Salp-falls in the Tasman Sea: a major food input to deep-sea benthos

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ABSTRACT: Large, fast-sinking carcasses (food-falls) are an important source of nutrition to deep-sea benthic communities. In 2007 and 2009, mass depositions of the salp *Thetys vagina* were observed on the Tasman Sea floor between 200 and 2500 m depth, where benthic crustaceans were observed feeding on them. Analysis of a long-term (1981 to 2011) trawl survey database determined that salp biomass (wet weight, WW) in the eastern Tasman Sea regularly exceeds 100 t km^{-3} yr^{-1}, with biomasses as high as 734 t km^{-3} recorded in a single trawl. With fast sinking rates, salp fluxes to the seafloor occur year-round. Salps, like jellyfish, have been considered to be of low nutritional value; however, biochemical analyses revealed that *T. vagina* has a carbon (31% dry weight, DW) and energy (11.00 kJ g^{-1} DW) content more similar to that of phytoplankton blooms, copepods and fish than to that of jellyfish, with which they are often grouped. The deposition of the mean yearly biomass (4.81 t km^{-2} WW) of salps recorded from the trawl database in the Tasman Sea represents a 330% increase to the carbon input normally estimated for this region. Given their abundance, rapid export to the seabed and high nutritional value, salp carcasses are likely to be a significant input of carbon to benthic food webs, which, until now, has been largely overlooked.

KEY WORDS: Benthic communities · Gelatinous zooplankton · Carbon cycling · Fluxes · Salp-fall · Jelly-fall

INTRODUCTION

Food-limited deep-sea benthic ecosystems rely on depositions of organic matter from the euphotic zone (Gooday 2002). Concentrated pulses of particulate organic matter (POM) derived from differing sources including phytoplankton blooms, other plant or algal matter, zooplankton faecal pellets and carcasses of larger fauna are major contributors of organic matter to the sea floor (Rowe & Staresinic 1979, Smith et al. 2008). Despite the majority of particles being small (<5 mm) (Alldredge & Silver 1988), these pulses are

an important source of nutrition for deep-sea benthic communities, promoting both species richness and abundance (Butman et al. 1995). Benthic ecosystem functions are also positively related to increasing POM supply, including sediment community respiration rates and organic matter remineralisation (Witte & Pfannkuche 2000, Smith et al. 2008, Sweetman & Witte 2008).

Large, fast-sinking particles, such as carcasses, provide food-fall events that augment the nutritional ecology of deep-sea benthic communities (Rowe & Staresinic 1979, Stockton & DeLaca 1982, Smith & Baco 2003). The 'gelatinous pathway' (Billett et al. 2006, Lebrato et al. 2012) was first discovered by Moseley (1880) and illustrates the potential for sinking carcasses of gelatinous organisms to contribute a large flux of organic matter to the benthic environment. Because of their swarming nature, depositions of gelatinous carcasses generally accumulate in high densities to the benthic environment in areas underlying large and persistent gelatinous populations (Billett et al. 2006, Lebrato & Jones 2009). For example, following swarms in surface waters (Wiebe et al. 1979, Grassle & Morse-Porteous 1987), dense concentrations of salp carcasses were observed nearby on the seafloor in the outer Hudson Canyon (3240 m) in 1975 and 1986 (Cacchione et al. 1978). Similarly, pelagic cnidarian deposits (jelly-falls) have been recorded on the sea floor off Oman (Billett et al. 2006), in the Sea of Japan (Yamamoto et al. 2008) and in a Norwegian fjord (Sweetman & Chapman 2011), while pyrosome carcasses have been observed on the Madeira Abyssal Plain (Roe et al. 1990) and on the seafloor off the Ivory Coast (Lebrato & Jones 2009).

During 2 benthic sampling research voyages, we observed mass depositions of the large salp *Thetys vagina* on the Tasman Sea floor, prompting an examination into their subsequent fate and the nutritional value provided by the carcasses to the deep-sea benthic communities. *T. vagina* reaches up to 306 mm in size (Nakamura & Yount 1958) and has a distribution spanning the top 200 m (Thompson 1948, Iguchi & Kidokoro 2006) of sub-tropical and temperate waters of the Mediterranean Sea and the Atlantic, Indian and Pacific oceans (Berrill 1950). Salp carcasses can potentially sink at rates of up to 1700 m d^{-1} (Lebrato et al. 2013), suggesting that little, if any, decomposition occurs during descent, and mass depositions of salp carcasses may represent an important and substantial food-fall event for the benthic ecosystem. Although several reports indicate that gelatinous organisms such as salps are important to the diet of some marine organisms (e.g. Duggins 1981, Clark et

al. 1989, Lyle & Smith 1997, Gili et al. 2006), they are still generally thought to be of low nutritional value (Moline et al. 2004). Therefore, to determine whether salp carcasses can positively contribute to the benthic ecosystem, it is necessary to identify the quality of food they provide.

In particular, we sought to (1) assess the frequency and abundance of salp swarms in the Tasman Sea and eastern New Zealand over 30 yr, (2) quantify the biomass and relative abundance of *Thetys vagina* carcasses on the sea floor, and (3) compare the energetic input and the biochemical composition of *T. vagina* carcasses with other gelatinous zooplankton.

MATERIALS AND METHODS

Study region

Long-term trawl surveys and 2 benthic sampling cruises were conducted in the southern Tasman Sea and Pacific Ocean east of New Zealand (Fig. 1A). For the first benthic study on board the RV 'Tangaroa' in June 2007 (TAN0707), sampling was carried out on the Challenger Plateau, a large submarine plateau extending from the west coast of central New Zealand and considered to be a region of low pelagic productivity (Wood 1991). In October 2009, on the second benthic study on board the RV 'Southern Surveyor' (SS03/2009), sampling occurred off southeastern Australia in Bass Canyon, one of the largest submarine canyons in the world (Mitchell et al. 2007).

Trawl data analysis

Trawl data were available from 2 sources: a long-term data series (30 yr) from the New Zealand fisheries research trawl database and pelagic trawls in the Tasman Sea over 3 yr. Salp and pyrosome biomass was obtained from analysis of the New Zealand fisheries database (stock assessment, research and observer-monitored commercial trawls) from 1981 to 2011 (n = 2044; see Fig 1A for sampling locations). As the majority of data was opportunistically sampled, sampling periods within a year are variable but on average include every month per year. Trawls (midwater or benthic) were towed at a mean depth of 563.17 ± 342.40 m, ranging from 33 to 2532 m. Where possible, recorded trawl dimensions and tow lengths were used. If details of trawl size or tow distance were not available, a standard averaged value calculated from all trawls was used (headline height = 8 m,
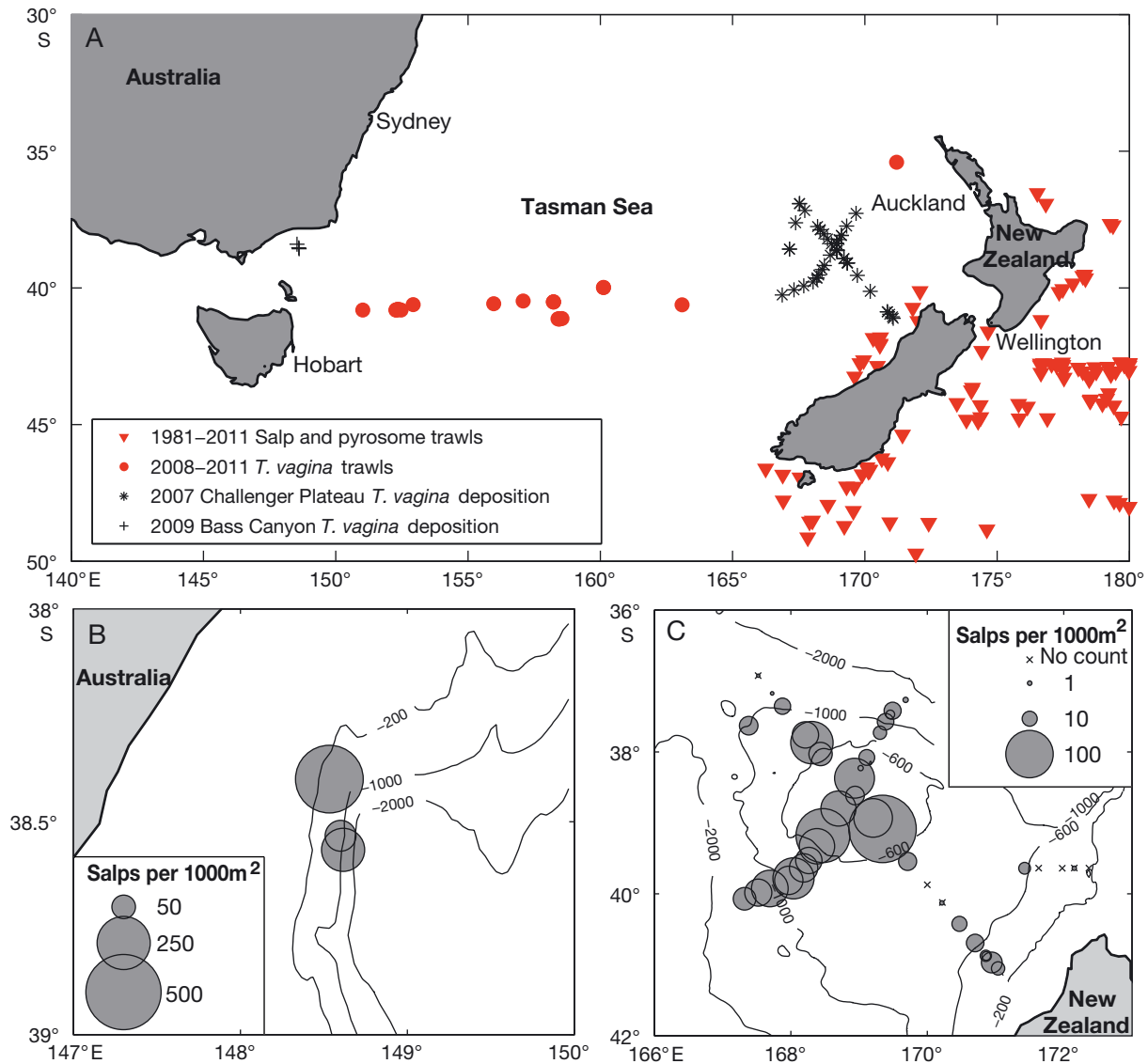
Fig. 1. (A) Survey area in the southern Tasman Sea and southwestern Pacific Ocean east of New Zealand showing trawl stations and benthic sampling stations. (B,C) Density distribution based on video footage/camera stills of *Thetys vagina* (ind. 1000 m⁻²) at different stations (B) in Bass Canyon and (C) on the Challenger Plateau. Depth contours are displayed in metres

wing distance = 30 m, tow distance = 4.4 km, tow speed = 6.5 km h⁻¹). Individuals were not classified into species. *Thetys vagina* biomass was obtained from 3 trans-Tasman cruises in 2008, 2009 and 2011 (n = 12). Depth-stratified midwater tows with a pelagic trawl were made at 200 m intervals to a maximum depth of 1000 m from the surface, with equal 20 min tows at 6.5 km h⁻¹. The biomass estimates of *T. vagina* from the trans-Tasman pelagic trawls were calculated from the net area with the smallest mesh size capable of capturing them (minimum 40 mm mesh). Graded mesh area information was not available for the nets used in the New Zealand fisheries database, and as a result, biomass estimates are more

conservative than data obtained from the trans-Tasman pelagic trawls. All biomass estimates are represented in wet weight (WW).

Benthic sample collection and analysis

At both benthic sampling locations, video surveys were conducted using towed camera platforms with video and still image cameras. All individual salps observed on the seabed were counted along the full length of each video transect. If necessary, still camera images taken every 2 min along the transects were used to aid in identification of individuals.

Deployments lasted from 30 to 60 min, at speeds of 0.25 to 0.50 ms^{-1}. On the Challenger Plateau, 46 deployments of the Deep Towed Imaging System (Hill 2009) were conducted at depths ranging from 237 to 1831 m. Both video and still cameras were oriented directly downwards, to facilitate scaling, and video frame width was calculated in ImageJ (http://rsbweb.nih.gov/ij/) by measuring widths of approximately 100 frame grabs using the camera's paired lasers (20 cm apart) as a reference. In Bass Canyon, the Benthic Optical and Acoustic Grab System (Sherlock et al. 2010) was deployed at 3 depths: 450, 650 and 1500 m. As the camera system did not have paired lasers, video frame width was measured by using the average (± SD) length of *Thetys vagina* species caught from the subsequent Bass Canyon trawls (55.66 ± 5.90 mm, n = 30) to approximate frame size from 17 randomly chosen screenshots containing *T. vagina*. Abundance of individuals per 1000 m^2 (ind. 1000 m^{-2}) was calculated by determining salps per corrected area of deployments (corrected area = transect seabed area × percentage of usable video footage). Video analyses were run in Ocean Floor Observation Protocol (http://ofop.texel.com); see methods in Bowden et al. (2011). Still image analyses used ImageJ software.

After each towed camera transect, benthic fauna were sampled at the same site using either a beam trawl (4 m mouth width, 10 mm mesh) or an epibenthic sled (1 m mouth width, 25 mm mesh). Trawls were towed for approximately 15 min at 0.75 m s^{-1}. Once back on deck, all fauna were sorted into species, weighed for biomass estimates and frozen (–20°C).

Salps were thawed, and total length and wet weight were measured for each individual. Guts were removed prior to biochemical analysis to ensure that only body tissue was analysed. Randomly selected individuals from each site were then freeze-dried and their dry weights (DW) recorded. To determine ash-free dry weight (AFDW) of the specimens, tissue samples were taken and combusted at 550°C for 24 h. All remaining tissue was ground in a ball mill to give a homogenous powder for biochemical analyses.

Biochemical analyses

Protein content of the salps was measured using the Bradford protein assay (Bradford 1976) with bovine serum albumin as the standard. Lipid content of the salps was estimated using a chloroform: methanol procedure after Folch et al. (1957) and carbohydrate content was estimated following Dubois et al. (1956) with D-glucose as the standard. Energetic values of the salps were determined with a Parr 6200 isoperibol calorimeter using a benzoic acid standard and as per the manufacturer's instructions (Parr Instrument Company 2008).

Carbon and nitrogen contents were measured by combusting the material and using gas chromatography to separate the resulting N$_2$ and CO$_2$ gases. The gases were then analysed with an Isoprime isotope ratio mass spectrometer to give total carbon and nitrogen content. An average of the carbon content (n = 68, 31.35% DW) per salp for both locations was used to calculate carbon standing stock (mg C m^{-2}) from the carcasses observed. All salps viewed in the video transects were assumed to have a DW of 0.38 g (the mean of n = 27 weighed individuals), allowing carbon standing stock to be calculated per square metre. While this is an approximation, we are confident that all carcasses seen in the video and captured in benthic gear were of similar size.

RESULTS

Observations of *Thetys vagina* on the sea floor

Carcasses of *Thetys vagina* were observed in all 3 video transects in Bass Canyon and in 38 out of 46 transects on the Challenger Plateau (Fig. 2A). In total, 368 carcasses were recorded in Bass Canyon comprising 47.8% of the total observed fauna over an area of 2118 m^2. The mean (± SD) density of *T. vagina* was 219 ± 168 ind. 1000 m^{-2}, with a minimum density of 85 and a maximum of 408 ind. 1000 m^{-2} (Fig. 1B). On the Challenger Plateau, 1400 individuals were observed, making up 9.8% of total observed fauna over an area of 72 995 m^2. In 11 transects where abundances of *T. vagina* were high (>20 ind. 1000 m^{-2}, Fig. 1B), *T. vagina* carcasses ranged from 19.6 to 48.7% of the total fauna observed, similar to that found in Bass Canyon. The mean (± SD) density of *T. vagina* on the Challenger Plateau was 26 ± 39 ind. 1000 m^{-2}, significantly lower than densities found in Bass Canyon (p < 0.001, $F_{1,48}$ = 40.1, ANOVA), with a minimum density of 0 and a maximum of 202 ind. 1000 m^{-2} (Fig. 1C). *T. vagina* comprised 19.0% of total haul biomass on the Challenger Plateau and 42.6% of total haul biomass in Bass Canyon and was the dominant organism in both locations (see Appendix 1). During one transect on the Challenger Plateau, the deep-water spider crab *Platymaia maoria* was twice observed directly feeding on *T. vagina* carcasses (Fig. 2B; Table 1). On 17 occasions across 9
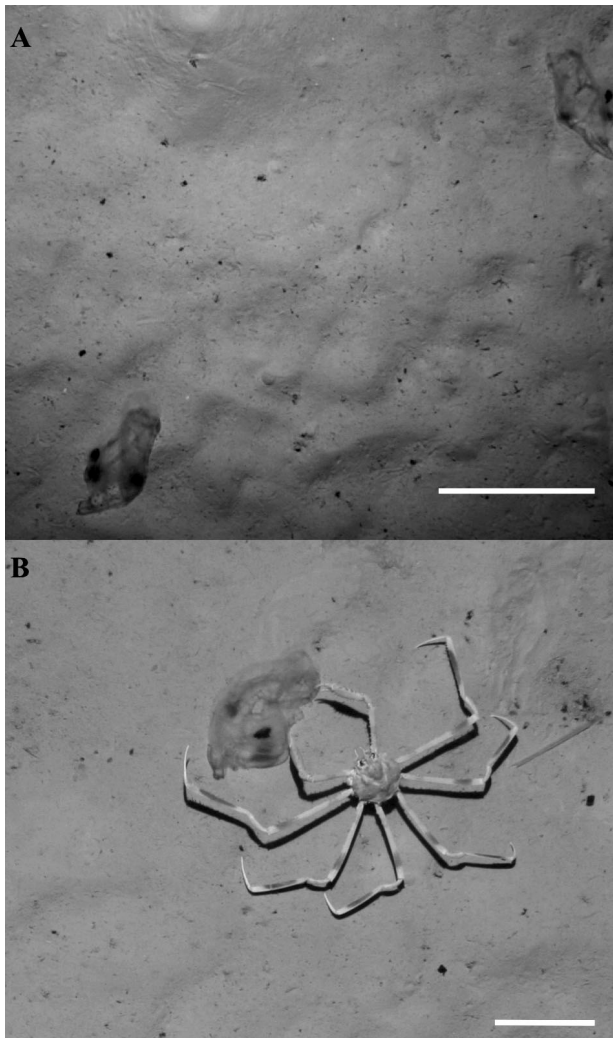
Fig. 2. Sea floor photographs from the Tasman Sea. Scale bars = 10 cm. (A) *Thetys vagina* carcasses at 1565 m depth taken in Bass Canyon. (B) *Platymaia maora* feeding on *T. vagina* carcass at 482 m on the Challenger Plateau

transects, demersal fish and sea stars were recorded near the carcasses (Table 1). The most common demersal fish were rattails *Coelorinchus* spp. and were found close to the carcasses on 10 occasions. At both locations, all *T. vagina* individuals observed on the sea floor were dead, whole and with no visible bacterial mats or biofilms.

Abundance of *Thetys vagina* and other large salps and pyrosomes in the Tasman Sea

Analysis of the New Zealand fisheries database from 1981 to 2011 determined that salp and pyrosome biomass exceeded 100 t km^{-3} WW (56 t km^{-2}) in approx-

Table 1. Megafaunal taxa observed directly feeding on or close to (potential feeders) *Thetys vagina* carcasses on the Challenger Plateau. Footnotes b to e denote previous records of taxa feeding on salps

	No. of events
Crustacea	
Platymaia maoria	2[a]
Fish	
Coelorinchus sp.[b]	10
Paraulopus sp.	1
Tripterophycis gilchristi	1
Helicolenus sp.[c]	1
Hoplichthys haswelli	1
Hydrolagus novaezelandiae[d]	1
Echinodermata	
Ophiuroidea	2
Asteroidea[e]	1

[a]Direct feeding observed; [b]Clark (1985); [c]Bax & Williams (2000); [d]Dunn et al. (2010); [e]Domanski (1984)

imately half of the years sampled (Fig. 3A). Biomass ranged from 0.006 t km^{-3} WW (0.003 t km^{-2}) to 1464 t km^{-3} WW (824 t km^{-2}), with a 30 yr average (±SD) of 8.54 ± 51.79 t km^{-3} WW (4.81 t km^{-2}). Salps and pyrosomes were present year-round but appear to form dense swarms an order of magnitude greater than their normal occurrence between December and June (Fig. 3B).

High densities of *Thetys vagina* were captured in 3 trans-Tasman cruises in 2008, 2009 and 2011 (Fig. 3A), with a maximum of 734 t km^{-3} WW (147 t km^{-2}) caught in 2009 (minimum = 0.003 t km^{-3} WW, mean (±SD) = 44.82 ± 158.20 t km^{-3} WW). Depth-stratified sampling showed that 98% of *T. vagina* biomass occurred in the top 200 m of the water column.

Biochemical composition of *Thetys vagina*

Lipids accounted for the highest proportion of macronutrients, making up a mean (±SD) of 10.5 ± 2.8% DW (Table 2). Protein constituted 3.4 ± 1.5% DW, and carbohydrates constituted 4.4 ± 1.9%. The mean (± SD) energetic content of *Thetys vagina* was 11.0 ± 1.4 kJ g^{-1} DW. AFDW was high, ranging from 33 to 88% DW, and total organic content of *T. vagina* represented only 31% of AFDW.

Mean (± SD) carbon content for *Thetys vagina* (31.4 ± 5.4% DW) was much higher than nitrogen content (2.8 ± 1.1% DW; Table 2). Carbon standing stock of the *T. vagina* deposition in Bass Canyon was 26.1 mg C m^{-2}. On the Challenger Plateau, carbon standing stock was lower, with a mean of 3.1 mg C m^{-2}

Table 2. *Thetys vagina*. Biochemical and elemental composition. n = number of individuals measured

	n	Mean ± SD	Range
Protein content (% DW)	68	3.42 ± 1.46	1.10–7.34
Lipid content (% DW)	31	10.50 ± 2.77	6.19–16.48
Carbohydrate content (% DW)	18	4.36 ± 1.92	1.34–7.77
Energetic content (kJ g^{-1} DW)	9	11.00 ± 1.38	8.91–13.33
Carbon content (% DW)	68	31.35 ± 5.34	18.77–42.68
Nitrogen content (% DW)	68	2.82 ± 1.13	1.52–8.09
C:N	68	12.03 ± 3.03	4.73–19.05

but reaching 24.1 mg C m^{-2} at some stations. Using C:N ratio and energetic content as an indicator of nutritional quality, *T. vagina* is nutritionally similar to phytoplankton (Fig. 4). Values for *T. vagina* are much greater than reported values for cnidarians and ctenophores.

DISCUSSION

Observations of *Thetys vagina* on the sea floor

Densities of *Thetys vagina* carcasses observed on the sea floor in this study are among the highest recorded for any gelatinous zooplankton deposition.

These mean densities of *T. vagina* (26 and 219 ind. 1000 m^{-2} for the Challenger Plateau and Bass Canyon, respectively) are much greater than those found for depositions of the giant jellyfish *Nemopilema nomurai* in the sea of Japan (1.1 ind. 1000 m^{-2}) (Yamamoto et al. 2008) and the deep-sea scyphozoan *Periphylla periphylla* in a Norwegian fjord (10 ind. 1000 m^{-2}) (Sweetman & Chapman 2011). Densities were similar to those of *Pyrosoma atlanticum* carcasses off the Ivory Coast (70.6 ind. 1000 m^{-2}) described by Lebrato & Jones (2009). The mass depositions of fresh carcasses observed in this study indicate the recent demise of swarms at both locations. On the Challenger Plateau, high densities of *T. vagina* were observed at the surface during sampling, suggesting that the swarm may still have been developing for several weeks after sampling. Sampling during an ongoing swarm may limit the accuracy of the deposition densities, as some salp and pyrosome species are known to migrate to sea floor depths (Roe et al. 1990, Gili et al. 2006). As *T. vagina* mainly occurs in the top 200 m of the water column and all carcasses viewed on the video were dead or moribund, it is unlikely that deposition abundances were overstated.
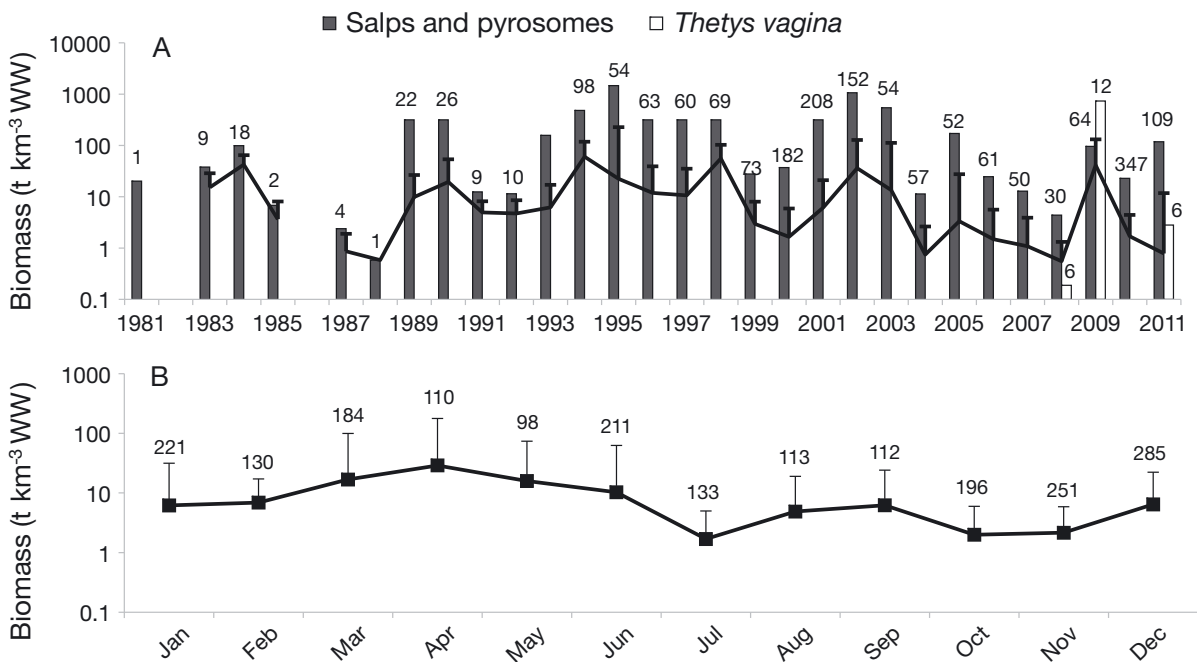

Fig. 3. (A) Maximum yearly biomass for salps and pyrosomes (dark grey bars; New Zealand fisheries database) from 1981 to 2011 and *Thetys vagina* (white bars; trans-Tasman pelagic trawls) in 2008, 2009 and 2011. Yearly mean (+SD) is represented by the solid line. Number of trawls per year is indicated above each bar. Station locations are presented in Fig. 1. (B) Mean (+SD) monthly biomass of salps and pyrosomes from 1981 to 2011. Number of trawls per month is indicated above each bar. WW = wet weight
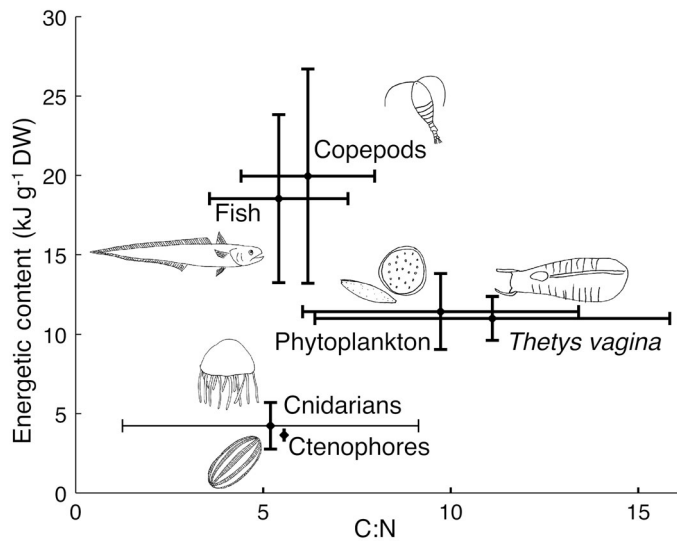
Fig. 4. Relationship between mean (±SD) energetic content and mean (±SD) C:N ratio as an indicator of quality of different marine organisms as a food item. Values for *Thetys vagina* obtained from this study. Other values obtained from previous studies: phytoplankton (Platt & Irwin 1973), copepods (Donnelly et al. 1994, Ikeda et al. 2006), cnidarians and ctenophores (Clarke et al. 1992) and fish (Childress & Nygaard 1973). DW = dry weight

Abundance of *Thetys vagina* and other large salps in the Tasman Sea

Other large salps such as *Salpa thompsoni* (Nishikawa et al. 1995, Perissinotto & Pakhomov 1998) and *S. aspera* (Wiebe et al. 1979, Madin et al. 2006) frequently form large swarms, but records of *Thetys vagina* are sparse. The largest swarm recorded of *T. vagina* occurred in 2004 in the Sea of Japan, with biomasses as high as 900 t km^{-3} WW (Iguchi & Kidokoro 2006), comparable to the maximum of 734 t km^{-3} WW recorded in this study. As New Zealand fisheries surveys were designed for the capture of large pelagic and demersal fish, they are likely to under-represent the true abundances of salps. Trawls would only spend approximately 35% of their time in the 0 to 200 m depth range that is preferred by the majority of large salps in the Tasman Sea (Thompson 1948). Regardless, abundances of salps across the 30 yr dataset indicate that salp biomass in the Tasman Sea often exceeded 100 t km^{-3} WW, which is considerably higher than previously thought.

Tranter (1962) recorded an average zooplankton biomass (excluding salps) of 36 t km^{-3} WW from 1959 to 1961 in the Tasman Sea, with salps accounting for an additional 53 t km^{-3} WW. Maximum swarm values from the present study show that large salp and pyrosome swarms in the Tasman Sea can frequently

exceed zooplankton biomass by 300%. Similarly, Young et al. (1996) sampled zooplankton in the Tasman Sea from 1992 to 1994 and found salps on average made up 30% of zooplankton biomass across the 3 yr and at some times up to 90%. To put salp biomass into perspective, hoki *Macruronus novaezealandiae* constitutes New Zealand's largest fishery (O'Driscoll 2004), with biomass estimated to be 1.2 t km^{-2} WW (based on an 8 yr average) and representing 97% of all fish biomass in the midwater depth range (Bull et al. 2001). The mean 30 yr average of large salp biomass (4.81 t km^{-2} WW) for the Tasman Sea and New Zealand region not only exceeds this value but also indicates the prevalence of salp swarms in the Tasman Sea.

Biochemical composition of large salps

This study provides the first data on the biochemical composition of *Thetys vagina*. Results obtained are within expected ranges observed for other large salps (Madin et al. 1981, Clarke et al. 1992, Dubischar et al. 2006). Similar to our salps, higher proportions of lipids to protein are found in the Antarctic species *Salpa thompsoni* (5.7 to 6.8% DW) (Dubischar et al. 2006), while the opposite trend is observed for North Atlantic salp species: 0.96, 0.25 and 0.97% DW for *Pegea confoderata, S. cylindrica* and *S. maxima*, respectively (Madin et al. 1981). Differences in the biochemical composition of salp species are likely to arise from either differing lipid concentrations within food sources (Larson & Harbison 1989) or environmental conditions inciting higher storage of lipids in cooler waters (Dubischar et al. 2006). Previous studies show that carbohydrate contents for salps are generally low (0.8 to 1.3% DW) (Madin et al. 1981, Clarke et al. 1992, Dubischar et al. 2006); however, this study recorded levels similar to those of protein. These higher values are consistent with expected results, as the salp tunic is mainly comprised of proteins and polysaccharides (Godeaux 1965).

Although the total organic content (lipids, proteins and carbohydrates) of an organism should equal its AFDW (Madin et al. 1981), high values of AFDW are characteristic for gelatinous zooplankton because of difficulties in removing 'water of hydration' (Madin et al. 1981) when freeze-drying. Similar AFDW values have been found for other salps: 27 to 62.7% DW for *Salpa thompsoni* (Huntley et al. 1989, Donnelly et al. 1994) and 66.4% DW for *S. fusiformis* (Clarke et al. 1992), with total organic contents ranging from 19 to 51% of AFDW (Madin et al. 1981, Dubischar et al.

2006). Apart from residual water, the most likely causes for the 'missing' compounds are those missed by the methodology. For example, as the nitrogen content of protein can be assumed to be 16% (protein = N × 6.25) (Madin et al. 1981), from the nitrogen values recorded here, protein content should have been as high as 17.6% DW, 4 times higher than our detected values. Similar problems detecting proteins in gelatinous zooplankton have been seen in previous studies (Clarke et al. 1992, Dubischar et al. 2006) and are thought to arise from problems with detecting cross-linked proteins.

Contribution to the benthic food web

Energetic content of *Thetys vagina* was higher than that of cnidarians and ctenophores (4.35 to 10.17 kJ g^{-1} DW) (Percy & Fife 1981) and other pelagic tunicates such as *Pyrosoma atlanticum* (4.94 ± 1.55 kJ g^{-1} DW) (Davenport & Balazs 1991) and almost as high as some crustacean species (14.77 ± 1.67 kJ g^{-1} DW) (Wacasey & Atkinson 1987). Of all gelatinous zooplankton studied to date, carbon content for *T. vagina* was second only to *P. atlanticum* (Davenport & Balazs 1991, Lebrato & Jones 2009). The energetic content and C:N ratios suggest that *T. vagina* carcasses have higher food value than other gelatinous zooplankton (cnidarians and ctenophores) (Fig. 4) and nutritionally are more similar to the phytoplankton blooms that normally sustain benthic communities (Rowe & Staresinic 1979, Smith et al. 2008) as well as fish and copepods. As only the tunic of *T. vagina* was analysed, nutritional quality has not been elevated by gut contents. Compared to smaller salps, the tunic of *T. vagina* is relatively thick and composed of densely packed fibrous material (Hirose et al. 1999), possibly resulting in elevated nutritional values. Based on maximum salp biomass values of 100 t km^{-3} WW, these deposition events can potentially export up to 616 GJ km^{-2} of energy, or 16 t km^{-2} of carbon, to the Tasman Sea benthos every year.

Several fish species feed exclusively on salps or have salps as a major component of their diets. These species tend to be opportunistic bentho-pelagic feeders, such as the black oreo *Allocyttus niger*, smooth oreo *Pseudocyttus maculatus*, spiky oreo *Neocyttus rhomboidalis*, carinate rattail *Macrourus carinatus* and small-scaled brown slickhead *Alepocephalus australis* (Clark et al. 1989, Lyle & Smith 1997). Our results suggest that the salp carasses often found in these fish guts may result from scavenging at the seafloor. Apart from fish, other benthic feeders

including sea stars (Domanski 1984), sea urchins (Duggins 1981), octocorallians (Gili et al. 2006), mushroom corals (Hoeksema & Waheed 2012) and, from this study, the deep-water spider crab *Platymaia maora* have been observed feeding on salps. Similarly, pyrosome carcasses have provided food for a range of megafauna including crustaceans, arthropods, anemones and echinoderms (Roe et al. 1990, Lebrato & Jones 2009), while anemones, shrimp, crabs and molluscs have been observed near and feeding on cnidarian carcasses (Yamamoto et al. 2008, Sweetman & Chapman 2011). As salp carcasses can sink at rates up to 1700 m d^{-1} (Lebrato et al. 2013), they will be able to reach the seafloor in less than 2 to 3 d, before significant bacterial degradation can take place. Preliminary experimental data suggest that at seafloor temperatures (4°C), *Thetys vagina* individuals will retain 68% of their mass after 28 d (N. Henschke unpubl. data). These results are slower than a model-calculated decomposition time of approximately 20 d for a gelatinous organism, which includes more labile cnidarians (Lebrato et al. 2011). As no bacterial mats or biofilms were observed on any of the *T. vagina* individuals viewed or collected in this study, slow decomposition rates of *T. vagina* would allow carcasses to remain on the sea floor until scavenged or eventually remineralised via the microbial loop.

Potential carbon standing stock

Studies in the world's oceans (Smith & Kaufmann 1999), including the Pacific Ocean near New Zealand (Nodder et al. 2003), have identified that food demand in the benthic community (sediment community oxygen consumption) often exceeds food supply (POM). Salp carcasses are not detected by traditional methods of sampling water column nutrient fluxes, such as sediment traps (Lebrato & Jones 2009), and consequently are not included in current carbon budget calculations, resulting in a considerable underestimation of the total flux. Hence, salp carcasses may be supplementing the smaller POM that can be collected by sediment traps, providing an extra source of nutrition for the benthic community. Since particles that generally make up the majority of measured carbon flux in the Tasman Sea are <1 mm (Kawahata & Ohta 2000), these salp deposition events provide a substantial contribution of much larger carbon parcels to the benthos. As swarms of *Thetys vagina* were still in surface waters during sampling on the Challenger Plateau, by the time the

entire population had collapsed, the input from both faecal pellets and carcasses would have been considerably higher than values estimated here.

Depositions of *Thetys vagina* on the Challenger Plateau in this study only represented 0.19% of the regional annual carbon flux, whereas carbon provided from the Bass Canyon deposition was 10-fold greater, representing 1.5% of the annual flux (Kawahata & Ohta 2000). Although gelatinous zooplankton depositions can occur across all bottom topographies, studies have identified much greater biomasses and carbon inputs when organisms are in environments that promote concentration, such as canyons or structures like pipelines (Cacchione et al. 1978, Lebrato & Jones 2009). Carbon standing stocks for cnidarian carcasses in the Arabian Sea have been reported as high as 78 g C m^{-2} in some areas, an order of magnitude higher than mean annual flux (Billett et al. 2006), and 22 g C m^{-2} has been reported for *Pyrosoma atlanticum* carcasses off the Ivory Coast, 13 times greater than the annual flux (Lebrato & Jones 2009). Future studies may benefit from incorporating bottom topographies when calculating the potential for gelatinous organisms to accumulate on the sea floor and their eventual contribution to carbon fluxes in the area.

Concluding remarks

Mass depositions of salp carcasses represent a significant pathway for the export of organic production from surface waters to the deep sea. Salp biomass in the Tasman Sea regularly exceeds 100 t km^{-3} WW, with deposition events likely to export at least 16 t km^{-2} of carbon, or 616 GJ km^{-2} of energy, to the benthos every year. With higher organic content than depositions of other gelatinous organisms, the input of large salp carcasses (salp-fall) is likely to be important to the nutritional ecology of the deep-sea benthos.

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Appendix 1. Percentage (wet weight, WW) of organisms and total haul weight (kg WW) across different depths from hauls performed on the Challenger Plateau, 2007, and in Bass Canyon, 2009. Values outside parentheses denote % contribution (WW) to haul including fish; values inside parentheses denote % contribution (WW) to haul excluding fish. **Bold** values indicate contribution of salps to the haul. n = number of hauls

	Challenger Plateau					Bass Canyon			
n	11	7	10	4	12	57	17	1	1
Water depth (m)	200–500	501–600	601–800	801–1000	1001–1800	421–441	800	1600–1631	2685
Fish	14.09	17.5	7.61	5.72	6.28	60.3	17	0	2.1
Tunicates – salps	**12.49 (14.54)**	**22.23 (26.95)**	**23.74 (25.70)**	**17.43 (18.49)**	**18.87 (20.13)**	**20.6 (51.89)**	**30.3 (36.51)**	**63.1 (63.10)**	**55 (56.24)**
Tunicates – other	0 (0)	0 (0)	0 (0)	0.02 (0.02)	0.15 (0.16)	1.1 (2.77)	0.5 (0.60)	0.6 (0.6)	11.4 (11.66)[a]
Sponges	0.01 (0.01)	11.73 (14.22)	15.14 (16.39)	0.16 (0.17)	4.48 (4.78)	10.2 (25.69)	1 (1.20)	0 (0)	0 (0)
Cnidarians	7.71 (8.98)	1.88 (2.28)	8.46 (9.16)	15.2 (16.12)	13.57 (14.48)	0.1 (0.25)	20.6 (24.82)	0.9 (0.90)	14.6 (14.93)
Echinoderms	22.71 (26.44)	12.89 (15.62)	12.52 (13.55)	14.94 (15.85)	21.67 (23.12)	2.6 (6.55)	23.8 (28.67)	29.9 (29.90)	15.7 (16.05)
Polychaetes	16.29 (18.96)	1.34 (1.62)	11.85 (12.83)	28.42 (30.15)	4.06 (4.33)	0.5 (1.26)	2.8 (3.37)	0.5 (0.50)	0.4 (0.41)
Sipunculids	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.7 (0.70)	0 (0)
Molluscs	6.53 (7.60)	8.87 (10.75)	4.81 (5.21)	7.47 (7.92)	14.24 (15.19)	1.1 (2.77)	1.2 (1.45)	3.2 (3.20)	0.6 (0.61)
Crustaceans	12.01 (13.98)	6.58 (7.98)	10.77 (11.66)	9.98 (10.59)	7.75 (8.27)	3.5 (8.82)	2.8 (3.37)	0.9 (0.90)	0.1 (0.10)
Other	8.15 (9.49)	16.98 (20.58)	5.09 (5.51)	0.65 (0.69)	8.93 (9.53)	0 (0)	0 (0)	0 (0)	0 (0)
Total haul (kg)	**3.38**	**92.35**	**9.54**	**12.00**	**25.03**	**13.22**	**2.64**	**1.90**	**5.27**

[a]Sample includes *Pyrosoma atlanticum*