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An observation of two oceanic salp swarms in the Tasman Sea: *Thetys vagina* and *Cyclosalpa affinis*

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Abstract

Background: Large oceanic salps are rarely encountered. The highest recorded biomasses of the salps *Thetys vagina* (852 g WW m^{-3}) and *Cyclosalpa affinis* (1149 g WW m^{-3}) were observed in the Tasman Sea during January 2009.

Results: Due to their fast sinking rates the carcasses and faecal pellets of these and other large salps play a significant role in carbon transport to the seafloor. We calculated that faecal pellets from these swarms could have contributed up to 67 % of the mean organic daily carbon flux in the area. This suggests that the flux of carbon from salp swarms are not accurately captured in current estimates.

Conclusion: This study contributes information on salp abundance and biomass to a relatively understudied field, improving estimates for biogeochemical cycles.

Background

The role of gelatinous zooplankton, such as salps, pyrosomes and cnidarians, in ocean food webs and biogeochemical cycling has garnered increased attention in recent years (Lebrato et al., 2011; Henschke et al., 2013; Lebrato et al., 2013; Smith et al. 2014). Salps (Phylum: Thaliacea, Order Salpidae) in particular, are significant contributors to oceanic carbon flux. They have the highest per-individual filtration rates of all marine zooplankton filter feeders (Alldredge and Madin, 1982) consuming particles across three orders of magnitude (1 μm up to 1 mm in size; Vargas and Madin, 2004; Sutherland et al., 2010) using a fine mucous net that is continuously secreted and fed toward the oesophagus. This efficient feeding mechanism and their alternating sexual and asexual life-cycle results in fast individual (up to 21 % in length h^{-1}; Heron, 1972a) and population (up to 2.5 d^{-1}; Heron, 1972b; Henschke et al., 2015) growth rates. As a result, salps form large swarms that often reach abundances greater than 1000 individuals m^{-3} (~6 kg WW m^{-3}; Henschke et al., 2014) and persist for up to 6 months (Smith et al. 2014). When salps occur in high abundances, their fast-sinking faecal pellets (Bruland and Silver, 1981) and carcasses (Henschke et al., 2013) can increase the carbon flux in an area up to ten-fold the daily average (Fischer et al., 1988) for a sustained period of time (Smith et al. 2014).

Due to their regular occurrence (Henschke et al., 2014) and coastal dominance (Henschke et al 2011), smaller salps such as *Thalia democratica* are studied with greater frequency. Although these smaller salps contribute significantly to biogeochemical cycling with fast growth rates (Heron, 1972a) and faecal pellets, carcasses of these smaller salps rarely sink as they are neutrally buoyant (Tsukamoto et al., 2009). The carcasses of larger salps however, sink rapidly and have the potential to reach the sea floor in less than 2 days (Henschke et al., 2013; Lebrato et al., 2013). Due to the combined input from both faecal pellets and carcasses, swarms of larger salps are thought to play a greater role in carbon export (Smith et al. 2014). Of significance however, is that very little is known about the distribution and abundance of larger salps as they are oceanic and rarely encountered. The aim of this study is to document swarm observations from the Tasman Sea of two large salps: *Thetys vagina* and *Cyclosalpa affinis* and compare these biomasses to previous observations.

Thetys vagina is often observed opportunistically as a single individual and little is known about their ecology (Nakamura and Yount, 1958; McAlice, 1986; Sims, 1996; Stone and Steinberg, 2014). Large biomasses (900 t WW km^{-3}) of *T. vagina* have been observed in the Japan Sea (Iguchi and Kidokoro, 2006) and Tasman Sea (Thompson,

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1948; Henschke et al., 2013). Although *T. vagina* has been found across a wide temperature (7–20 °C) and salinity (33.9–35.6) range (Thompson, 1948; Iguchi and Kidokoro, 2006; Henschke et al., 2013), there appears to be no seasonality to *T. vagina* swarms (Henschke et al 2013). In the Japan Sea and Tasman Sea, higher *T. vagina* biomass occurred in areas of higher chlorophyll *a* (Iguchi and Kidokoro, 2006; Henschke et al., 2013). As seamounts have been found to promote localised upwelling (Boehlert and Genin, 1987; Suthers, 1996), this is one factor that may have encouraged the *T. vagina* population to aggregate around Gascoyne Seamount in this report.

Although the ecology of *Cyclosalpa affinis* is well studied (e.g. Madin, 1974; Madin et al., 1981; Vargas and Madin, 2004), their distribution is not well known. Unlike *T. vagina,* the relationship between upwelling events and *C. affinis* populations is unknown. Long-term studies have found that *C. affinis* generally occurs in low numbers (<30 g WW m^{-3}) and has been characterised as a cool-phase species, occurring after intrusions of cooler high latitude water (Lavaniegos and Ohman, 2003). However, *C. affinis* has also been found in the subtropical Tasman Sea (32.8°S and 32.57°S) and the warmer parts of the Indian, Pacific and Atlantic oceans (Thompson, 1948) suggesting that its temperature tolerance may be quite broad.

Methods

Salp samples were collected onboard the R.V. *Southern Surveyor* in the austral summer (25–29 January 2009) in the western Tasman Sea (Fig. 1). Sampling stations were located at Gascoyne Seamount ($n = 5$) and on the Challenger Plateau ($n = 1$). Gascoyne Seamount is part of the Tasmantid Seamount Chain in the Tasman Sea, and rises to 93 m below the surface from a bottom depth of 4000 m (Quilty, 1993). The Challenger Plateau is a large submarine plateau west of New Zealand, with depths varying from 500 to 1500 m, and is considered to be a region of low pelagic productivity (Wood, 1991).

At each sampling station a Seabird SBE911-plus Conductivity–Temperature–Depth (CTD) recorder equipped with an AquaTracker Mk3 fluorometer (Chelsea, UK) was used to record salinity, temperature, and fluorescence, respectively. Salps were sampled at the surface with a neuston net (0.75 m × 0.75 m, 500 μm mesh; $n = 2$) and from 0 to 40 m using a rectangular mid-water trawl (RMT; 1 m × 1 m, 1 mm mesh, double-oblique tows; $n = 1$). The neuston net was towed for 5 min, and the RMT for 30 min, both at 1.5 m s^{-1}. All tows were undertaken at night (2100–0200 h). Immediately after sampling, zooplankton were preserved in 5 % formaldehye solution. Salps were identified to species and total length and wet

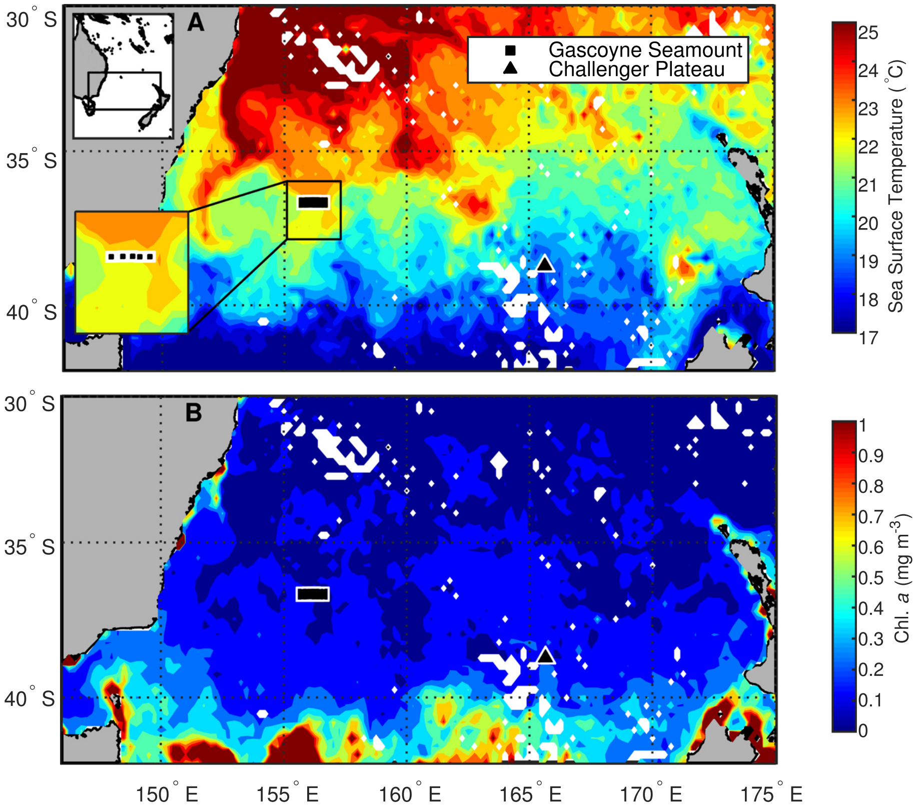

Fig. 1 Location plot showing sampling locations in the Tasman Sea. Overlaid is satellite derived **a**) sea surface temperature and **b**) chlorophyll *a*. Sampling stations on Gascoyne Seamount are represented by squares ($n = 5$) and Challenger Plateau is represented by triangles ($n = 1$)

weight was measured for each individual. Due to salps being damaged in the RMT net, total length of salps from the RMT samples could not be measured. Carbon calculations were based on carbon-length relationships previously established for *T. vagina* (Henschke et al., 2013) and *C. affinis* (Madin et al., 1981). Pearson correlations were undertaken to determine if there were any relationships between salp biomass and location to the seamount.

Results and discussion

The Gascoyne Seamount transect extended for 38 km crossing west-east over the seamount. At the time of sampling, sea surface temperature at Gascoyne Seamount was ~22 °C compared to Challenger Plateau which was cooler (~19 °C) and had higher chlorophyll *a* concentrations (Fig. 1). *Thetys vagina* was present at all Gascoyne Seamount stations ($n = 5$) but absent at Challenger Plateau ($n = 1$) where only *Cyclosalpa affinis* occured. Biomass of *T. vagina* did not significantly differ with distance to the seamount (Pearson correlation, R = -0.36, $p = 0.55$).

Biomass and abundance

At Gascoyne Seamount, mean (±SE) surface biomass of *Thetys vagina* was 444.9 ± 249.8 g WW m^{-3} (6.6 mg C m^{-3}) and the mean (±SE) oblique biomass was 851.7 ± 280.6 g WW m^{-3} (12.7 mg C m^{-3}; Fig. 2d). These values are higher than biomasses previously sampled in the Japan Sea (maximum of 0.9 g WW m^{-3}; Iguchi and Kidokoro, 2006) and Tasman Sea (maximum of 0.7 g WW m^{-3}; Henschke et al., 2013). At one station during sampling, the weight of high abundances of *T. vagina* tore the RMT net. Higher biomasses in the oblique tows (vs. neuston tows) suggest that *T. vagina* were more abundant deeper in the water column (Fig. 2d). Aggregation of salp biomass in the top 40 m is consistent with previous research that has found that 98 % of *T. vagina* abundances occurred in the top 200 m during both day and night (Henschke et al., 2013). There is no known data on vertical migration by *T. vagina* and all samples in this study were undertaken only at night, but anecdotal observations from this cruise and previous cruises suggest they are not present in surface waters during the day.

Cyclosalpa affinis was only observed at the Challenger Plateau, with a surface biomass of 1148.6 g WW m^{-3} (4.3 mg C m^{-3}) and oblique biomass of 2251.4 g WW m^{-3} (8.3 mg C m^{-3}; Fig. 2h). Compared to Gascoyne seamount, the water was cooler and less saline at the Challenger Plateau with a 100 m depth-integrated temperature of 15 °C compared to 19 °C (Fig. 2e,f). The fluorescence at Challenger Plateau was higher in the surface waters,

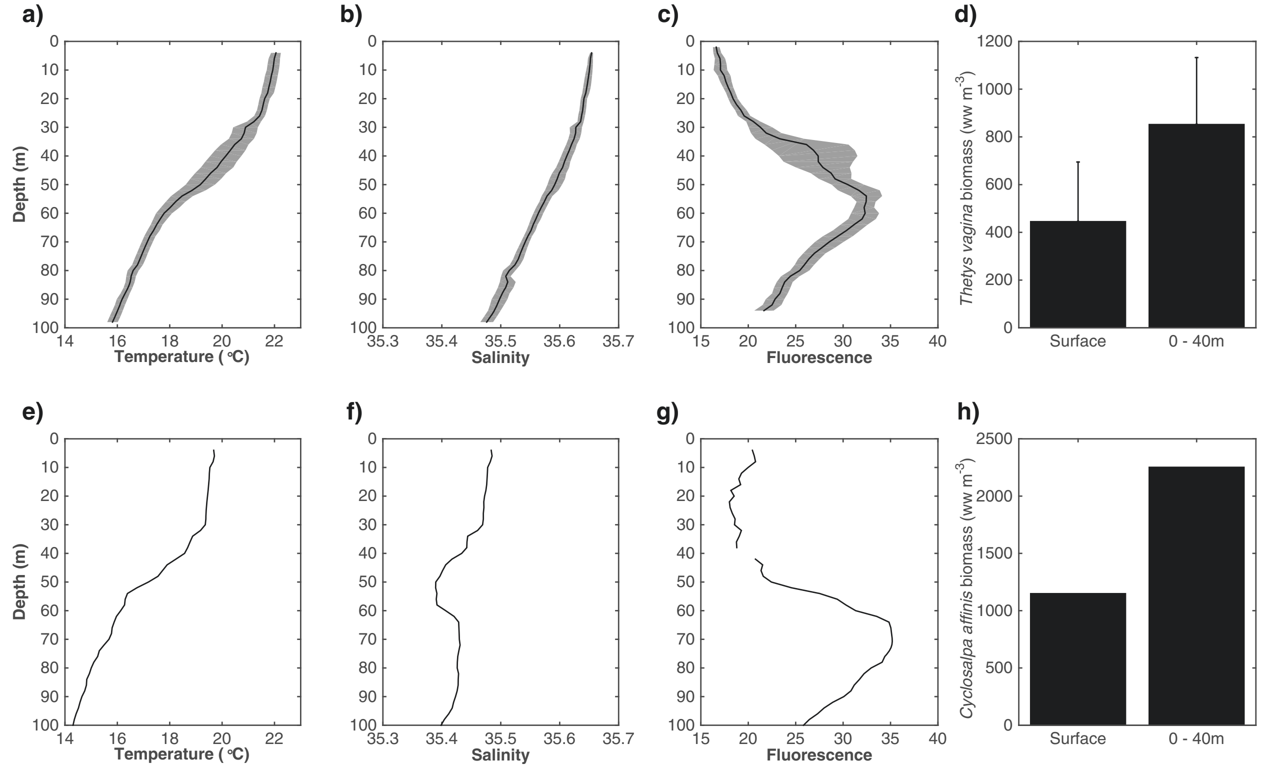

Fig. 2 Depth stratified temperature (**a**,**e**), salinity (**b**,**f**) and fluorescence (**c**,**g**) values for Gascoyne Seamount (top row) and Challenger Plateau (bottom row) sampling stations. Shaded values indicate standard error around the mean. Mean (±SE) **d**) *Thetys vagina* and **h**) *Cyclosalpa affinis* biomass at the surface and oblique (0–40 m) depths are represented in the bar chart. As only one station was sampled at Challenger Plateau, standard errors around the mean could not be calculated for temperature, fluorescence or salp biomass

but showed a similar sub-surface maximum at 60 m to Gascoyne Seamount (Fig. 2c,g). *C. affinis* is not believed to undergo diel-vertical migration (Madin et al., 1996) and to date this is the largest observed biomass of *C. affinis* population.

Size structure

Thetys vagina aggregates ranged from 21 to 135 mm in size (mean = 48 mm, *n* = 179), and solitaries ranged from 11 to 178 mm (mean = 27 mm, *n* = 25; Fig. 3a). Despite the large size range, the majority of aggregate and solitary individuals were small with respective modes of 39 and 19 mm. Fully grown *T. vagina* individuals are reported to be up to 306 mm for solitary forms (Nakamura and Yount, 1958) and 190 mm for aggregate forms (Thompson 1948). It is unknown what size aggregate *T. vagina* embryos are when they are born, however, McAlice (1986) observed developing embryos between 10 and 15 mm inside a solitary individual. The abundance of small individuals (<40 mm) suggests that the *T. vagina* swarm observed at Gascoyne seamount had recently developed.

C. affinis aggregates ranged from 9 to 77 mm in length (mean = 37 mm, *n* = 36; Fig. 3b). Unlike *T. vagina*, there appears to be two distinct aggregate size classes in the *C. affinis* population with respective modes of 14 (*n* = 4) and 66 mm (*n* = 3). Only 3 solitaries were measured and lengths ranged from 56 to 96 mm (mean = 74 mm) with no developing buds observed. *C. affinis* aggregates reach a maximum size of 80 mm (Thompson, 1948), suggesting that the swarm has been developing for a while, and a cohort of solitary buds may have already been released from the larger aggregates.

Potential carbon input

Salps are significant contributors to oceanic carbon flux (Henschke et al., 2013; Smith et al. 2014). The defecation rate of *Cyclosalpa affinis* has been calculated at 9.9 μg C mg body C h^{-1}, and although no defecation rate has been calculated for *Thetys vagina*, we can assume an average defecation rate of 11.8 μg C mg body C h^{-1} based on a range of salp species (Madin and Deibel, 1998). Therefore, using the mean surface salp biomass from this study (and assuming a 1:1 conversion for m^3:m^2), *T. vagina* faecal pellets would have contributed ~2 mg C m^{-2} d^{-1} at Gascoyne Seamount, and *C. affinis* would have contributed ~1 mg faecal carbon m^{-2} d^{-1} at the Challenger Plateau. These carbon flux values are likely to be an underestimation, as we have not considered population growth and the carbon input from carcasses. Considering the mean organic carbon flux in the area has been calculated as 4.5 mg C m^{-2} d^{-1} (Kawahata and Ohta, 2000), it is likely that the contribution from salp swarms is not accurately captured in current estimates.

Conclusion

This study confirms recent literature that has identified that swarms of large salps frequently occur in the Tasman Sea (Henschke et al., 2013), and this is likely the case in oceans around the world. Large salps have recently been found to be nutritionally important for several marine organisms and salp faecal pellets and carcasses play a large role in carbon export (Henschke et al., 2013). As salp remains are rarely found in sediment traps (Rowe and Staresinic, 1979), this suggests the

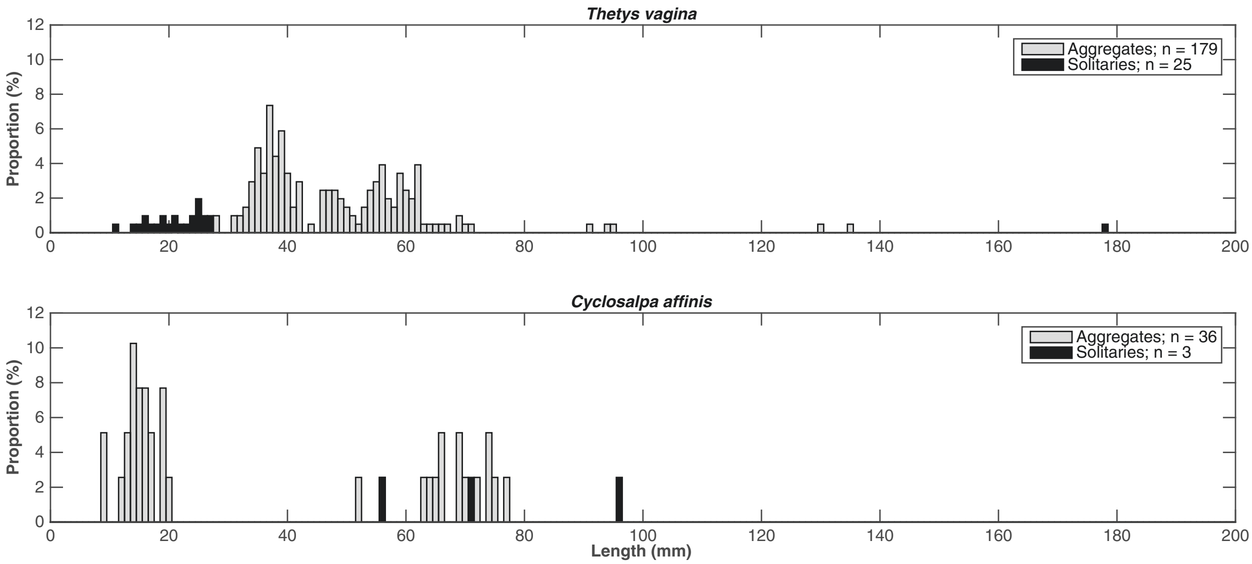

Fig. 3 Size histograms for the *Thetys vagina* (top) and *Cyclosalpa affinis* (bottom) swarms. Aggregates are represented by grey bars and solitaries by black bars

biogeochemical carbon budgets of the area are significantly underestimated. To incorporate salps into ecosystem models, it is important to understand which environmental factors promote high abundances of large salps in order to have accurate representations of their abundance and distribution. Their ephemeral nature will continue to make sampling of large oceanic salps difficult, but improved reporting of all encountered salp blooms will allow their contribution to global biogeochemical cycles to be better estimated.

Competing interests

The authors declare that they have no competing interests.

Authors' contributions

NH, JDE and IMS designed the study, analysed the data and wrote the manuscript. IMS collected the data. All authors read and approved the final manuscript.

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