical migration behavior. *Deep-Sea Res. II* 52, 217–245.
- Coyle, K.O., Cheng, W., Hinckley, S., Lessard, E.J., Whitlege, T., Hermann, A.J., Hedstrom, K., 2012. Model and field observations of effects of circulation on the timing and magnitude of nitrate utilization and production on the northern Gulf of Alaska shelf. *Prog. Oceanogr.* 103, 16–41.
- Coyle, K.O., Gibson, G.A., Hedstrom, K., Hermann, A.J., Hopcroft, R.R., 2013. Zooplankton biomass, advection and production on the northern Gulf of Alaska shelf from simulations and field observations. *J. Mar. Syst.* 128, 185–207.
- Deibel, D., 1985. Blooms of the pelagic tunicate, *Doliolotta geggenbarui*: Are they associated with Gulf Stream frontal eddies?. *J. Mar. Res.* 43, pp. 211–236.
- Deibel, D., Paffenhöfer, G.A., 2009. Predictability of patches of neritic salps and doliolids (Tunicata, Thaliacea). *J. Plankton Res.* 31, 1571–1579.
- Doubleday, A., Hopcroft, R.R., 2015. Interannual patterns during spring and late summer of larvaceans and pteropods in the Coastal Gulf of Alaska, and their relationship to pink salmon survival. *J. Plankton Res.* 37, 134–150.
- Freeland, H.J., 2006. What proportion of the North Pacific Current finds its way into the Gulf of Alaska? *Atmosphere–Ocean* 44, 321–330.
- Freeland, H.J., Cummins, P., 2005. Argo: a new tool for environmental assessment and monitoring of the world's oceans. *Prog. Oceanogr.* 64, pp. 31–44.
- Fiechter, J., Moore, A.M., 2009. Interannual spring bloom variability and Ekman pumping in the coastal Gulf of Alaska. *J. Geophys. Res.* 114, C06004. <http://dx.doi.org/10.1029/2008JC005140>.
- Godeaux, J., Bone, Q., Braconnot, J.C., 1998. Anatomy of Thaliacea. In: Bone, Q. (Ed.), *The Biology of Pelagic Tunicates*. Oxford University Press, New York, NY, pp. 1–24.
- Harbison, G.R., McAlister, V.L., Gilmer, R.W., 1986. The response of the salp, *Pegea confederata*, to high levels of particulate material: starvation in the midst of plenty. *Limnol. Oceanogr.* 31, 371–382.
- Harbison, G.R., Gilmer, R.W., 1976. The feeding rates of the pelagic tunicate *Pegea confederata* and two other salps. *Limnol. Oceanogr.* 21, 517–528.
- Henschke, N., Everett, J.D., Doblin, M.A., Pitt, K.A., Richardson, A.J., Suthers, I.M., 2014. Demography and interannual variability of salp swarms (*Thalia democratica*). *Mar. Biol.* 161, 149–163.
- Hereu, C.M., Lavaniegos, B.E., Gaxiola-Castro, G., Ohman, M.D., 2006. Composition and potential grazing impact of salp assemblages off Baja California during the 1997–1999 El Niño and La Niña. *Mar. Ecol. Prog. Ser.* 318, 123–140.
- Heron, A.C., 1972. Population Ecology of a colonizing species: the pelagic tunicate *Thalia democratica* I. Individual growth rate and generation time. *Oecologia* 10, 294–312.
- Heron, A.C., Benham, E.E., 1984. Individual growth rates of salps in three populations. *J. Plankton Res.* 6, 811–828.
- Huntley, M.E., Sykes, P.F., Marin, V., 1989. Biometry and trophodynamics of *Salpa thompsoni* Foxtton (Tunicata: Thaliacea) near the Antarctic peninsula in Austral summer, 1983–1984. *Polar Biol.* 10, 59–70.
- Huskin, I., Elices, M.A., Anadon, R., 2003. Salp distribution and grazing in a saline intrusion off NW Spain. *J. Mar. Syst.* 42, 1–11.
- Iguchi, N., Kidokoro, H., 2006. Horizontal distribution of *Thetys vagina* Tilesius (Tunicata, Thaliacea) in the Japan Sea during spring 2004. *J. Plankton Res.* 28, 537–541.
- Kawaguchi, S., Siegel, V., Litvinov, F., Loeb, V., Watkins, J., 2004. Salp distribution and size composition in the Atlantic sector of the Southern Ocean. *Deep-Sea Res. II* 51, 1369–1381.
- Ladd, C., Stabeno, P., Cokelet, E.D., 2005. A note on cross-shelf exchange in the northern Gulf of Alaska. *Deep-Sea Res. II* 52, 667–679.
- Lavaniegos, B.E., Ohman, M.D., 2003. Long-term changes in pelagic tunicates of the California Current. *Deep Sea Res. II* 50, 2473–2498.
- Lavaniegos, B.E., Ohman, M.D., 2007. Coherence of long-term variations of zooplankton in two sectors of the California Current System. *Prog. Oceanogr.* 75, 42–69.
- Liu, H., Hopcroft, R.R., 2008. Growth and development of *Pseudocalanus* spp. in the northern Gulf of Alaska. *J. Plankton Res.* 30, 923–935.
- Liu, Y.Q., Sun, S., Zhang, G.T., 2012. Seasonal variation in abundance, diel vertical migration and body size of pelagic tunicate *Salpa fusiformis* in the Southern Yellow Sea. *Chin. J. Oceanol. Limnol.* 30, 92–104.
- Loeb, V.J., Santora, J.A., 2012. Population dynamics of *Salpa thompsoni* near the Antarctic Peninsula: growth rates and interannual variations in reproductive activity (1993–2009). *Prog. Oceanogr.* 96, 93–107.
- Mackas, D.L., Coyle, K.O., 2005. Shelf-offshore exchange processes, and their effects on mesozooplankton biomass and community composition patterns in the northeast Pacific. *Deep-Sea Res. II* 52, 707–725.
- Mackas, D.L., Batten, S.D., Trudel, M., 2007. Effects on zooplankton of a warming ocean: recent evidence from the Northeast Pacific. *Prog. Oceanogr.* 75, 223–252.
- Mackas, D.L., Thomson, R.E., Galbraith, M., 2001. Changes in the zooplankton community of the British Columbia continental margin, 1985–1999, and their covariations with oceanographic conditions. *Can. J. Fish. Aquat. Sci.* 58, 685–702.
- Mackas, D.L., Peterson, W.T., Zamon, J.E., 2004. Comparisons of interannual biomass anomalies of zooplankton communities along the continental margins of British Columbia and Oregon. *Deep-Sea Res. II* 51, 875–896.
- Mackas, D.L., Galbraith, M.D., 2002. Zooplankton distribution and dynamics in a North Pacific eddy of coastal origin: I. Transport and loss of continental margin species. *J. Oceanogr.* 58, 725–738.
- Mackas, D.L., Tsurumi, M., Galbraith, M.D., Yelland, D.R., 2005. Zooplankton distribution and dynamics in a North Pacific eddy of coastal origin: II. Mechanisms of eddy colonization by and retention of offshore species. *Deep-Sea Res. II* 52, 1011–1035.
- Madin, L.P., Cetta, C.M., 1984. The use of gut fluorescence to estimate grazing by oceanic salps. *J. Plankton Res.* 6, 475–492.
- Madin, L.P., Deibel, D., 1998. Feeding and energetics of Thaliacea. In: Bone, Q. (Ed.), *The Biology of Pelagic Tunicates*. Oxford University Press, New York, NY, pp. 81–104.
- Madin, L.P., Kremer, P., Hacker, S., 1996. Distribution and vertical migration of salps (Tunicata, Thaliacea) near Bermuda. *J. Plankton Res.* 18, 747–755.
- Madin, L.P., Purcell, J.E., Miller, B.C., 1997. Abundance and grazing effects of *Cyclosalpa bakeri* in the subarctic Pacific. *Mar. Ecol. Prog. Ser.* 157, 175–183.
- Madin, L.P., Purcell, J.E., 1992. Feeding, metabolism, and growth of *Cyclosalpa bakeri* in the subarctic Pacific. *Limnol. Oceanogr.* 37, 1236–1251.
- Madin, L.P., Kremer, P., Wiebe, P.H., Purcell, J.E., Horgan, E.H., Nemazie, D.A., 2006. Periodic swarms of the salp *Salpa aspera* in the Slope Water off the NE United States: biovolume, vertical migration, grazing, and vertical flux. *Deep-Sea Res. I* 53, 804–819.
- Ménard, F., Dallot, S., Thomas, G., Braconnot, J.C., 1994. Temporal fluctuations of two Mediterranean salp populations from 1967 to 1990. Analysis of the influence of environmental variables using a Markov chain model. *Mar. Ecol. Prog. Ser.* 104, 139–152.
- Okkonen, S.R., Weingartner, T.J., Danielson, S.L., Musgrave, D.L., 2003. Satellite and hydrographic observations of eddy-induced shelf-slope exchange in the northwestern Gulf of Alaska. *J. Geophys. Res.* 108, 3033. <http://dx.doi.org/10.1029/2002JC001342>.
- Paffenhöfer, G.A., Atkinson, L.P., Lee, T.N., Verity, P.G., Bulluck III, L.R., 1995. Distribution and abundance of thaliaceans and copepods off the southeastern U.S. A. during winter. *Cont. Shelf Res.* 15, 255–280.
- Parsons, T.R., Maita, Y., Lalli, C.M., 1984. *A Manual for Chemical and Biological Methods in Seawater Analysis*. Pergamon Press, Toronto, Canada.
- Perissinotto, P., Pakhomov, E.A., 1998. Contribution of salps to carbon flux of marginal ice zone of the Lazarev Sea, Southern Ocean. *Mar. Biol.* 131, 25–32.
- Pinchuk, A.I., Coyle, K.O., Hopcroft, R.R., 2008. Climate-related variability in abundance and reproduction of euphausiids in the northern Gulf of Alaska in 1998–2003. *Prog. Oceanogr.* 77, 203–216.
- Purcell, J.E., Madin, L.P., 1991. Diel patterns of migration, feeding, spawning by salps in the subarctic Pacific. *Mar. Ecol. Prog. Ser.* 73, 211–217.
- Royer, T.C., Grosch, C.E., 2006. Ocean warming and freshening in the northern Gulf of Alaska. *Geophys. Res. Lett.* 33, L16605. <http://dx.doi.org/10.1029/2006GL026767>.
- Stabeno, P.J., Bond, N.A., Hermann, A.J., Kachel, B., Mordy, C.W., Overland, J.E., 2004. Meteorology and oceanography of the Northern Gulf of Alaska. *Cont. Shelf Res.* 24, 859–897.
- Stabeno, P.J., Bond, N.A., Kachel, N.B., Ladd, C., Mordy, C.W., Strom, S.L., 2016. Southeast Alaska: currents, mixing and chlorophyll-a. *Deep-Sea Res. II*, this issue [doi: 10.1016/j.dsr2.2015.06.018].
- Stone, J.P., Steinberg, D.K., 2014. Long-term time-series study of salp population dynamics in the Sargasso Sea. *Mar. Ecol. Prog. Ser.* 510, 111–127.
- Strom, S.L., Fredrickson, K.A., Bright, K.J., 2016. Spring phytoplankton in the eastern coastal Gulf of Alaska: photosynthesis and production during high and low bloom years. *Deep-Sea Res. II*, this issue [doi: 10.1016/j.dsr2.2015.05.003].
- Strom, S.L., Olson, M.B., Macri, E.L., Mordy, C.W., 2007. Cross-shelf gradients in phytoplankton community structure, nutrient utilization, and growth rate in the coastal Gulf of Alaska. *Mar. Ecol. Prog. Ser.* 328, 75–92.
- Tsuda, A., Nemoto, T., 1992. Distribution and growth of salps in a Kuroshio warm-core ring during summer 1987. *Deep-Sea Res.* 39, S219–S229.
- van Soest, R.W.M., 1998. The cladistics biogeography of salps and pyrosomas. In: Bone, Q. (Ed.), *The Biology of Pelagic Tunicates*. Oxford University Press, New York, NY, pp. 231–249.
- Vargas, C.A., Madin, L.P., 2004. Zooplankton feeding ecology: clearance and ingestion rates of the salps *Thalia democratica*, *Cyclosalpa affinis* and *Salpa cylindrica* on naturally occurring particles in the Mid-Atlantic Bight. *J. Plankton Res.* 26, 827–833.
- Weingartner, T.J., Coyle, K., Finney, B., Hopcroft, R., Whitlege, T., Brodeur, R., Dagg, M., Farley, M., Haidvogel, D., Halderson, L., Hermann, A., Hinkley, S., Napp, J., Stabeno, P., Kline, T., Lee, C., Lessard, E., Royer, T., Strom, S., 2002. The Northeast Pacific GLOBEC Program: Coastal Gulf of Alaska. *Oceanography* 15, 48–63.
- Wiebe, P.H., Madin, L.P., Haurly, L.R., Harbison, G.R., Philbin, L.M., 1979. Diel vertical migration by *Salpa aspera* and its potential for large-scale particulate organic matter transport to the deep-sea. *Mar. Biol.* 53, 249–255.
- Wickett, P.W., 1967. Ekman transport and zooplankton concentration in the North Pacific Ocean. *J. Fish. Res. Board Can.* 24, 581–594.
- Zeldis, J.R., Davis, C.S., James, M.R., Ballara, S.L., Booth, W.E., Chang, F.H., 1995. Salp grazing: effects on phytoplankton abundance, vertical distribution and taxonomic composition in a coastal habitat. *Mar. Ecol. Prog. Ser.* 126, 267–283.