Deep-Sea Research II 132 (2016) 136–145

Contents lists available at ScienceDirect

Deep-Sea Research II

journal homepage: www.elsevier.com/locate/dsr2

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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ARTICLE INFO

Available online 20 April 2016

Keywords:
Thaliacean
Salpa aspera
Cyclosalpa bakeri
Salp bloom
Gulf of Alaska

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 ± 0.64 mg C m^{-3} in southeastern Alaska during spring then decreased to 0.03 ± 0.12 mg C m^{-3} during summer. Estimated biomass of *C. bakeri* was 0.03 ± 0.06 mg C m^{-3} over the entire sampling domain during spring, then rose to 0.15 ± 0.25 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.

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 ind. m^{-3}) under favorable conditions (Andersen, 1998). Salps have some of the highest clearance rates of any zooplankton – up to several liters h^{-1} 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 100s 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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http://dx.doi.org/10.1016/j.dsr2.2016.04.009
0967-0645/

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 (Lavaniegos 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., 2016), 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