

Distribution of life-history stages of the salp *Thalia democratica* in shelf waters during a spring bloom

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ABSTRACT: Swarms of the salp *Thalia democratica* periodically occur off southeast Australia following the austral spring bloom of phytoplankton. The present study aimed to determine the abundance and size/stage distribution of *T. democratica* and their relationship with copepods in 3 water types of the western Tasman Sea. Samples were taken from vertical net hauls along 4 cross-shelf transects spaced along 200 km of the New South Wales coast, from the East Australian Current (EAC) separation zone, around 32.5° S, to off Sydney (34° S). Temperature–salinity signatures grouped stations into 3 distinct water types: inner shelf water, EAC and upwelled water. Although common across all stations, *T. democratica* was significantly more abundant in inner shelf waters compared to both EAC and upwelled water. Analysis of population structure (aggregate buds, aggregate females, aggregate males, immature solitaries and mature solitaries) also identified higher proportions of reproductive aggregates and their offspring in inner shelf water. This salp population structure was significantly different in the EAC regions, characterised by a paucity of the solitary stages, higher temperatures and lower chlorophyll *a* concentrations. A weak negative correlation was identified between *T. democratica* and copepod abundance. In the present study, the maximum abundance of *T. democratica* was twice the highest globally recorded abundance and 10-fold greater than maximum abundances sampled from the continental shelf and slope waters off southeast Australia during the period from 1938 to 1942.

KEY WORDS: *Thalia democratica* · Salps · Life cycle · Zooplankton · Water types · Population structure · East Australian Current

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INTRODUCTION

Salps are an ecologically and biogeochemically important class of gelatinous zooplankton. Among the fastest growing metazoans on earth, they can short-circuit traditional food webs through their ability to continuously filter-feed on a range of particles over 3 orders of magnitude in size (Kremer & Madin 1992). Salps also alter carbon fluxes within the ocean (Phillips et al. 2008). They produce rapidly sinking faecal pellets that are rich in carbon (up to 37%), and it has

been suggested that salps can quickly contribute to the vertical transport of carbon, up to 88 mg C m⁻² d⁻¹ (Perissinotto & Pakhomov 1998), an amount 10-fold greater than the average daily flux in areas without salp swarms (Fischer et al. 1988).

Swarms of the salp *Thalia democratica* periodically occur in continental shelf waters off southeast Australia during the austral spring and summer (Thompson 1948, Heron 1972a, Deibel & Paffenhofer 2009). High densities of *T. democratica* have also reoccurred in the Californian Current (Blackburn 1979), west

Mediterranean (Licandro et al. 2006) and South Africa (Gibbons 1997). Occasional swarms of gelatinous species, including salps, are well known historically, but recent reports indicate that these are increasing in frequency and magnitude as a result of human-induced stresses such as eutrophication and climate change (Hay 2006).

Salp swarms are possible as a result of their life cycle involving the obligatory alternation between aggregated sexual and solitary asexual generations (Fig. 1), allowing *Thalia democratica* populations to grow exponentially while maintaining genetic variability (Godeaux et al. 1998). The aggregate stage begins life as a chain of genetically identical individuals ('buds' or A1) and reproduces sexually. Born female, aggregates separate and are externally fertilised immediately after release from their parent, and an embryo grows internally (A2). Once the embryo is born, female aggregates develop testes and function as a male (A3). These males (A3) then fertilise the recently released buds (A1) before dying shortly thereafter. The embryo is the start of the solitary generation (S1) that asexually produces up to 3 chains, each with between 20 and 80 individual aggregates (A1). Once mature (S2), solitaries release each chain separately (Heron & Benham 1985).

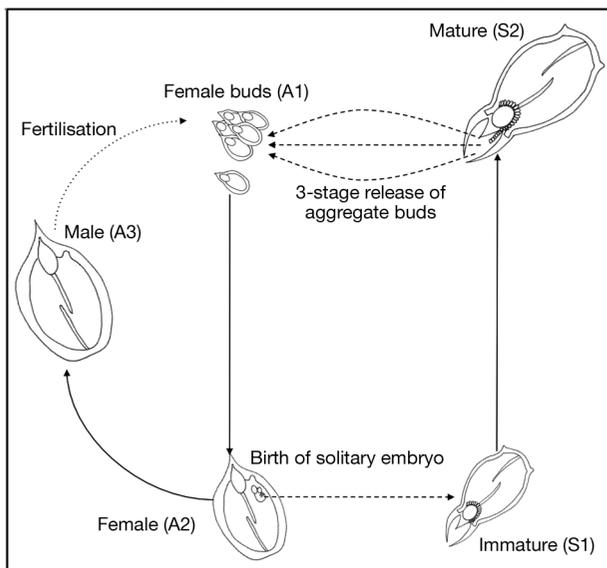


Fig. 1. Life cycle of the salp *Thalia democratica*, demonstrating alternation between aggregated sexual (A1 to A3) and solitary asexual (S1 and S2) generations (Heron & Benham 1985). Aggregate female buds (A1) are fertilised immediately upon release by mature male aggregates (A3). These female buds then grow an embryo internally (A2). Once the embryo is born, the aggregate female develops testes and functions as a male (A3). The embryo is the start of the solitary generation. The immature solitary (S1) develops up to 3 chains of between 20 and 80 aggregate buds, released by mature solitaries (S2). Dashed lines represent the shift in generation. Dotted line represents external fertilisation

Growth rates of up to 10% in length per hour (Heron 1972a) and efficient feeding strategies (Vargas & Madin 2004) also contribute to the high population growth of *Thalia democratica*. These adaptations appear to have an impact on other zooplankton within the marine community. It has been identified that copepods can be scarce when salps are abundant over an extended period of time (Humphrey 1963, Silver 1975). As salps can consume particles from a wide size range, they can remove copepods through consumption of copepod eggs and small nauplii (Vargas & Madin 2004), as well as remove enough particulate matter from the water column to exclude copepods (Nishikawa et al. 1995). Although *T. democratica* has also been reported to have a prey-predator relationship with the copepod *Sapphirina angusta* (Heron 1973), abundances of *S. angusta* throughout our study were negligible, so their effect on *T. democratica* was not considered.

Blooms of phytoplankton form along the continental shelf of eastern Australia as a result of the upwelling of cool nutrient-rich slope waters (Hallegraeff & Jeffrey 1993). These slope-water intrusions occur as a result of either current or wind-driven upwelling (for further information see: Roughan & Middleton 2002). Under upwelling-favourable conditions water can be brought to the surface, resulting in phytoplankton blooms (Cresswell 1994, Baird et al. 2006). Although it has been difficult to relate abundances of *Thalia democratica* to physical conditions, swarms of *T. democratica* have been commonly associated with processes such as upwelling or slope-water intrusions (Tranter 1962, Heron & Benham 1984).

The first extensive study of zooplankton in the western Tasman Sea quantified abundance of salps in net tows from 1938 to 1942 (Thompson & Kesteven 1942). *Thalia democratica* occurred at 80% of the 304 stations, although swarming occurred from September to January, the warmer months, and peaked in November (Thompson 1948). Along the New South Wales coast (28 to 37° S), Thompson took 236 samples from a 50 m to the surface vertical haul with a N70 net (see 'Materials and methods'). The maximum abundance recorded was 350 ind. m⁻³, with a mean of 16 ± 40 ind. m⁻³.

Other observations of salp swarms off southeast Australia have been recorded. Large swarms of *Thalia democratica* were observed at the Port Hacking 50 m station (34° 05' S, 151° 13' E) in 1959 and 1960, with the total zooplankton biomass (dominated by salps) reaching 1187 and 2399 mg m⁻³ (wet weight) (Tranter 1962). Humphrey (1963) observed a reduction in the spring bloom of phytoplankton as a result of 1959 and 1960 salp swarms. Further salp swarms were observed at the Port Hacking 100 m station (34° 05' S, 151° 15' E) from August to October and in December 1978 (Halle-

graeff 1981). Young (1989) also found high concentrations of salps on the outside and on the edge of a warm-core eddy (centred at 33° 30' S, 153° 30' E) in September and October 1979. Recent studies have identified the possibility to predict patches of salps based on meteorological and oceanographic data (Deibel & Paffenhofer 2009). The initial response of the salp population to oceanographic conditions should be evident in the population structure. Given the unusual life-history stages of *T. democratica*, the quantification of population structure is quite feasible. However, no study has quantified the 2 alternate life-history stages during bloom formation.

In the present study, we determined the spatial distribution and abundance of *Thalia democratica* in the western Tasman Sea in relation to water types following an austral spring bloom of phytoplankton. We identified hydrographic conditions that support the formation of *T. democratica* swarms by comparing the spatial distribution of size and population structure with water types. We also investigated the relationship between the abundance of *T. democratica* and copepods to examine the ecological impacts of these swarms.

MATERIALS AND METHODS

Study site. The surveyed area extended off southeast Australia in the Southwest Pacific Ocean, from Broughton Island in the north (32° 30' S, 152° 30' E) to Sydney in the south (34° S, 151° 30' E; Fig. 2). Four transects perpendicular to the New South Wales coast were sampled from 15 to 19 October 2008 aboard the RV 'Southern Surveyor'. These transects were made up of from 6 to 10 equidistant stations and were located with the aid of daily Moderate Resolution Imaging Spectroradiometer (MODIS) and Advanced Very High Resolution Radiometer (AVHRR) satellite imagery. Transects were identified as oceanographic points of interest that were most likely to stimulate strong biological responses. These hydrographic features included a cyclonic eddy off Sydney, continental slope water off Broken Bay and upwelling sites off Stockton Bight and Broughton Island (Fig. 2).

Sampling procedure. At stations along each transect, the vessel's Seabird SBE911-plus conductivity-temperature-depth (CTD) recorder equipped with a Chelsea AquaTracker Mk3 fluorometer was used to

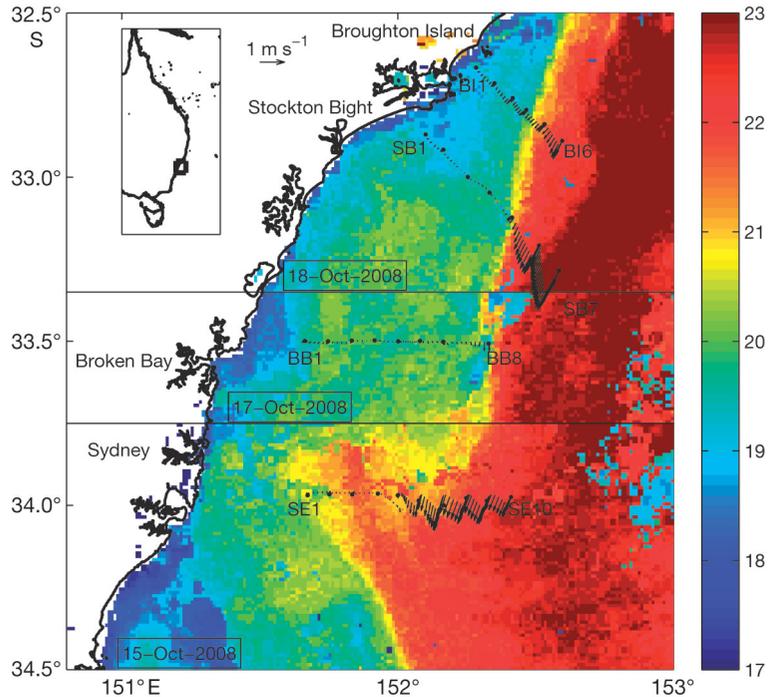


Fig. 2. Study area with sea-surface temperature (SST; °C) and surface current vectors overlaid. Dates refer to SST conditions on the day of sampling. Current vectors are shown from the vessel's Acoustic Doppler Current Profiler. The first and last sampling locations are labelled. BI: Broughton Island; SB: Stockton Bight; BB: Broken Bay; SE: Sydney Eddy. Data were sourced from archived Legacy Bureau of Meteorology SST Mosaic (LBoMSST), a $0.01^\circ \times 0.01^\circ$ gridded composite product. This product is based on a running weighted mean of observations over a 14 d period, with the most recent observations given the greatest weight. Due to the compilation of multiple satellite sources in the LBoMSST product and limited satellite passes, the oceanographic features are not always displayed exactly at the location of sampling within this image. The SST data for the present study were for within 24 h of the date shown for the Broken Bay, Broughton Island and Stockton Bight transects. The Sydney Eddy transect data were 1 to 2 d old

record salinity, temperature and fluorescence. The CTD was mounted on a rosette frame holding 10 l Niskin bottles. Water was collected in the Niskin bottles for chlorophyll *a* extraction at the surface and the fluorescence maximum. The fluorescence maximum depth was determined as the depth of the maximum fluorescence reading on the downcast. Water was filtered through 47 mm diameter, 0.7 μm Whatman glass fibre filters under low vacuum (<20 mm Hg) immediately after collection. The filter papers were then folded, blotted dry, wrapped in aluminium foil and frozen (-20°C) until laboratory analysis. Chlorophyll *a* concentration was determined using a Turner Trilogy fluorometer (Turner designs) according to the methodology of Parsons et al. (1984). Fluorescence readings were calibrated against measures of chlorophyll *a* concentrations from both surface and fluorescence

maximum depths at each CTD station ($n = 62$, chlorophyll $a = 0.1423[\text{fluorescence}] - 2.967$; $b = 0.142$, $t = 8.48$, $p < 0.001$, $R^2 = 0.55$).

To determine the spatial distribution of *Thalia democratica*, 2 replicate vertical hauls of a N70 net were made at the 31 CTD stations. The N70 net was used extensively during the 1938 to 1942 MV 'Warreen' cruises to sample zooplankton off southeast Australia (Thompson & Kesteven 1942). The use of the old net design was to facilitate comparison with the most comprehensive earlier study of zooplankton in the region. The N70 net was designed for the capture of medium and smaller size organisms (Kemp & Hardy 1929) and was modified for the present study to suit modern materials. This modified N70 net had a 70 cm opening and was made up of 3 sections: a 53 cm long, 4 mm mesh section near the mouth (formerly $\frac{1}{4}$ inch mesh); a 97 cm long, 400 μm mesh section (formerly silk, 70 mesh/inch); and a 135 cm long, 225 μm mesh section (formerly silk, 200 mesh/inch). The N70 net was hauled vertically from a depth of 50 m to the surface at a speed of 1 m s^{-1} . The samples were collected and immediately preserved in 5% formaldehyde in seawater. Samples that were collected during either dawn or dusk were not considered in the present study due to synchronised mating aggregations and release of buds that bias observations at those times of day (Heron 1972a,b, Heron & Benham 1984, Miller & Cosson 1997).

Laboratory procedure. The methods for calculation of *Thalia democratica* abundance were based on those of the 'Warreen' cruises (Thompson & Kesteven 1942). Samples from the N70 net were filtered through a 200 μm sieve and concentrated to 100 ml with a 5% formalin solution. If the concentrated sample exceeded 100 ml, a Folsom plankton splitter was used to distribute the sample into 2 jars. The 100 ml sample was gently mixed to ensure an even consistency of organisms suspended in the solution before two 1 ml replicate subsamples were taken with a wide-mouth pipette.

The first 60 *Thalia democratica* individuals, both aggregate and solitary forms, within each subsample

were measured and photographed using image analysis software (Image Pro Plus 5.1; Media Cybernetics). Measurements followed a standard method for the measurement of salps that involved the measurement of salp length from oral opening to the posterior ridge of the gut, exclusive of the outer test (Foxton 1966). A minimum of 100 zooplankton individuals per subsample were counted, with extra subsamples being examined if necessary. Organisms were classified into the following categories enumerating major taxonomic groups known to frequently occur off southeast Australia, following Thompson & Kesteven (1942): salps, doliolids, crustaceans, larvaceans, chaetognaths, *Noctiluca* and other zooplankton. In the present paper, only salp and copepod abundance is considered. Further community composition analysis was undertaken by Henschke (2009).

Analysis. Distinctions between water types were based upon a combination of temperature and salinity data obtained from CTD casts, as well as sea-surface temperature imagery (MODIS, AVHRR). Differences among water types were tested with analyses of similarity (ANOSIM). Zooplankton abundance was converted to abundance (individuals per m^3) using the towed volume. Towed volume was calculated from the mouth area of the net and multiplied by the distance towed (50 m). Statistical significance was assumed when $p < 0.05$, and normality was assessed through the use of a normal probability plot and the Shapiro-Wilk test (Shapiro & Wilk 1965). Data were $\log_{10}(x + 1)$ transformed if necessary to obtain normal distribution, and the assumption of homoscedasticity was tested with Levene's test. An unbalanced 1-way analysis of variance (ANOVA) was used to test the null hypothesis of no significant difference in *Thalia democratica* abundance among water types. Tukey's analysis was used for *a posteriori* pairwise comparisons between factor levels for all ANOVAs.

Analysis of population structure used different life-history stages based on length distinctions derived from Heron (1972a) and Heron & Benham (1985) (Table 1). The *Thalia democratica* life-history stages

Table 1. Life-history distinctions of *Thalia democratica* based on classifications identified by Heron & Benham (1985) and shown in Fig. 1. Duration is based on optimal growth conditions, whereby generation times are as short as 48 h (Heron 1972a)

Generation	Life-history stage	Size (mm)	Duration (h)	Notes
Aggregate	Buds (A1)	0–3	5	Released from solitary form
	Female (A2)	3–8	18	Female form supporting growth of solitary embryo
	Male (A3)	>8	2	Male form that fertilises buds upon release
Solitary	Immature (S1)	0–8	24	Brooding aggregate buds
	Mature (S2)	>8	24	Released first (of 3) chain of aggregate buds. Subsequent chains released every 5 h thereafter

examined in the present study include: aggregate buds (A1), aggregate females (A2), aggregate males (A3), immature solitaries (S1) and mature solitaries (S2) (Fig. 1, Table 1). For the remainder of our paper, life-history stages will be referred to as A1, A2, A3, S1, or S2. Frequency distributions for each life-history stage were used to create a matrix. Matrix data were \log_{10} -transformed to construct the Bray-Curtis similarity matrix. Hierarchical clustering was used to identify common groups of population structure. Similarity profile (SIMPROF) permutation procedure was used to identify the significance of the clusters ($p < 0.05$). To identify the life-history stages contributing most to similarities within clusters, as well as dissimilarity among clusters, similarity percentage analysis (SIMPER) was undertaken. Principal coordinates analysis (PCO) was then undertaken to highlight relationships between clusters and water types.

Regression analyses were used to examine correlations between *Thalia democratica* abundance and abundances of copepod crustaceans. They were performed with R, Version 2.9.1 (R Development Core Team). Other parametric tests were performed with Predictive Analytics Software, Version 18 (SPSS Inc.),

and all multivariate non-parametric tests were performed with PRIMER, Version 6 (PRIMER-E; Clarke & Warwick 2001, Clarke et al. 2008).

RESULTS

Hydrological environment

The EAC is the poleward-flowing western boundary current of the South Pacific. The study site is located in the region where the EAC becomes unstable and the coherent flow of further north develops into a meso-scale eddy field (Cresswell & Legeckis 1986). Depending on the location of these eddies, the EAC flow in the study region can either be directed in a poleward, along-shore direction, or offshore, as part of the Tasman Front (Baird et al. 2008).

In mid-September 2008, the EAC had a weak flow, with an average temperature range from 20 to 22°C and a significant retroflexion around 33° 30' S (Fig. 3a). By the commencement of sampling in October 2008, the EAC centre had warmed to 23°C and a strong eastward flow along the Tasman Front was pre-

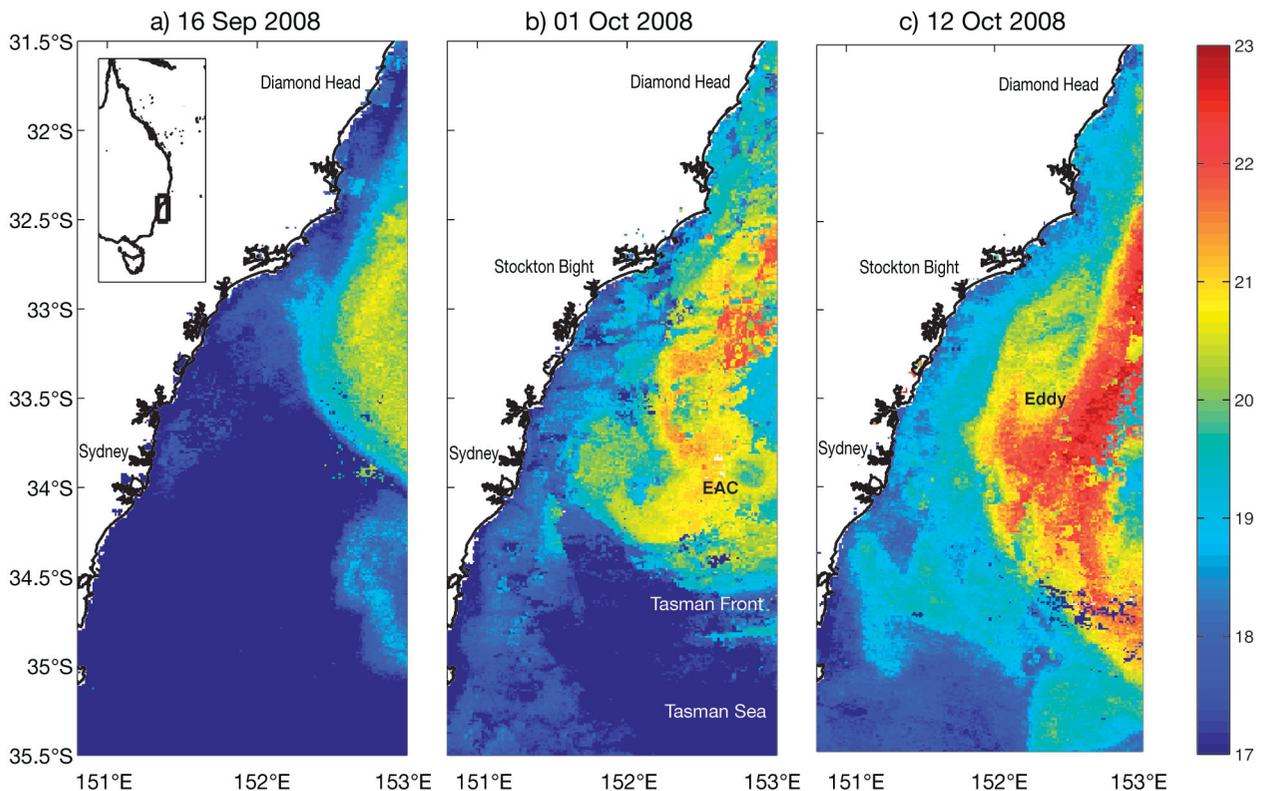


Fig. 3. Study area with sea-surface temperature (SST; °C) overlaid. Images are given for: (a) 1 mo prior (16 September 2008), (b) 2 wk prior (1 October 2008) and (c) at the formation (12 October 2008) of the coastal eddy centred at 33°S, 152° 30' E. The locations of the East Australian Current (EAC), Tasman Front, Tasman Sea and the cold core eddy (Eddy) are indicated

sent (Fig. 3b). The EAC temperature during this time was approximately 1 to 2°C warmer than the average over the previous 50 yr (from CSIRO Atlas of Regional Seas [CARS], Version 2006a. For further information see: Ridgway et al. 2002).

A small cyclonic eddy (40 km in diameter) formed between 10 and 12 October 2008, north of Sydney at 33°S, 152°30' E (Fig. 3c). This eddy was created from a filament of cold upwelled water, and, by 15 October 2008, it had been advected south by the adjacent EAC to 34°S, 152° E, where the Sydney eddy (SE) transect bisected it (Fig. 2). Due to the EAC meandering adjacent to the Sydney transect, the parallel Broken Bay (BB) transect did not intersect the EAC, only sampling inner shelf water adjacent to the Sydney eddy. On 17 October 2008, a chlorophyll *a*-rich filament had formed at the Seal Rocks coast (32.5°S) and extended offshore and southwards along the 200 m isobath to 33°30' S. The Stockton Bight (SB) and Broughton Island (BI) transects intersected this filament, as well as the EAC.

The characterisation of 3 water types follows those identified by Cresswell for the region (Plate II in Cress-

well 1994): inner shelf water, EAC water and upwelled water (Fig. 4; Table 2). EAC water is advected south from the Coral Sea and is warmer, but also typically fresher, than the surrounding waters (Fig. 2 in Baird et al. 2011; based on the CARS 2006a climatology, for further information see: Ridgway et al. 2002). The upwelled water has been lifted from the continental slope through the interaction of the EAC and the shelf (Roughan & Middleton 2002) and is therefore cooler and fresher. At the time of sampling, inspection of AVHRR and geostrophic currents (not shown) suggests inner shelf water is composed primarily of an earlier pulse of the EAC that moved onto the shelf in late September. The high salinity of inner shelf water suggests there has been little entrainment of upwelled water or freshwater inputs, although some mixing with saltier waters from further south along the shelf is possible.

During our observations, inner shelf water was more saline than both EAC and upwelled waters. This contrasts with other shelf systems where freshwater inputs often reduce salinity. Off southeast Australia there is little freshwater run-off, and the EAC is generally fresher than the surrounding Tasman Sea waters.

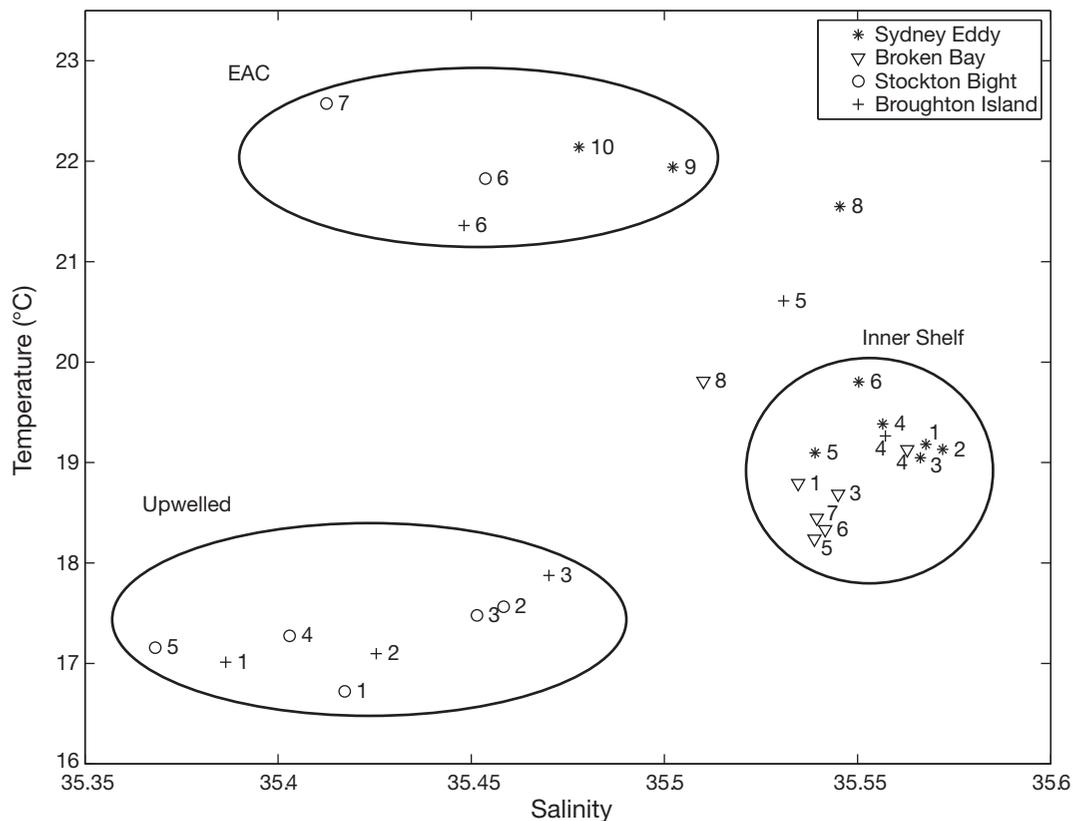


Fig. 4. Temperature–salinity diagram of depth-averaged (to 50 m) CTD values from inshore transects. Transects are numbered from west to east (see Fig. 2). Three groups of water types are circled and labelled. Stns SE8, BB8 and BI5 (not circled; $n = 3$) were removed from further analysis as they encompassed mixed water. EAC: East Australian Current

Table 2. Mean characteristics (\pm SD) of the 3 water types identified. Values are depth averaged over the top 50 m of the water column. The surface mixed layer depth is calculated from the minimum depth at which $T < T(10\text{ m}) - 0.4^\circ\text{C}$ or $S > S(10\text{ m}) + 0.03\text{ PSU}$ following Condie & Dunn (2006). Stations corresponding to each water mass are labelled. Values in parentheses correspond to ranges. n: number of stations; EAC: East Australian Current

Water type	n	Stations	Temperature ($^\circ\text{C}$)	Salinity	Surface mixed layer depth (m)	Fluorescence	Chlorophyll a ($\mu\text{g l}^{-1}$)
Inner shelf	13	BI4; BB1,3–7; SE1–6	18.96 \pm 0.45 (18.24–19.80)	35.55 \pm 0.01 (35.53–35.57)	29 \pm 14 (14–48)	29.13 \pm 3.44 (24.12–33.70)	1.18 \pm 0.49 (0.46–1.83)
EAC	5	SB6–7; BI6; SE9–10	21.97 \pm 0.44 (21.36–22.58)	35.46 \pm 0.03 (35.41–35.50)	41 \pm 6 (32–48)	24.95 \pm 6.51 (17.36–35.19)	0.68 \pm 0.80 (0–2.04)
Upwelled	8	SB1–5; BI1–3	17.27 \pm 0.36 (16.72–17.88)	35.42 \pm 0.04 (35.37–35.47)	19 \pm 12 (4–24)	34.73 \pm 2.71 (29.63–37.55)	1.97 \pm 0.39 (1.25–2.38)

Water type characteristics were depth averaged over the top 50 m of the water column to coincide with the zooplankton sampling depth (Fig. 4, Table 2). Stations SE8, BB8 and BI5 were classified as mixed water, as temperature–salinity signatures of these stations were a composite of the 3 previously distinguished water types; thus, they were removed from further analysis. Upwelled waters could be further distinguished from the EAC and inner shelf water by higher chlorophyll a concentrations (Table 2). ANOSIM results further confirmed that each water type was significantly different ($R = 0.96$, $p = 0.001$; Table 3).

Abundance and horizontal distribution

Salps were the most dominant zooplankton group in all samples, constituting 59% of total zooplankton, and

Table 3. Results of analyses of similarity (ANOSIM) among water types. Factors used in analyses were 50 m depth-averaged temperature, salinity and fluorescence and compared differences between water types. EAC: East Australian Current

Groups compared	Global R	p-value
EAC, Inner shelf	0.960	0.002
EAC, Upwelled	0.967	0.001
Inner shelf, Upwelled	0.979	0.001

this group was comprised exclusively of *Thalia democratica*. *T. democratica* aggregates were found across all stations (Table 4, Fig. 5) and were significantly more abundant than solitary forms ($F_{1,100} = 54.2$, $p < 0.001$), with a geometric mean abundance (\pm SD) of $334.29 \pm 6.95\text{ ind. m}^{-3}$ compared to $20.84 \pm 6.28\text{ ind. m}^{-3}$. Solitaries were absent at BI1 and SE10 (Fig. 5). Both geometric mean aggregate and solitary abundance differed significantly between water types ($F_{2,50} = 14.3$, $p < 0.001$; $F_{2,50} = 16.5$, $p < 0.001$). Tukey's post hoc analysis identified significantly greater numbers of aggregates and solitaries in inner shelf water relative to upwelled and EAC waters ($p < 0.001$).

Population structure

Similar trends in population structure were observed across water types (Fig. 6). The abundances of A1 and A2 individuals were significantly greater than abundances of A3 individuals across all water types ($F_{2,78} = 81.7$, $p < 0.001$), and S1 individuals were present at significantly higher abundances than S2 across all water types ($F_{1,52} = 10.7$, $p = 0.002$).

SIMPER analysis detected the life-history stage contributing most to similarities and dissimilarities among cluster groups. Cluster analysis on life-history stages defined 3 groups that could not be significantly further differentiated ($p < 0.05$; Fig. 7). Cluster A was defined by high proportions of A1 and A2 indi-

Table 4. Abundance (ind. m^{-3}) of aggregate and solitary forms of *Thalia democratica* in Tasman Sea water types during October 2008. n: number of stations; GM: geometric mean (\pm SD); AM: arithmetic mean (\pm SD); EAC: East Australian Current

Water type	n	Aggregate			Solitary		
		GM	AM	Range	GM	AM	Range
Inner shelf	25	1044.99 \pm 1.62	1165.09 \pm 551.06	407.35–2344.07	67.99 \pm 2.95	93.08 \pm 59.25	0–245.06
EAC	9	59.36 \pm 6.06	241.14 \pm 366.97	12.47–916.84	5.67 \pm 5.65	19.17 \pm 28.99	0–81.86
Upwelled	16	148.92 \pm 10.46	579.23 \pm 619.33	0–1613.83	6.83 \pm 5.48	23.50 \pm 48.34	0–196.47

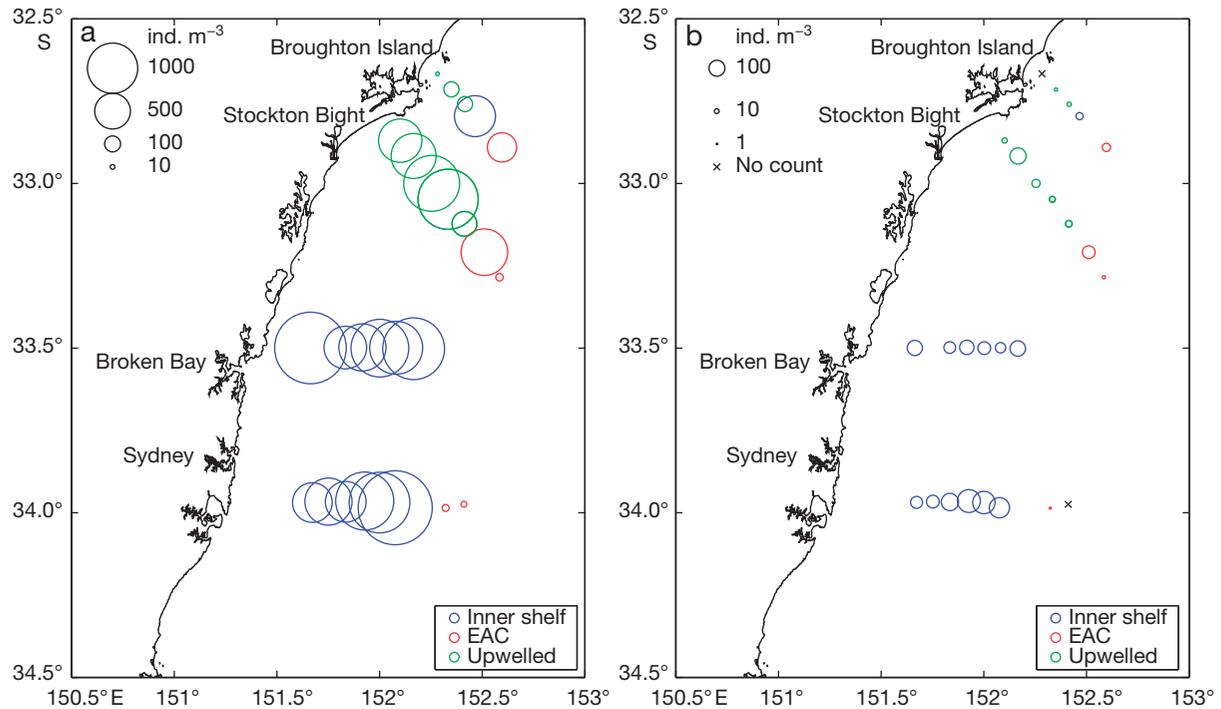


Fig. 5. Abundance distributions of *Thalia democratica* (a) aggregate and (b) solitary forms (ind. m⁻³). Colours represent water type classifications according to the key. Stations where no individuals were found are also shown (x). EAC: East Australian Current

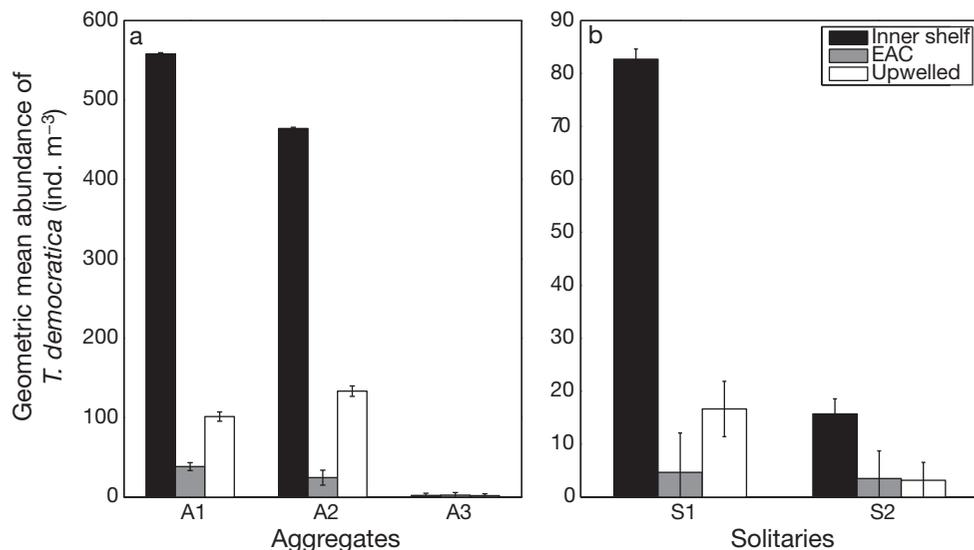


Fig. 6. Geometric mean abundance (ind. m⁻³, \pm SD) of *Thalia democratica* (a) aggregate and (b) solitary life-history stages, separated by water type. Refer to Fig. 1 for life-history classifications. EAC: East Australian Current

viduals and minimal proportions of other life-history stages. Clusters B and C were defined by high proportions of A1 and A2 individuals and high proportions of S1 and S2 individuals (Fig. 8). Dissimilarity between Clusters A and C (62%) and Clusters A and B (49%) were driven by the proportion of A2 individ-

uals. The dissimilarity between Clusters B and C (25%) was driven by the proportion of A1 individuals. The cluster groups also differed with abundances. The geometric mean abundance of *Thalia democratica* (aggregates and solitaries) within Cluster A was 14.55 ± 1.88 ind. m⁻³ compared to 99.30 ± 2.19 ind.

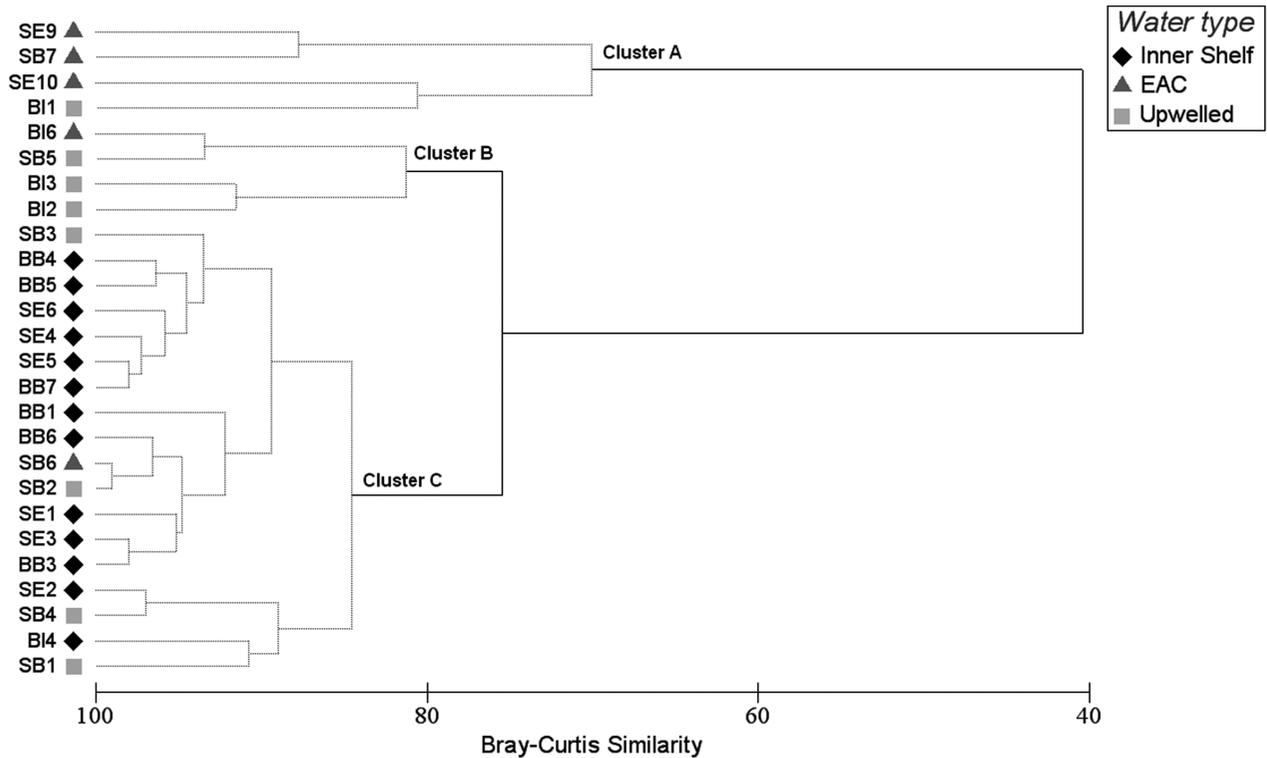


Fig. 7. Cluster analysis of *Thalia democratica* population structure. Dotted lines connect groups that are not significantly different ($p = 0.05$). Three main cluster groups were identified: Clusters A, B and C

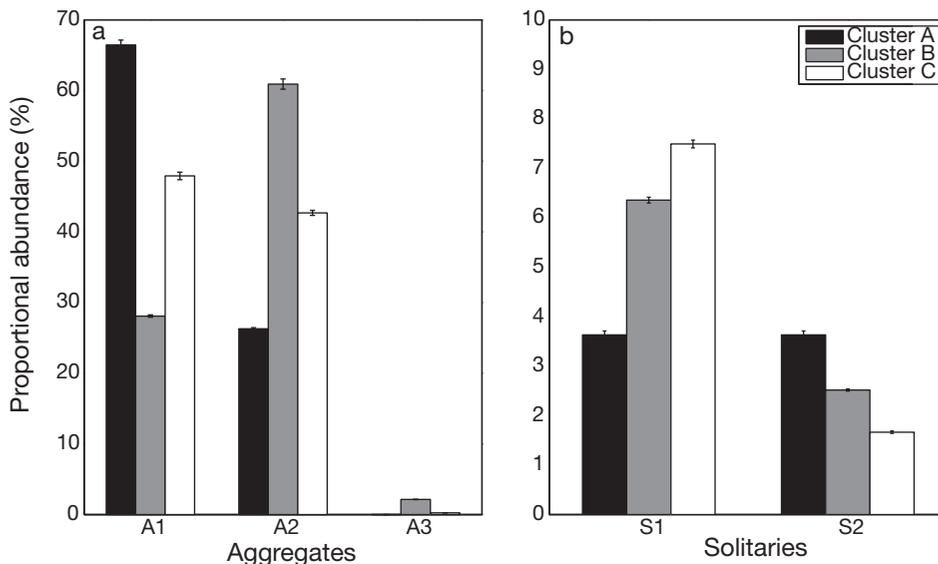


Fig. 8. Proportional abundance of *Thalia democratica* life-history stages (%; \pm SD) per cluster group

m^{-3} and $1010.07 \pm 1.81 \text{ ind. } m^{-3}$ for Clusters B and C, respectively (Table 5). Water types further distinguished cluster groups. Cluster A was made up mostly of EAC stations (75%); Cluster B, by upwelled stations (75%); and Cluster C, by inner shelf stations

(72%). Vectors overlaid on PCO analysis indicate that Cluster A is more strongly influenced by temperature, whereas Clusters B and C are more strongly influenced by chlorophyll *a* concentration and salinity (Fig. 9, Table 5).

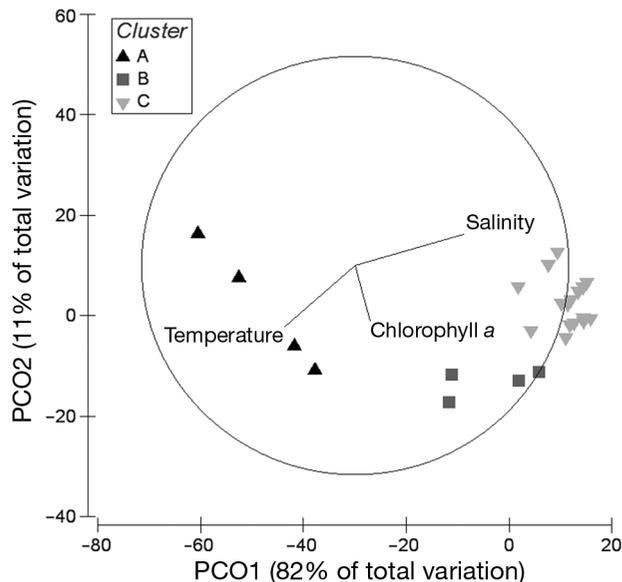


Fig. 9. Ordination of *Thalia democratica* population structure separated by cluster groups using principal coordinates analysis. Vectors overlaid are multiple correlations of water type variables (temperature, salinity and chlorophyll *a*)

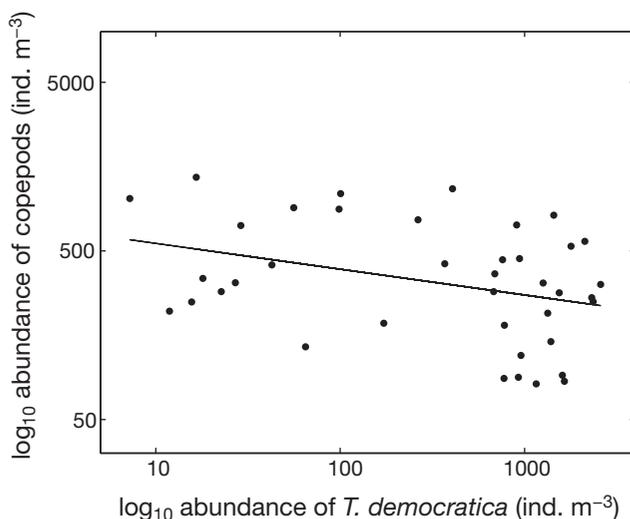


Fig. 10. Regression analysis between $\log_{10}(x + 1)$ -transformed copepod abundance and *Thalia democratica* abundance ($R^2 = 0.16$)

Table 5. Biological and hydrographic characteristics of cluster groups. Variables include *Thalia democratica* abundance (GM), temperature, salinity and chlorophyll *a*. Hydrographic variables are 50 m depth averaged. GM: geometric mean (\pm SD)

Cluster group	GM	Temperature (°C)	Salinity	Chlorophyll <i>a</i> ($\mu\text{g l}^{-1}$)
A	14.55 \pm 1.88	20.92 \pm 2.62	35.44 \pm 0.05	0.79 \pm 0.94
B	99.30 \pm 2.19	18.37 \pm 2.02	35.43 \pm 0.04	2.22 \pm 0.14
C	1010.07 \pm 1.81	18.74 \pm 1.13	35.52 \pm 0.05	1.23 \pm 0.55

Interactions with copepods

Copepods were the second most dominant zooplankton after *Thalia democratica*, constituting 23% of the total zooplankton abundance. Regression analysis identified a negative relationship between *T. democratica* abundance and copepod abundance ($b = -0.19$, $t = -2.92$, $p = 0.025$; Fig. 10). No other significant relationship was identified between *T. democratica* and any other zooplankton (Henschke 2009).

DISCUSSION

This is the first study of *Thalia democratica* abundance and distribution within the western Tasman Sea in over 60 yr. *T. democratica* constituted 59% of the total zooplankton sampled, and was the only salp species found throughout sampling (although *Thetys vagina* was occasionally found in other net types in low numbers). In the present study, the maximum abundance of *T. democratica* (2115 ind. m^{-3} at BB1) was double the highest globally recorded abundance (1000 ind. m^{-3}) (Andersen 1998) and almost an order of magnitude greater than maximum abundances sampled from the continental shelf and slope waters off southeast Australia during the period from 1938 to 1942 using similar sampling procedures (Thompson 1948, Baird et al. 2011). Isolated observations of salp swarms, particularly those in 1959 and 1960 (Tranter 1962), during which zooplankton biomass rather than counts of individuals was recorded, may have been of a similar size as the 2008 swarm.

Abundance and horizontal distribution

Three discrete inshore water types were identified based on satellite imagery and 50 m depth-averaged temperature–salinity signatures: inner shelf water, EAC water and upwelled water (Fig. 4). Abundances of aggregate and solitary forms of *Thalia democratica* were significantly greater in inner shelf water compared to other water types. Inner shelf waters were characteristically cooler than the EAC waters, with moderate surface chlorophyll *a* concentrations (Table 2). Phytoplankton analysis performed during the voyage confirmed higher proportions of diatoms ($>20 \mu\text{m}$) at stations located within the inner shelf water, whereas the EAC stations were dominated by smaller dinoflagellates and prochlorophytes that are indicative of tropical and EAC

waters (Hassler et al. 2011). Phytoplankton analyses were not undertaken for stations within the upwelled water; however, it has been reported that the frequent upwelling occurring within these stations characteristically promote diatom blooms (Dela-Cruz et al. 2007).

Thalia democratica feeds on a particle range of from <1 μm to 1 mm, but with maximum efficiency on diatoms and ciliates between 20 and 50 μm (Vargas & Madin 2004). This suggests that the differences in abundance of *T. democratica* between inner shelf and EAC water types may be driven by differences in phytoplankton community composition. Despite having a potentially preferable phytoplankton community composition, lower abundances of *T. democratica* were found within upwelled sites. A recent study suggests that there appears to be an inverse correlation between *T. democratica* abundance and phytoplankton abundance off southeast Australia (Deibel & Paffenhofen 2009). Abundances of *T. democratica* at the chlorophyll *a*-rich station (SB5; 263 ind. m^{-3} ; 3.5 $\mu\text{g l}^{-1}$) were almost equal to the maximum abundance calculated between 1938 and 1942 (350 ind. m^{-3}) (Thompson & Kesteven 1942) and were similarly high at other upwelled stations of high chlorophyll *a* concentrations (Table 4). Some species of salps become clogged in areas of high particulate material, although it is believed that subtle differences in feeding mechanisms or behaviour exist for other species like *T. democratica* that are able to exploit regions of increased productivity (Harbison et al. 1986). It has been observed that *T. democratica* may be able to regulate food intake when encountering areas of high particulate material by halting feeding or 'backwashing' to expel water (Deibel 1985). A more reasonable hypothesis explaining the lower abundances of salps within the upwelled stations appears to be the 'age' of the water. As the water sampled was upwelled a day earlier (for considerations of time-scales of advection of upwelled water in this region see: Macdonald et al. 2009), it is possible that the salps at these stations had not had enough time to take advantage of the available chlorophyll *a* resources, resulting in lower abundances compared to those in the inner shelf water. Interestingly, salp populations sampled during the present study in an offshore eddy characterised by old, nutrient-poor water (3 to 4 mo old) had a paucity of solitaries and were in very low abundances (for further information see: Henschke 2009).

Population structure

Marked zonation between distinct size ranges of *Thalia democratica* were not found in the present study. This contrasts with findings for populations of

Salpa thompsoni in the Southern Ocean (Kawaguchi et al. 2004), and is most likely due to the rapid growth and short generation times of *T. democratica*. Instead, 3 distinct groups of population structure were identified from cluster analysis. Cluster A was the most distinct, whereas Clusters B and C were only dissimilar by 25%.

Lower proportions of immature solitaries (S1 individuals) in Cluster A, as well as the absence of reproducing aggregates (A3), indicate slow rates of population growth and incomplete generations. This is also apparent in the density of the *Thalia democratica* populations, as Cluster A was comprised of stations with the lowest abundance of salps. High population density and abundances of A3 individuals are necessary for successful mating swarms (Heron 1972a). It is not likely that the populations within Cluster A will reach swarm levels, instead they are much like the sparse winter populations identified by Heron and Benham (Fig. 4 in Heron & Benham 1985).

In Clusters B and C, higher proportions of reproductive aggregates (A2 and A3) and their offspring (S1) suggest faster growing populations and mating success. Similar to the densely populated spring and summer populations (Heron & Benham 1985), these swarms were predominantly present in inner shelf and upwelled water. The hydrographic conditions that support these successful swarming aggregations were cooler temperatures and moderate chlorophyll *a* levels (Table 5). This is consistent with long term-trends observed in the Mediterranean Sea, which found significant correlations between increases in *Thalia democratica* swarm occurrence and cool, diatom-dominated waters (Licandro et al. 2006), as well as studies in the central Pacific Ocean (Yount 1958). Despite having similar hydrographic conditions, the salp population within the single upwelled station (BI1) in Cluster A was slow growing. The most recently upwelled station in the present study, as mentioned above, the salp community found at BI1, may not have had enough time to take advantage of the available food resources by the time of sampling.

Temperature has been identified as an important trigger promoting blooms of *Thalia democratica* within the Mediterranean Sea (Licandro et al. 2006); however, phytoplankton concentration also appears to influence *T. democratica* growth rates. At 20°C and with optimal food abundance, it has been found that *T. democratica* can grow at rates of 10% in length per hour, completing both generations within 2 d (Heron 1972a). In contrast, *T. democratica* growth rates (at 20°C) can be as low as 0.3 to 0.9% in length per hour when food sources are low (Deibel 1982). Based on these observations, it can be hypothesised that the characteristically warm, oligotrophic EAC waters are not suitable for

supporting the formation of salp swarms. Cluster A stations are more strongly driven by temperature (Fig. 9), and were comprised mainly of EAC stations. Cluster A populations are dominated by A1 and A2 individuals that were produced asexually. This suggests that an optimal food source is needed for growth and maturation of a salp population to include A3, and thus to promote sexual reproduction and successful completion of both generations.

Two EAC stations within this study (BI6 and SB6) were grouped in Clusters B and C, confounding this hypothesis. However, these stations are located on the EAC front, between EAC waters and the inner shelf (Fig. 2) and were characterised by phytoplankton communities indicative of inner shelf waters (higher abundance of diatoms as opposed to tropical communities) (Djajadikarta 2009). This is further supported by the high variability in chlorophyll *a* concentrations within EAC stations (Table 3) and the PCO analyses indicating that chlorophyll *a* is more strongly driving differences in Cluster B compared to in Cluster A (Fig. 9). Similarly, previous studies have also identified greater concentrations of salps and other zooplankton at temperature and salinity fronts (Atkinson et al. 1978, Deibel 1982), as fronts are generally thought to have greater phytoplankton abundance than adjacent waters (Graham et al. 2001).

Interactions with copepods

Despite the dominance of *Thalia democratica* throughout the majority of stations, abundances of copepods remained high (Fig. 10). The *T. democratica* population structure across each station illustrated that all populations were relatively young (dominated by A1). As *T. democratica* filtration rates increase with increasing size (Deibel 1985), more mature blooms would have a greater impact on copepod abundances through exploitative competition. Similar results were found in a study by Atkinson et al. (1978), where weak negative correlations were identified between crustacean zooplankton and a recently developed bloom of doliolids. However, enumerating gelatinous zooplankton as individuals to compare with other zooplankton may be misrepresentative due to high water content and size differences. Although it has been found that *T. democratica* has a tissue density more similar to crustaceans than other gelatinous zooplankton (Heron et al. 1988), more specialised sampling methods are necessary to provide more insight into the ecological impacts caused by salp swarms.

The results of the present study outline the prevalence of *Thalia democratica* during spring in the western Tasman Sea. It is often difficult to determine accu-

rate abundances of salps, as abundance and biomass can fluctuate depending on time of day, growth rate, or presence of mating aggregations (Heron 1972b). As we used identical methods to those used in the 'Warreen' cruises (Thompson & Kesteven 1942), abundances between studies can be reasonably compared. In our study, *T. democratica* were found to be approximately an order of magnitude more abundant than between 1938 and 1942 (Thompson & Kesteven 1942), and dominated the zooplankton community. Studies over a larger temporal scale are needed to identify whether abundances of *T. democratica* are increasing, or whether the observed swarm was an extreme event. As our study provides evidence for the potential competition that occurs within the zooplankton community as a result of salp swarms, it is necessary to further examine this theory.

The analysis of population structure was a novel and useful way to identify conditions supporting swarms of *Thalia democratica* and showed that swarming aggregations of *T. democratica* are dependent upon favourable hydrographic conditions. Within the western Tasman Sea, the inner shelf water appears to be a favourable environment for swarms. By examining the proportions of different life-history stages, one can determine the most sensitive stages driving high abundances, as well as identify the characteristics of the swarm to decide whether it is likely to be slow or fast growing. The present study provides a tool that can help determine the processes influencing the creation of salp swarms. Similar hydrographic conditions occur along other western boundary currents, such as the Gulf Stream or the Kuroshio Current, which also report frequent outbreaks of *T. democratica* swarms (Deibel & Paffenhofer 2009). As concerns are rising over shifts towards the dominance of gelatinous species within marine ecosystems (Richardson et al. 2009), it is important to examine the effects of increases in salp swarm frequency and occurrence on the marine environment. Implementing the use of population structure will help increase our understanding of the interaction between salp swarm dynamics and oceanographic processes.

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