Grazing impact of salp (Tunicata, Thaliacea) assemblages in the eastern tropical North Pacific

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Salps are gelatinous filter-feeders that can intermittently contribute significantly to the cycling of organic matter in the world's oceans. We estimated the grazing impact of salp assemblages on phytoplankton biomass and rates of primary production (PP) in the eastern tropical North Pacific off Mexico during two cruises in February and November of 2003. Salp biomass comprised a large proportion of the preserved zooplankton biomass (21–525 mL per 10^3 m^3) at stations where large salps were present. Of the 19 species found in the area, *Thalia democratica* (and closely related species) comprised 11–100% of total salp abundance but were surpassed in dominance at some locations by *Metcalfina hexagona* (49%) and an unidentified *Cyclosalpa* (29%). In February, salp abundance ranged from 6 to 1901 salps m^{-2} (0.1–13.5 mg C m^{-2}); in November, values ranged from 54 to 631 salps m^{-2} (1–193 mg C m^{-2}). Ingestion rates by the salp assemblage, estimated from gut pigment content, were moderate and highly variable. *Thalia* exerted a low impact on phytoplankton stocks and PP, whereas moderate aggregations of co-occurring *M. hexagona*, *Cyclosalpa* sp. and *Pegea confoederata* exerted a higher impact when present. Salp assemblages ingested 0.01–3.5% of chlorophyll standing stock daily. The proportion of PP removed by salps was estimated to range from 0.1 to 24.5% day^{-1}, suggesting a significant role for salps in the grazing mediated carbon fluxes in these stratified waters.

KEYWORDS: salp distribution; gut pigment content; eastern tropical North Pacific; ETNP; Mexico

INTRODUCTION

Salps are pelagic tunicates widely distributed throughout the world's oceans. They feed at high rates while moving through the water column and can remove minute particles with relatively high efficiency (Andersen, 1998). These feeding characteristics mean that these organisms are very well adapted to the relatively low food concentrations typical of oceanic waters. Though salps are usually found at low densities, under favorable conditions they can form dense aggregations or swarms as a result of high population growth rates and the alternation of sexual and asexual reproduction (Madin and Deibel, 1998). Swarms can last from days to months and have been found at high and

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mid latitudes (Bathmann, 1988; Huntley *et al.*, 1989; Madin *et al.*, 1997; Huskin *et al.*, 2003) as well as in productive shelf and coastal waters (Zeldis *et al.*, 1995; Lavaniegos and Ohman, 2003; Hereu *et al.*, 2006; Iguchi and Kidokoro, 2006; Madin *et al.*, 2006). Conditions required for the formation and maintenance of swarms are moderate to high rates of primary production (PP) that are capable of supporting high salp biomass (Andersen, 1998; Madin *et al.*, 2006; Deibel and Paffenhöfer, 2009). However, in much of the open ocean, where oligotrophic conditions prevail, the abundance of salps is low and dense aggregations are rarely seen (Madin *et al.*, 1996, 2006).

The euphotic zone of the eastern tropical North Pacific (ETNP) off Mexico has two to three layers. An oligotrophic surface mixed layer overlies a steep nutricline where the primary chlorophyll maximum is located. Below this, there is an oxygen minimum zone (OMZ) where a secondary chlorophyll maximum is found when the top of the OMZ penetrates into the euphotic zone (Goericke *et al.*, 2000a; Pennington *et al.*, 2006; Almazán-Becerril and García-Mendoza, 2008). Owing to its vicinity to the productive California Current (CC) System, offshore waters may sustain moderate phytoplankton standing stocks and rates of PP. In contrast, coastal areas sustain high levels of PP via macronutrient supply associated with thermocline shoaling and wind-driven upwelling (Pennington *et al.*, 2006). The phytoplankton community in the euphotic zone is dominated by small picoplankton and nanophytoplankton that contribute most of the chlorophyll biomass and PP (Goericke *et al.*, 2000a; Lara-Lara and Bazán-Guzmán, 2005; Almazán-Becerril and García-Mendoza, 2008).

In tropical pelagic communities, organic carbon is normally transferred from primary producers to the zooplankton primarily via microzooplankton grazing (Landry and Calbet, 2004). Only a small fraction is due to direct grazing by the mesozooplankton and other larger organisms (Calbet, 2001). Pelagic tunicates and cladocerans are an exception among mesozooplankters, in that these animals efficiently exploit smaller phytoplankters which are responsible for most of the PP in oligotrophic ecosystems. Salps in particular can ingest a wide spectrum of food particle size, ranging from <1 μm to 1 mm (Madin and Deibel, 1998), so they can directly consume the smallest particles (i.e. picoplankton) as well as the various protists of the microbial food web (Vargas and Madin, 2004; Madin *et al.*, 2006). However, limited information exists on salp abundance and their impact on planktonic food webs (Calbet, 2001; Barber, 2007).

In the open ocean, a large fraction of the biogenic material is transported to deeper layers in the form of fecal pellets, so changes in herbivore species composition in the upper ocean will affect the dynamics and chemistry of materials entering deep waters (Michaels and Silver, 1988). Salp fecal pellets are commonly collected by sediment traps in ETNP waters (Small *et al.*, 1983; Goericke *et al.*, 2000b). The pellets showed evidence that salps feed on the abundant prokaryote *Prochlorococcus* (<1 μm) and therefore would contribute significantly to the carbon flow through pellet production in these waters (Goericke *et al.*, 2000a, b). To understand the role of salps in the cycling of energy and matter in the open ocean and in particular their role in mediating fluxes of carbon from the euphotic zone to the deep ocean, their feeding capacity, abundance and their distribution must be studied in greater detail (Michaels and Silver, 1988; Fortier *et al.*, 1994; Andersen, 1998; Barber, 2007).

Here, we report on the distribution, abundance and feeding rates of salps in the ETNP. We studied the area extending from southwest Punta Eugenia (25°N) to Manzanillo (18°N), including the entrance of the Gulf of California (GC). This sector constitutes the transition zone between the CC System, a temperate productive system, and the equatorial Pacific. Previous studies off Baja California, i.e. north of our study area, reported that dense patches of salps were frequently found (Lavaniegos and Ohman, 2003; Hereu *et al.*, 2006). Estimates of the impact of salps as grazers highlight their role as consumers, mediating the export of carbon out of the euphotic layer (Silver, 1971; Landry *et al.*, 1994a, b; Hereu *et al.*, 2006). In this report, we show that although salp abundance is normally low in this region, at times they can form patches that exert a moderate grazing pressure on phytoplankton and, therefore, can contribute considerably to carbon export from the euphotic zone.

METHOD

Sampling

The observations reported here were made during two expeditions to the ETNP (25°–15°N) in 2003, one from February 4 to March 8 (herein February) and the other from November 8 to December 3 (herein November). We sampled along two transects (Fig. 1): Transect 1, of ~900 km length oriented northwest–southwest and Transect 2, extending from Manzanillo to ~1600 km off the coast (~120°W).

Hydrographic properties (temperature, salinity and oxygen) were measured and water for analysis was collected with standard Seabird CTD/rosette bottles.

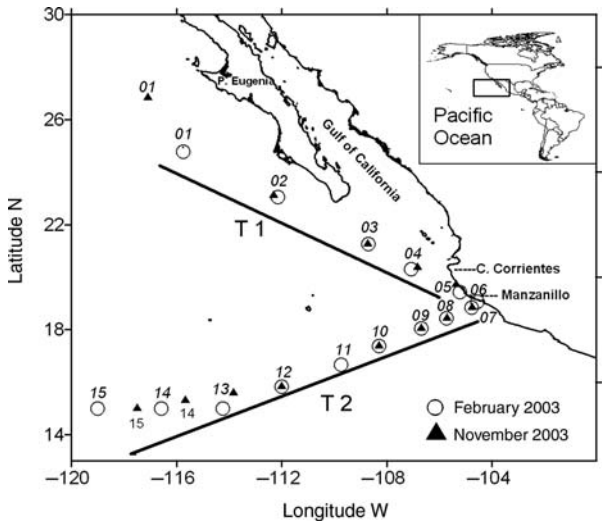

Fig. 1. Cruise track in the ETNP off Mexico in February 2003 (circles) and November 2003 (triangles). T 1, Transect 1; T 2, Transect 2.

Concentrations of chlorophyll *a* (Chl *a*) and pheopigments were determined using the fluorometric method (Holm-Hansen *et al.*, 1965). Pheopigment concentrations are expressed as Chl *a* equivalents. Samples of 250 or 500 ml seawater were filtered on 25 mm Whatman GF/F filters and, in the case of size fractionation measurements, on 1 (November only), 3 and 8 μm Nuclepore filters and 20 μm Nitex circles. Filtrations for size fractionation measurements were carried out in parallel and in triplicate. The filters were extracted for 24 h in 90% acetone at −18°C. Concentrations of Chl *a* were determined on a Turner Designs 10AU fluorometer from fluorescence measurements before and after acidification with 2 drops of 1 N HCl.

Salp abundance was estimated from vertical/oblique tows. Zooplankton was collected with a conical net of 1 m mouth diameter, equipped with a flowmeter attached to the mouth. The mesh size of the net was 505 μm in February and 333 μm in November. The net was either vertically towed from ∼70−100 m to the surface (February) or obliquely from 150 m to the surface (November), filtering on average 207 and 365 m^3 per tow in February and November cruises, respectively. All zooplankton tows were done at night (about 6:00 p.m. to 4:00 a.m.).

Samples were fixed and preserved in 4% buffered formaldehyde for identification in the laboratory. Salp abundance was estimated from both vertical and oblique tows. All salp species in the preserved samples were identified following Van Soest (Van Soest, 1972), Godeaux (Godeaux, 1998) and Esnal and Daponte (Esnal and Daponte, 1999). When necessary, abundant species were counted from a subsample (1/2 to 1/8) and the rest of the sample was also analyzed to determine the presence of rare species. Species that were not collected in vertical/oblique tows but were registered from horizontal tows (see below) are also reported.

Zooplankton and salp biomass

Total zooplankton biomass (including salps) was determined on the preserved sample by the displacement volume method (Smith and Richardson, 1977). When large organisms were present in the sample, they were removed and their volume was measured separately. This fraction, considered "large biomass", was composed mainly of large salps (>80 mm length), jellies and fish juveniles (65−145 mm length). This large biomass value was then summed with the remaining fraction (small biomass) to obtain the total zooplankton biomass. The result was standardized to milliliter displacement volume of preserved sample per 10^3 m^3.

Salp carbon biomass (mg C m^{-2}) was estimated using carbon regressions on length listed in Madin and Deibel (Madin and Deibel, 1998) for all salps present in a sample collected by vertical and oblique tows. The length used in carbon conversions was corrected considering 10% shrinkage due to the preservation in formaldehyde in *Thalia* spp. (Heron *et al.*, 1988) and 20% in the remaining species (Madin *et al.*, 1981; Nishikawa and Terazaki, 1996).

Gut pigment content and ingestion rates

Salps of different species and sizes were selected to estimate their ingestion rates by the gut pigment method (Mackas and Bohrer, 1976). To use the gut pigment approach, it is necessary to measure gut pigment content (GPC) for freshly collected salps, determine the background fluorescence signal for cleared guts and gut evacuation rates (Madin and Kremer, 1995). After vertical/oblique tows at each station, additional tows were done with a 1 m diameter, 1:5 aspect ratio, 202 μm net equipped with a large (1 gallon) cod end to collect organisms for gut pigment analysis and experiments on board. Subsurface horizontal tows were done at 10−20 m depth at speeds of 0.5−0.8 knots. Tows lasted 15−20 min. Additional short tows were done to collect salps for experiments on board to determine gut pigment destruction and gut passage time (GPT). On some occasions, salp chains were easily visible from deck and were collected with buckets minimizing handling prior to experimentation.

Salp body length was measured to the nearest millimeter under a stereomicroscope as the distance from oral to atrial openings. In February, the salp guts were excised and placed on GF/F filters, frozen in liquid nitrogen and later stored at −40°C until pigment extraction in the laboratory. In November, samples for gut pigment analysis were analyzed aboard the ship shortly after collection.

GPC (ng Chl *a* salp^{-1}) was determined by extracting the gut in 90% acetone at −18°C in the dark for 24 h, centrifuging the sample and measuring concentrations of Chl *a* and pheopigments as described above.

The background fluorescence signal of empty guts (Bp, ng pigments salp^{-1}) was determined by placing salps in 1–5 L containers filled with filtered seawater (Millipore cartridge nominal size <1 μm) until their guts seemed translucent, i.e. ~4.5–18 h depending on salp size and species. Empty guts were analyzed in the same way as full guts. For some species, background values were taken from the literature (Table I).

GPT (h) was determined only for the two species for which a sufficient number of organisms were collected (i.e. *Thalia democratica* and *Metcalfina hexagona*) by two different methods. Other species were not present in sufficient abundance for these measurements. The first method consisted of placing salps in unfiltered seawater and feeding them with colored particles (i.e. carmine dye) to estimate the time elapsed from feeding until the appearance of the red marker in the feces. The other method consisted of keeping freshly collected salps of the same size in filtered seawater and removing animals at time steps of 30 min following methodology detailed in Båmstedt *et al.* (Båmstedt *et al.*, 2000). For other species, GPT values reported in the literature were used (Table II).

We performed pigment budget experiments to determine the gut pigment destruction factor (Pd) which is a source of error in the pigment measurement due to degradation of Chl *a* to non-fluorescing Chl *a* degradation products in the gut (Madin and Cetta, 1984; Madin and Kremer, 1995). Experiments were carried out with *T. democratica* solitaries fed the diatom *Thalassiosira weissflogii* and with *M. hexagona* aggregates of 14–16 mm length fed the prymnesiophyte *Isochrysis galbana*. Two to four salps, previously kept in filtered water to empty their guts, were placed in 1 L aluminum-

Table I: Background pigment (Bp) values or range for salp species

Species	Length (*L*, mm)	Background pigment [Bp (ng Chl *a* salp^{-1})]	Zooid	Reference
Cyclosalpa bakeri	ND	0	ND	2
Metcalfina hexagona	13–15	33.7–73	A	5[a]
	48–55	250	S	5
Pegea confoederata	7–18	8.6–80.5	A	5[a]
	19–55	50	A	2[a]
Salpa aspera	<20	50	A	4
	40	400	A	4
Salpa cylindrica	4–29	0	A	5
	30–36	$L - 10$	S	1[b]
Thalia	1–10	0	A–S	3, 5
Salpa maxima	17–55	$10 \times L - 70$	A	1[b]

Length ranges correspond to salps for which Bp was determined either in this (Ref. 5) or other studies (Ref. 1–4). References: 1, Madin and Cetta (1984); 2, Madin and Kremer (1995); 3, Gibbons (1997); 4, Madin *et al.* (2006); 5, present study.
[a]Lowest value of a group of data was considered in this study. [b]Regression of background pigments (Bp) of empty salp stomachs on length (*L*, mm) taken from literature.

Table II: GPT (h) as a function of live body length (L, mm)

			Gut passage time					
Species	Length (min–max)	*T* (°C)	Min–Max	Regression	*N*	Zooid	r^2	Ref.
Cyclosalpa bakeri	15–90	11	0.4–2.6	$0.02 \times L + 0.73$	59	A–S	0.42	2
Metcalfina hexagona	13–30	27	2.0–10.3	$0.28 \times L - 1.76$	9	A	0.60	4[a,b]
Pegea confoederata	27–65	ND	3.2–8.3	$0.08 \times L + 2.28$	13	A	0.62	1
Salpa aspera	10–90	21–24	2.0–15.0	$0.17 \times L$	12	A–S	0.90	3
Salpa maxima	32–77	ND	3.2–12.3	$0.15 \times L - 0.52$	18	A	0.71	1
Thalia spp.	4–7	24	0.4–2.0	$0.54 \times L - 1.78$	9	S	0.61	4[a]

T, ambient temperature (°C). Minimum–maximum length and number of salps for either this (Ref. 4) or other studies (Refs 1–3) are given. Zooid: A, aggregate; S, solitary. References: 1, Madin and Cetta (1984); 2, Madin and Purcell (1992); 3, Madin *et al.* (2006); 4, present study ($P<0.01$) from carmine dye[a] or decrease of gut pigment over time[b], see results.

wrapped containers filled with phytoplankton cultures. Experimental controls (no salps) and treatments (with salps) were carried out in duplicate or in triplicate when possible. After several hours, salps were removed and their guts analyzed as described above. About 200 mL of water from controls and treatments were filtered and the pigments extracted. All fecal material was removed from the bottom of the bottles and pigments were extracted as described above.

For ingestion rate calculations, pigment content of every gut analyzed was plotted against body length for each salp species. The equations obtained after fitting data to a linear or exponential model (whichever resulted in a higher r^2) were used to estimate ingestion rates of salp assemblages.

Individual ingestion rates (I, ng pigment salp^{-1} h^{-1}) were obtained by dividing the gut content (after correction for background pigment and pigment destruction) by GPT [Eq. (1)].

$$I = \frac{(\mathrm{GPC} - \mathrm{Bp}) \times \mathrm{Pd}}{\mathrm{GPT}} \quad (1)$$

An individual ingestion rate was calculated for each size class of a species. This individual ingestion rate, corresponding to one size class, was multiplied by the size class abundance (ind. m^{-2}) of the species. The result corresponding to each size class was summed for the entire size range to obtain the population ingestion rate of each species. Community ingestion rate (Ic, μg pigments m^{-2} day^{-1}) at each station was calculated as the sum of the ingestion rates of all species. This result was combined with integrated Chl *a* standing stock to estimate daily grazing impact (GI, % day^{-1}) as the percentage of phytoplankton standing crop (Pw, μg Chl *a* m^{-2}) grazed by salps as follows:

$$\mathrm{GI} = \frac{\mathrm{Ic}}{\mathrm{Pw}} \times 100 \quad (2)$$

Daily rates were calculated assuming constant feeding over 24 h. Since we used oblique/vertical tows to estimate salp abundance, we also assumed a uniform vertical distribution of salps and phytoplankton over the sampling depth interval for calculations of community ingestion rates. Chlorophyll concentrations were converted to carbon biomass using a carbon to chlorophyll ratio of 114 (Welschmeyer and Lorenzen, 1985) for the estimation of the grazing impact of salps in terms of PP.

In order to assess if our clearance rates (CR, mL ind. h^{-1}) are reasonably relative to those reported for the same or related species from gut pigment or other methods, we estimated CR of salps as the individual ingestion rate divided by the average amount of pigment in the water (Madin and Kremer, 1995). For this calculation, we considered the total amount of pigment present including particles that may be not retained by salps with 100% efficiency.

RESULTS

Hydrography

A noticeable latitudinal gradient of surface temperature was evident between stations 1 and 5 of Transect 1, particularly in February (Fig. 2). The weak thermocline at 50–90 m off Baja California changed to a steeper thermocline (40–60 m) close to the mouth of the GC (Fig. 2A and E). The colder and fresher water at ~100 m denoted the influence of the CC, with salinities <34 (Fig. 2B and F) and high oxygen concentrations at station 1 during both periods (Fig. 2C and G). The CC intrusion was more marked in February (Fig. 2A–D). Southerly subsurface influence of salty and poorly oxygenated waters was evident at stations 3–5. In February, stations at the entrance of the GC were influenced by saltier waters, probably Gulf Water (salinity >34.9; Castro *et al.*, 2006).

Along Transect 2, fully developed characteristics of the ETNP were evident with the typical east–west gradients in temperature and oxygen concentrations (i.e. thermocline and oxycline deepening from east to west, Fig. 3). In general, the thermocline was shallower (<30 m) inshore (stations 7–8) compared with offshore (>50 m). The upper layer (40 m) was slightly warmer in November (Fig. 3E). A strong oxycline was characteristic of the ETNP transect, reaching oxygen concentrations below 20 μM (Goericke *et al.*, 2000a). The depth of the oxycline varied along this transect from 60 to 150 m depth (Fig. 3C) in February and from 40 m to 110 m in November (Fig. 3G). A particular feature during November was the doming of isopycnals at ~200 km off the coast (Fig. 3E–H), possibly due to the presence of an eddy that often forms in this area (Zamudio *et al.*, 2001, 2007).

Chlorophyll biomass

Surface Chl *a* was low (<0.3 μg L^{-1}) along Transects 1 and 2 during both cruises (Figs 2D, H and 3D, H). Chl *a* maxima along Transect 1 were shallower (40 m) with higher concentrations of Chl *a* at station 5 (0.7 and 2.04 μg L^{-1} in February and November, respectively). Along Transect 2, the depth of the Chl *a* maximum (Fig. 3D and H) deepened from east (30 m) to west (60–80 m). In February, higher subsurface maximum values

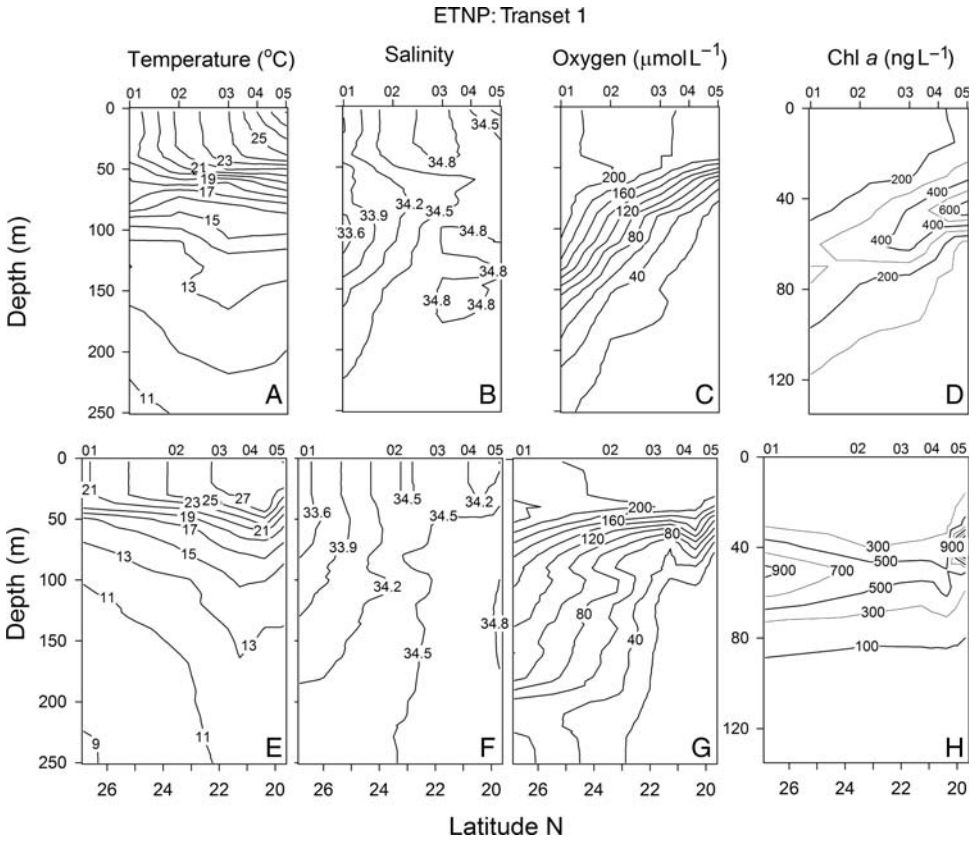

Fig. 2. Hydrographic properties plotted against depth and latitude for Transect 1 (stations 1–5) during February 2003 (**A**–**D**) and November 2003 (**E**–**H**). Temperature (A and E), salinity (B and F), oxygen (C and G) and total Chl *a* (D and H). Note the different depth range for Chl *a* plot.

(~0.7 μg L^{-1}) occurred near the coast (stations 6–7) and further offshore in November (stations 8–10). Despite the differences in Chl *a* profiles (not shown), integrated biomass (0–130 m) was relatively similar along both transects during both periods, ranging from 20 to 35 mg Chl *a* m^{-2}, except for two stations in November (stations 1 and 5) with values >40 mg m^{-2} (Fig. 4). While the high Chl *a* biomass at station 1 could be related to the influence of the CC, the high peak at station 5 could be the result of a local process (see above) that seems not to have influenced station 7. Station 5 was shallower (bottom depth <100 m) and closer to the coast than station 7. This station showed the lowest integrated Chl *a* biomass (Fig. 4) and the lowest value at the subsurface chlorophyll maximum (0.38 μg L^{-1} Chl *a*) during the cruise. Phytoplankton communities were dominated by small cells (<3 μm) during both cruises (Table III).

Zooplankton biomass

Zooplankton biomass of the preserved samples was below 80 mL per 10^3 m^3 during February except for stations near the coast. At station 4, a peak in zooplankton biomass (227 mL per 10^3 m^3) was observed; at this station three jellyfish contributed 12% of total zooplankton (Fig. 4). Along Transect 2, high zooplankton biomass (>100 mL per 10^3 m^3) occurred close to the Manzanillo coast. At station 13, the biomass of a large salp contributed 62% of the total zooplankton biomass (Fig. 4). November was characterized by high zooplankton biomass along Transect 1 and inshore stations from Transect 2. Large salps dominated the large fraction of zooplankton biomass at those inshore stations (Table IV, Fig. 4). Low zooplankton biomass occurred at offshore stations on Transect 2, where jellyfish and the pelagic red crab *Pleuroncodes planipes* (not shown) were common.

Salp composition and abundance

We observed 19 of the 24 salp species known to occur in the eastern tropical Pacific (Van Soest, 1998) when including the species captured by horizontal tows that were not caught in vertical/oblique tows (Table IV). The genus *Thalia* (*T. democratica*, *T. cicar*, *T. orientalis* and

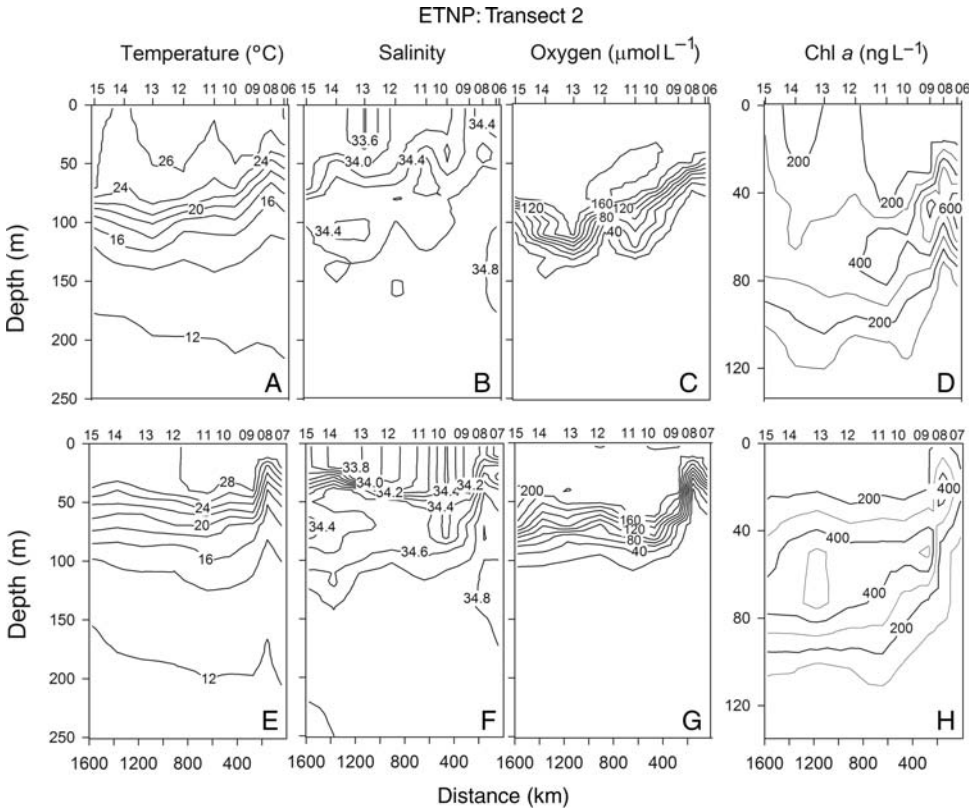

Fig. 3. Hydrographic properties plotted against depth and distance from the Mexican coast for Transect 2 (stations 6–15) during February 2003 (**A**–**D**) and November 2003 (**E**–**H**). Temperature (A and E), salinity (B and F), oxygen (C and G) and total Chl *a* (D and H). Note the different depth range for Chl *a* plot.

T. rhomboides) numerically dominated the salps captured at the stations along Transect 1 (87–100%) and most of the stations from Transect 2 (11–100%). At station 8 in November, *Thalia* was outnumbered by *M. hexagona* and one unidentified *Cyclosalpa* (presumably *C. affinis*) comprising 49% and 29% of the salps, respectively. A similar pattern of dominance occurred in terms of salp biomass (Fig. 5).

Total salp abundance ranged from 6 to 1901 salps m^{-2} (0.07–36.5 salps m^{-3}) in February and from 54 to 631 salps m^{-2} (0.4–4.2 salps m^{-3}) in November. Large differences between cruises were also evident for salp biomass with ranges of 0.1–13.5 mg C m^{-2} in February and 1–193 mg C m^{-2} in November (Table IV). Though a seasonal difference in salp abundance is possible, it could also be related to changes in sampling depth and towing method. In this area, zooplankton occur primarily in the upper 150 m of the water column (Blackburn, 1966). However, some salp species tend to be present in the surface layer (<100 m) (Gibbons, 1997; Andersen, 1998; Tew and Lo, 2005) and may be better sampled using tows in the upper 100 m.

Gut pigment content and ingestion rates

Most of the salps used to quantify GPC or used for onboard experiments were collected at stations along Transect 2. Ambient pigment concentration seems to have a strong effect on feeding behavior (Madin and Kremer, 1995; Phillips *et al.*, 2009). However, we did not observe any pattern in the amount of gut pigment relative to pigment concentration in the water where the salps were collected. Consequently, we combined all gut content data from both cruises to obtain the length–gut pigment regression for each species and further calculations of ingestion rates. Gut contents were linearly (*Salpa aspera*, *Salpa cylindrica* and *Thalia* spp.) or exponentially (*Cyclosalpa sewelli*, *M. hexagona*, *Pegea confoederata* and *Salpa maxima*) related to body length (Fig. 6). A wide range of gut content values were found, ranging from <1 ng Chl *a* for a 1 mm long aggregate of *Thalia* sp. to 17 μg Chl *a* for a 140 mm long solitary of *Cyclosalpa polae*. Although some species were collected and their guts analyzed (*S. aspera*, *S. maxima* and *Salpa younti*), they were absent from vertical/oblique tows and their population ingestion rate could not be estimated. Other

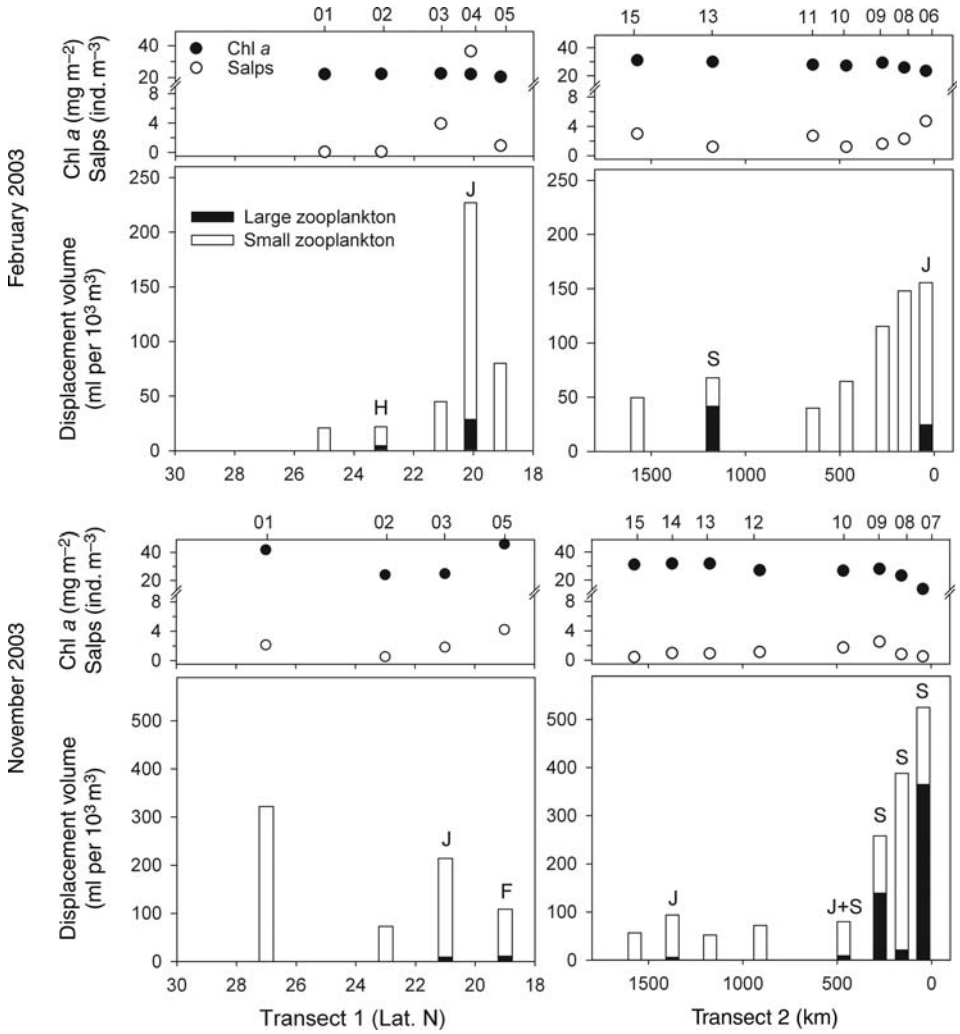

Fig. 4. Zooplankton (small and large fraction) biomass (displacement volume, mL per 10^3 m^3), salp abundance (ind. m^{-3}) and integrated chlorophyll biomass (mg Chl *a* m^{-2}) during February and November 2003. Letters refer to composition of the large fraction of zooplankton biomass: F, juvenile fishes; J, jellyfish; H, heteropods; S, salps.

Table III: Results from size-fractionation measurements on samples from the mixed layer at stations with Chl a concentrations <0.3 μg L^{-1} for the February and November 2003 cruises in the ETNP

	Chl *a*	<1 μm	1–3 μm	<3 μm	3–8 μm	8–20 μm	>20 μm
February 2003							
n = 10	0.17	ND	ND	86.0%	6.8%	3.8%	3.3%
SD	0.05	ND	ND	6.6%	1.2%	2.4%	4.1%
November 2003							
n=18	0.19	78.8%	12.7%	91.5%	3.6%	2.9%	2.0%
SD	0.05	4.6%	3.9%	4.4%	2.2%	1.8%	1.4%

Number of measurements (*n*), average and standard deviation (SD) of the Chl *a* concentration (μg L^{-1}) and average and standard deviation (SD) of % contributions of different size classes to total Chl *a*. Measurements to determine Chl *a* in the <1 μm size fraction were not carried out in February 2003.

species were present in vertical/oblique tows, but their abundance was too low to determine their GPC and ingestion rate (*Brooksia rostrata, Iasis zonaria, Ihlea punctata* and *Ritteriella amboinensis*).

The amount of pigment in Fig. 6 represents the gut content in salps before correcting for background pigments (Bp). Background pigments values used for each species in Eq. (1) are listed in Table I. For the species

Table IV: Salp species length range for aggregates (A) and solitaries (S), total abundance and biomass from vertical (February) and oblique (November) tows conducted in the ETNP in 2003.

		Abundance per species (ind. per 10^3 m^3)																	Total per station		
	Station	*Bros*	*Cbak*	*Cpol*	*Cqua*	*Csew*	*Cyc.* sp.	*Izon*	*Ipun*	*Mhex*	*Pcon*	*Ramb*	*Sasp*	*Scyl*	*Smax*	*Syou*	*Tvag*	*Thalia* sp.	Abundance (ind. m^{-3})	Abundance (ind. m^{-2})	Biomass (mg C m^{-2})
Length range (A/S)		2.5–6.3/ 3.8–12.5	3.8–12.5/ 12.5			5–18.8/ 6.3–15.0	6.3–47.5[a]	6.3–18.8/ 10.0	2.5–6.3/ 12.5–27.5	16.3–37.5/ 62.5–162.5	5.0–37.5/ 18.8–50.0	1.3–25.0/ 10.0–50.0		2.5–17.5/ 3.8–37.5				1.1–6.6/ 1.1–10.0			
February 2003	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	74	0.1	7	0.1
	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	[b]	—	55	0.1	6	ND
	3	—	—	—	—	—	—	—	—	—	—	10	—	—	—	—	—	3851	3.9	271	2.2
	4	—	19	—	—	—	—	—	—	—	—	10	—	39	—	—	—	36 484	36.5	1901	13.5
	5	5	5	—	—	[b]	—	30	5	—	[b]	75	[b]	[b]	—	[b]	—	765	0.9	39	1.8
	6	—	—	—	—	—	—	5	40	—	—	150	—	—	—	—	—	4500	4.7	329	ND
	8	5	—	—	—	—	–	5	134	[b]	—	96	[b]	134	—	[b]	—	1903	2.3	159	5.3
	9	12	—	—	—	6	17	162	—	[b]	[b]	46	—	[b]	—	[b]	[b]	1321	1.6	110	4.8
	10	[b]	[b]	[b]	[b]	65	—	5	—	[b]	[b]	10	[b]	71	—	[b]	—	1084	1.2	83	1.6
	11	—	—	[b]	—	17	—	—	—	[b]	[b]	—	—	17	—	—	—	2683	2.7	193	1.9
	13	16	—	—	—	[b]	—	—	—	5	[b]	—	—	5	—	—	—	1234	1.2	128	12.9
	15	—	—	[b]	—	15	—	[b]	—	[b]	—	—	[b]	[b]	—	[b]	—	3015	3.0	212	1.8
November 2003	1	—	—	—	—	—	21	—	30	—	—	4	—	186	—	—	—	1900	2.1	321	8.9
	2	—	—	—	—	4	—	—	—	—	[b]	—	—	—	—	—	—	447	0.5	68	1.3
	3	—	—	—	—	—	—	—	—	236	3	—	[b]	—	—	—	—	1547	1.8	268	49.9
	5	29	—	—	—	—	—	5	—	[b]	[b]	27	—	5	—	—	—	4147	4.2	631	6.6
	7	—	3	—	—	—	—		72	159	164	3	—	—	[b]	—	—	179	0.5	88	118.3
	8	—	—	–	–	—	224	22	3	386	59	8	[b]	—	—	[b]	—	86	0.8	118	193.2
	9	—	—	—	—	—	—	[b]	—	13	5	5	—	—	—	3	—	2487	2.5	377	41.3
	10	7	—	—	—	[b]	—	—	—	149	[b]	—	—	5	[b]	—	—	1587	1.7	262	6.8
	12	3	—	—	—	3	—	—	—	—	[b]	—	[b]	21	—	—	—	1113	1.1	171	1.6
	13	—	—	—	—	—	—	—	—	—	—	—	—	6	—	—	—	874	0.9	132	1.5
	14	—	—	—	—	[b]	—	—	—	—	[b]	—	—	[b]	—	—	—	954	1.0	143	1.0
	15	2	—	—	—	—	—	—	5	—	—	—	—	—	—	—	—	354	0.4	54	1.1

Length ranges are estimated live lengths (mm) based on live-preserved ratios. Species: *Brooksia rostrata* (Bros), *Cysclosalpa bakeri* (Cbak), *C. polae* (Cpol), *C. quadriluminis* (Cqua), *C. sewelli* (Csew), *Cyclosalpa* sp. (Cyc sp.), *Iasis zonaria* (Izon), *Ihlea punctata* (Ipun), *Metcalfina hexagona* (Mhex), *Pegea confoederata* (Pcon), *Ritteriella amboinensis* (Ramb), *Salpa aspera* (Sasp), *S. cylindrica* (Scyl), *S. maxima* (Smax), *S. younti* (Syou), *Thetys vagina* (Tvag).

[a]No distinction between aggregate and solitary.

[b]Presence of a species from horizontal surface tows. ND, salp length not measured.

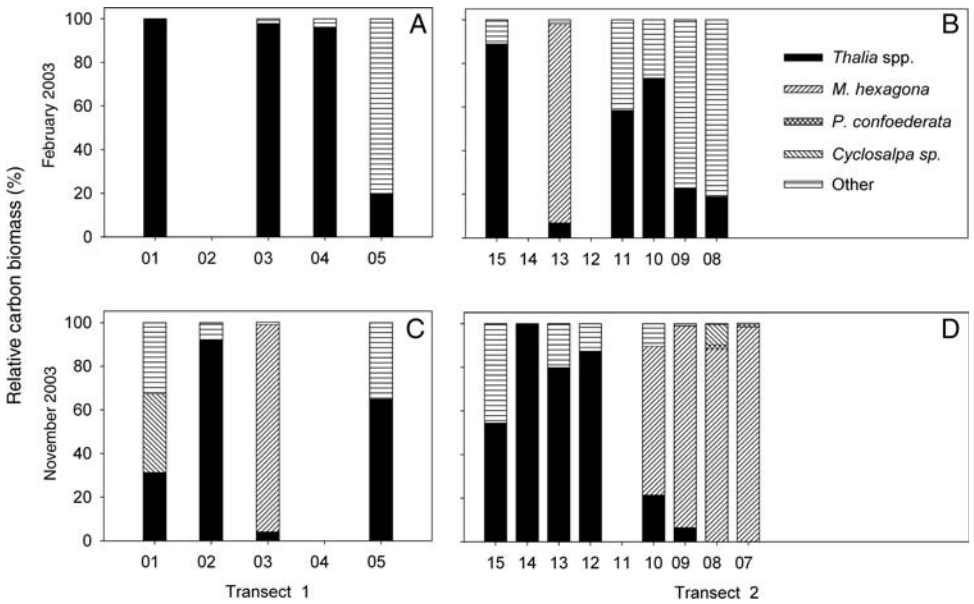

Fig. 5. Relative carbon biomass (%) per species during February (**A** and **B**) and November (**C** and **D**) 2003. See Table IV for a list of "other" species present at each station.

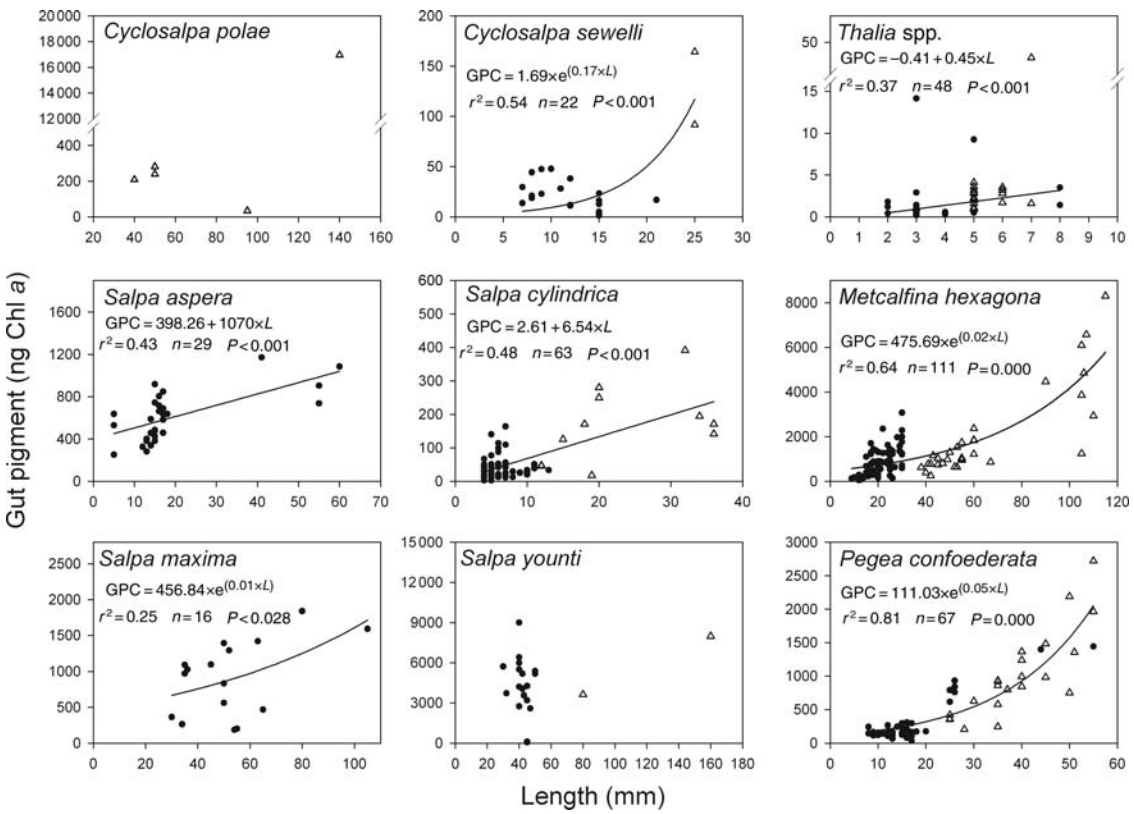

Fig. 6. Relationship between individual gut content (GPC, ng Chl *a*) and live body length (*L*, mm). Black dots are for aggregates and open triangles are for solitaries.

P. confoederata and *M. hexagona*, we considered Bp the smallest value obtained for a determined size range instead of the average (Madin and Kremer, 1995). For those species for which we could not determine Bp, we used reported values (Table I). In all cases, corrections for background pigment were <5% of the total signal.

Only two experiments out of the seven performed to determine the amount of pigment degraded during digestive process succeeded. The main problem we encountered was the low survival at the end of the time series probably due to prolonged confinement in small volume containers. The most satisfactory results (100% survival in all replicates) were obtained in an experiment with *T. democratica* solitaries fed with *Thalassiosira* and another experiment with *M. hexagona* aggregates fed with *I. galbana*. Replicates within time series experiments resulted in 16% and 36% (mean 26%) of pigment degradation for *Thalia* and 20%, 21% and 45% (mean 29%) for *M. hexagona*. An average value of 27% of Chl *a* degradation in guts was used to correct pigment ingestion values in all species [Pd in Eq. (1)].

Madin and Kremer (Madin and Kremer, 1995) reported that evacuation rates are highly variable, depending on the species and method used. The values of GPT for *M. hexagona* derived from the regression we obtained (Table II, Fig. 7A) are high when compared with other species, particularly for larger individuals.

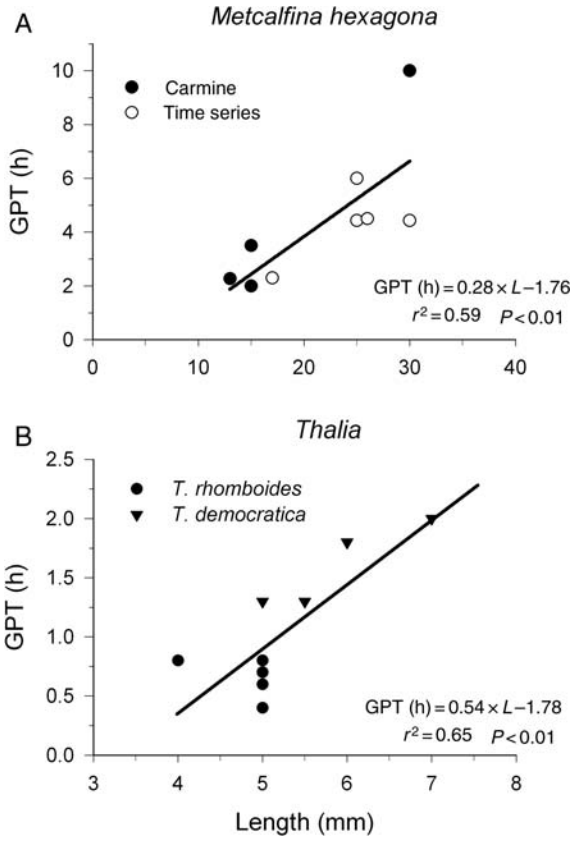

Fig. 7. Regression of *GPT* (h) on salp length (*L*, mm) for *M. hexagona* and *Thalia* sp. For GPT determination, two approaches were used for *M. hexagona* (carmine dye and time series) and one for *Thalia* spp. (carmine dye). See text for methods.

To determine lower and upper boundaries [Eq. (1)], we computed two "possible" ingestion rates for this species: a "low" ingestion rate (I_L) considering the high value of GPT (values obtained from the present study) and a "high" ingestion rate (I_H) considering a shorter GPT (in this case, we considered the regression of GPT reported for *S. maxima*, Table II). For *Thalia*, contrary to expectations, ingestion rate decreased with size (for salps >4 mm), so we also estimated two possible ingestion rates, I_L (with the GPT obtained from our regression, Fig. 7B) and I_H (fixing GPT as a function of size: 0.30 h for salps <4 mm and 0.38 h for salps ≥4 mm; Table II). This correction on GPT resulted in I_H 1.1 times higher than I_L for *Thalia* and two times higher for *M. hexagona*. Reported estimates of GPT for *S. cylindrica* are available only for solitaries longer than 25 mm (Madin and Cetta, 1984), so we considered a GPT for this species of 0.5 h for salps <8 mm and 1.0 h for salps of length ≥8 mm. The GPT of *C. sewelli* was obtained from regressions reported for *Cyclosalpa bakeri* (Madin and Purcell, 1992) considering a $Q_{10} = 2$. Values for *Pegea* were also taken from the literature (Madin and Cetta, 1984) (Table II).

On the basis of "high" ingestion rate (I_H) estimates, grazing by the salp assemblages in February ranged from 0.4 to 82.5 μg Chl *a* m^{-2} day^{-1} (Table V). In spite of the peak in salp abundance at the mouth of the GC (station 4), their ingestion did not surpass 0.4% day^{-1} of the Chl *a* biomass. Considering reported values of PP for the study area (Gaxiola-Castro and Alvarez-Borrego, 1986; Lara-Lara and Bazán-Guzmán, 2005; Pennington *et al.*, 2006), we estimated a mean value of 0.38 g C m^{-2} day^{-1}. Assuming a carbon to chlorophyll ratio of 114 (Welschmeyer and Lorenzen, 1985), salps ingested <1% of the daily PP at all stations except at station 4 where maximum grazing was 2.5% day^{-1} of PP. The low grazing impact during February occurred when the community was dominated by small salps, i.e. *Thalia* size ranging 1–8 mm, *Cyclosalpa* species ranging 4–19 mm and *S. cylindrica* from 3 to 38 mm of body length. In November, although grazing was low at most of the stations, several patches of larger salps were observed and determined to exert a higher grazing pressure on phytoplankton standing stock and PP. High daily ingestion estimates ranged from 5.4 to 815.6 μg Chl *a* m^{-2} day^{-1}, equivalent, to 0.02–3.5% day^{-1} of Chl *a* standing stock or 0.2–24.5% day^{-1} of the PP. Grazing impact at the mouth of the gulf (station 3) where large numbers of *M. hexagon*a aggregates (16-32 mm length) were found was among the highest observed (1.2% day^{-1} of Chl *a* biomass) in this study. A higher impact resulted at inshore stations on Transect 2 where larger *M. hexagona* (25–162 mm) dominated

Table V: Salp ingestion and grazing impact on chlorophyll standing stock (Chl a) and PP during February 2003 in the ETNP

Station	Species	Abundance (salps m^{-2})	Biomass (mg C m^{-2})	Chl *a* (mg m^{-2})	Ingestion (μg Chl *a* m^{-2} day^{-1})		Consumption			
							% Chl *a*		% PP	
					I_L	I_H	I_L	I_H	I_L	I_H
1	*Thalia* spp.	7	0.07	11.6	—	0.4	—	<0.01	—	<0.1
3	*Thalia* spp.	270	2.20	20.7	12.0	13.0	0.06	0.06	0.4	0.4
4	*Thalia* spp.	1897	13.10	20.4	67.0	78.0	0.35	0.40	2.1	2.5
	Cyclosalpa bakeri	1	0.05		0.3	0.3				
	Salpa cylindrica	2	0.38		4.2	4.2				
5	*Thalia* spp.	34	0.40	12.5	1.7	2.1	0.02	0.02	0.1	0.1
	Cyclosalpa bakeri	0.2	0.10		0.2	0.2				
8	*Thalia* spp.	133	1.00	24.7	6.8	7.2	0.09	0.09	0.7	0.7
	Salpa cylindrica	9	0.10		16.0	16.0				
9	*Thalia* spp.	92	1.10	21.1	4.7	6.3	0.03	0.03	0.2	0.2
	Cyclosalpa sewelli	0.4	0.06		0.3	0.3				
	Cyclosalpa sp.	0.8	0.04		0.3	0.3				
10	*Thalia* spp.	76	1.10	15.6	5.1	6.5	0.07	0.07	0.3	0.3
	Cyclosalpa sewelli	5	0.10		2.9	2.9				
	Salpa cylindrica	1	0.02		2.2	2.2				
11	*Thalia* spp.	191	1.70	12.3	9.5	11.1	0.10	0.11	0.4	0.4
	Cyclosalpa sewelli	0.8	0.20		0.9	0.9				
	Salpa cylindrica	1	0.01		1.6	1.6				
13	*Thalia* spp.	124	0.90	16.2	6.2	6.3	0.08	0.12	0.4	0.6
	Metcalfina hexagona	0.5	11.70		3.9	10.5				
	Salpa cylindrica	0.5	0.30		2.4	2.4				
15	*Thalia* spp.	211	1.60	23.1	10.3	11.3	0.05	0.06	0.4	0.4
	Cyclosalpa sewelli	0.9	0.17		1.5	1.5				

Left (right) columns for daily ingestion per species and consumption for all species in a station combined (as % Chl *a* and % PP) correspond to estimates when lower I_L (higher I_H) ingestions rates were considered. Chlorophyll integrated in 0–70 m.

together with other large salps (*P. confoederata* and *Cyclosalpa* sp., Tables IV and VI), resulting in a consumption of 2.7 and 3.5% day^{-1} of Chl *a* at those stations, respectively (Table VI). It should be noted that individual ingestion rate of the larger *Cyclosalpa* sp. at station 8 seemed to be high compared with those of other salps with the same size. While CR determined for *C. sewelli* and *C. polae* were within values reported for related species (Fig. 8C), CR for *Cysclosalpa* sp. individuals >30 mm were up to ~13 times higher than CR of *C. polae* (Fig. 8). In order to derive a conservative estimate for the larger (30–47 mm) salps of *Cyclosalpa* sp., feeding rates were estimated basing on a gut content corresponding to a 30 mm salp (Fig. 6; Table VI).

Integrated Chl *a* values (Tables V and VI) include pigment from small phytoplankton cells, which can be retained by salps but rarely with 100% efficiency (Kremer and Madin, 1992; Vargas and Madin, 2004). So, the overall impact of salps ingestion on the phytoplankton available to them was low considering that most of the Chl *a* biomass within the mixed layer was from cells <3 μm (Table III). However, if we assume that salps only graze on the phytoplankton fraction >3 μm (with an average percentage of contribution listed in Table III), maximum Chl *a* consumption by the salp assemblage in February and November will be up to 2.8 and 42.0% day^{-1} of the phytoplankton stock, respectively.

To determine if clearance rates we measured were consistent with reports by others, we calculated CR from individual ingestion rates and the average Chl *a* concentration in the water at each station and compared these with reported values (Fig. 8). However, estimates of CR (mL $salp^{-1}$ h^{-1}) determined from concentrations of pigments in the water and ingestion by salps will be underestimates of true CR if a substantial fraction of the phytoplankton is too small to be grazed on effectively by salps. It is likely that this is the case for our system, since more than 86% of phytoplankton pigment biomass is associated with particles <3 μm in diameter. For those species for which we estimated I_H and I_L, we present two possible CR values (Fig. 8A and E). When multiple estimates of CR were made for the same size in a species, they were averaged and presented as a single point. We did not find the usual exponential relationship between clearance rate and length of salp (Madin and Deibel, 1998) probably as a result of the combination of data. Clearance rates determined in this study showed great variability. In general, smaller salps (which included mainly the

Table VI: Salp ingestion and grazing impact on chlorophyll standing stock (Chl a) and PP during November 2003 in the ETNP

Station	Species	Abundance (salps m^{-2})	Biomass (mg C m^{-2})	Chl *a* (mg m^{-2})	Ingestion (μg Chl *a* m^{-2} day^{-1})		Consumption			
							% Chl *a*		% PP	
					I_L	I_H	I_L	I_H	I_L	I_H
1	*Thalia* spp.	285	2.80	41.8	18	19.3	0.22	0.22	2.7	2.8
	Salpa cylindrica	28	2.50		62.5	62.5				
	Cyclosalpa sp.	3	3.20		10	10				
2	*Thalia* spp.	67	1.20	23.9	5	6.6	0.02	0.03	0.2	0.2
	Cyclosalpa sewelli	1	0.15		0.6	0.6				
3	*Thalia spp.*	232	2.05	24.8	11.2	12.7	0.71	1.20	5.3	9.0
	Metcalfina hexagona	35	47.50		164.8	285.8				
	Pegea confoederata.	0.5	0.39		2.3	2.3				
5	*Thalia* spp.	621	4.32	45.8	24.4	27.4	0.06	0.07	0.8	0.9
	Salpa cylindrica	0.7	0.28		2.9	2.9				
7	*Thalia spp.*	27	0.24	13.7	1.2	1.3	1.63	2.69	6.7	11.0
	Metcalfina hexagona	24	116.21		176.8	322.0				
	Pegea confoederata	25	1.39		44.9	44.9				
	Cyclosalpa bakeri	0.5	0.05		0.1	0.1				
8	*Thalia* spp.	13	0.09	23.2	0.7	0.7	2.70	3.52	18.8	24.5
	Metcalfina hexagona	58	166.13		236.9	427.3				
	Pegea confoederata	9	3.83		28.1	28.1				
	Cyclosalpa sp.	34	22.61		359.5	359.5				
9	*Thalia* spp.	373	2.70	27.9	16.4	18.2	0.11	0.16	1.0	1.4
	Metcalfina hexagona	2	37.90		12.6	24.5				
	Pegea confoederata	0.8	0.38		2.3	2.3				
10	*Thalia* spp.	238	1.46	26.6	9.6	10.2	0.06	0.06	0.4	0.5
	Metcalfina hexagona[a]	0.4	4.58		1.7	3.4				
	Salpa cylindrica	0.7	0.34		3.3	3.3				
12	*Thalia* spp.	167	1.39	27.0	8.3	9.2	0.06	0.07	0.5	0.5
	Salpa cylindrica	3	0.10		7.6	7.6				
	Cyclosalpa sewelli	0.4	0.04		0.3	0.3				
13	*Thalia* spp.	132	1.22	31.7	5.9	6.7	0.03	0.03	0.3	0.3
	Salpa cylindrica	0.7	0.26		3.1	3.1				
14–15[b]	*Thalia* spp.	98	0.82	31.0	5.0	5.4	0.02	0.02	0.2	0.2

Left (right) columns for daily ingestion per species and consumption for all species in a station combined (as % Chl *a* and % PP) correspond to estimates when lower I_L (higher I_H) ingestions rates were considered. Chlorophyll integrated in 0–130 m.
[a]A chain of small (<10 mm) aggregates not included for grazing estimates.
[b]Average for stations 14 and 15.

aggregate form) had high clearance rates compared with solitaries. This pattern was also observed in other studies (Huskin *et al.*, 2003; Madin *et al.*, 2006). Since most of the studies listed in Fig. 8 did not include the same length range that we present here, comparisons rely on extrapolation of reported regressions to length ranges from this study. Individual CR for several species were higher (Fig. 8A and E) or similar (Fig. 8C, D and F) than related species for the smaller size salps and similar or lower rates for the larger individuals (Fig. 8C–F). Apparently, our estimated *I* for *S. cylindrica* are high (see Discussion) and this resulted in high CR for aggregates of this species. For a 4 mm aggregate, we estimated an average CR of 271 mL ind. h^{-1}, 15 and 43 times higher, respectively, than reported values of 444 and 151 mL ind.$^{-1}$ day^{-1} for aggregates of this species (Vargas and Madin, 2004). As Madin and Kremer (Madin and Kremer, 1995) noted, it is very difficult to get realistic results for this species in particular. Nonetheless, the range of variation in clearance rates estimated by different methods including the gut pigment method would be within 2- to 10-fold, depending on the size of salps and species.

DISCUSSION

Oceanographic conditions and biological patterns

In this study, the spatial variability of salp populations was related to the physical features that likely affect biological production (cf., Blackburn *et al.*, 1970; Fernandez-Alamo and Farber-Lorda, 2006; Pennington *et al.*, 2006). High zooplankton biomass (>100 mL 10^{-3} m^{-1}) coincided with areas with a markedly

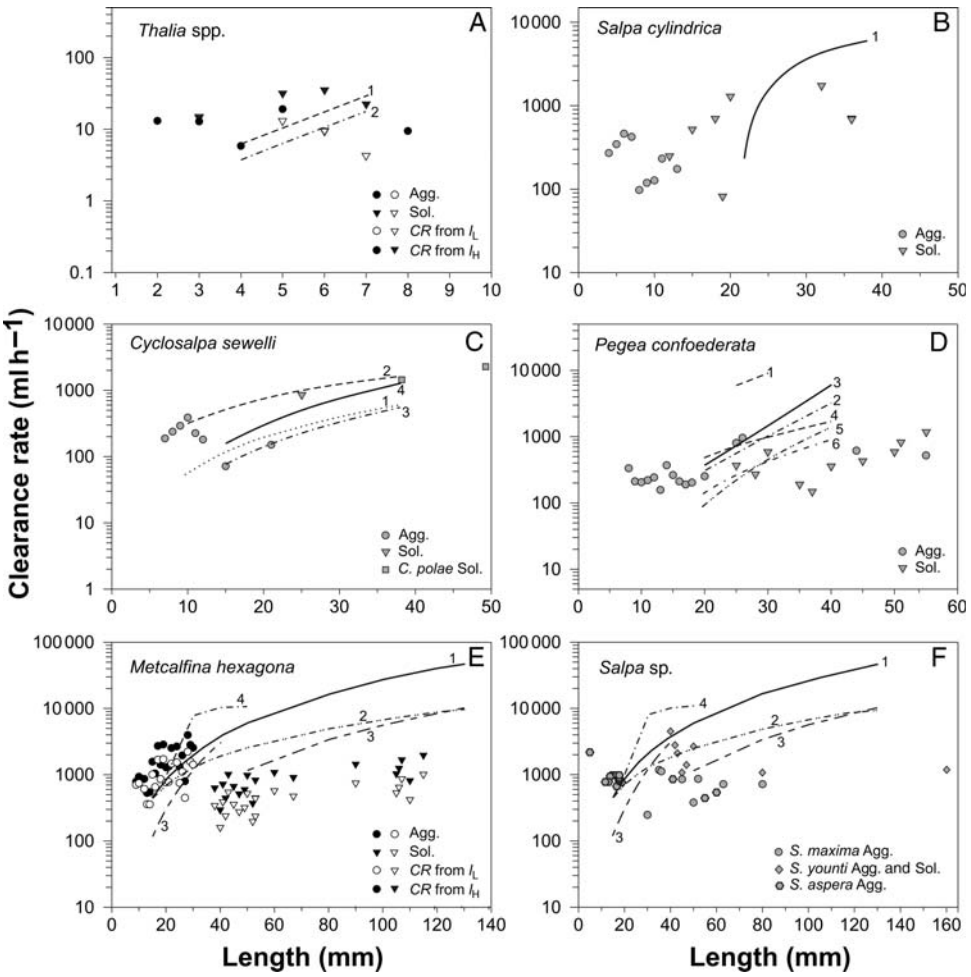

Fig. 8. Relation of salp clearance rates (CR, mL salp^{-1} h^{-1}) and body length (L, mm) estimated from ingestion rates and pigment in the water. Separated generations are shown in **A**–**E**: aggregates (circles) and solitaries (triangles), and combined in **F**. Two estimations of clearance rates are shown for *Thalia* spp. and *M. hexagona*, derived from low (white) and high (black) ingestion rates; gray symbols are used for the rest of species. Clearance rates functions determined by different methods are plotted for comparison in panels: (A) *Thalia* spp.: 1, particle depletion rate from Deibel (Deibel, 1982); 2, radiotracer rates from Mullin (Mullin, 1983); (B) *Salpa cylindrica*: 1, pumping rate (Madin and Kremer, 1995); (C) *Cyclosalpa sewelli* aggregates (>22 mm) and solitary (25 mm): 1, *C. polae* solitary; 2, *C. affinis* solitary from particle clearance experiments (Harbison and McAlister, 1979); 3 and 4, *C. bakeri* (both generations) from uncorrected gut pigment and diatom counts, respectively (Madin and Purcell, 1992); (D) *Pegea confoederata*: 1, pumping rate (Madin and Kremer, 1995); 2 and 3, gut pigment method (Madin and Kremer, 1995); 4, gut pigment method (Madin and Cetta, 1984); 5 and 6, particle depletion rates from Harbison and Gilmer (Harbison and Gilmer, 1976), for aggregates and solitaries, respectively; (E) *M. hexagona*: 1, clearance rate for *S. maxima* aggregates from particle depletion (Harbison and Gilmer, 1976); 2, from gut pigment (Madin and Cetta, 1984); 3, particle clearance experiments for *S. fusiformis* aggregates (<40 mm) and solitaries (>40 mm) (Andersen, 1985); 4, pumping rate for *S. maxima* (Madin and Kremer, 1995); (F) *Salpa* sp., lines 1–4 references as in E.

shallower thermocline, i.e. at the stations located in the mouth of the GC and near Manzanillo, up to 300 km off the coast. High zooplankton biomass at the mouth of the Gulf was described by Farber-Lorda *et al.* (Farber-Lorda *et al.*, 2004) based on more intense sampling in the area. These authors pointed out that centers of high biomass around Cape San Lucas and Cape Corrientes are possibly a fairly stable feature year round related to the mixing of CC waters with Gulf waters off Cape San Lucas and the vorticity effect off Cape Corrientes. For the same area, Torres-Orozco *et al.* (Torres-Orozco *et al.*, 2005), using satellite observation, described a frontal zone in the area during March 2003 generated by the interaction between cold upwelled waters near Cape Corrientes and warmer surrounding waters. According to these authors, interactions between coastal topography, bathymetry and variations in wind stress can induce the formation of filaments in the upwelling zone, favoring the fertilization of the euphotic layer offshore. Thus, these processes could explain the formation of patches with high zooplankton biomass (>100 mL 10^{-3} m^{-3}) as we have

observed in this study at the mouth of the Gulf and around Cape Corrientes and Manzanillo.

The small observed changes in euphotic zone Chl *a* standing stocks along Transect 2 are consistent with previous studies which have also shown that Chl *a* biomass only varies slightly in eastern tropical Pacific waters, with a maximum between April and September ($\sim$30 mg Chl *a* m^{-2}) and a minimum between October and January with a 2-fold difference among periods (Blackburn *et al.*, 1970).

Salp abundance and biomass

Our results show that salps are a common component of the meso and macrozooplankton community of the ETNP off Mexico. Salp abundance is dominated by cosmopolitan small species such as *Thalia* spp., which can dominate salp biomass as well when they bloom. Similarly, larger species, which were present in moderate abundance, can comprise an important fraction of zooplankton biomass.

Almost all of the 19 species collected in the area are among the 23 species reported by Esnal (Esnal, 1976) from nine cruises during the EASTROPAC expedition (1967–1968) and the 24 species reported by Van Soest (Van Soest, 1998) from several expeditions to the tropical Pacific, in which the study of Esnal was not included. Van Soest did not report *B. rostrata* listed by Esnal and observed in this study. However, these authors did not report *Thalia cicar* in the area, which has been commonly found in tropical waters (this study; Godeaux, 1977; Esnal, 1978; Amaral *et al.*, 1997) and off central Baja California (Hereu *et al.*, 2006). Surprisingly, *Salpa fusiformis* was absent from our samples during both periods. This is one of the most widely distributed species in all oceans and is usually found between 40°N and 40°S (Van Soest, 1998). This species usually forms swarms in the CC System mainly between 37°N and 25°N (Berner, 1967; Lavaniegos and Ohman, 2003; Hereu *et al.*, 2006) and also occurs conspicuously in the eastern tropical Pacific, appearing year round in offshore waters and mainly at the equator with maximum abundance in April–May (Esnal, 1976; Small *et al.*, 1983).

Salp abundance during February and November 2003 was in general low to moderate, but similar to values reported for other oligotrophic areas (Madin *et al.*, 1996). Patches with moderate abundance were found to be associated with a shallower thermocline. In this study, the highest salp abundance was associated with a patch of *Thalia rhomboides* (36 ind. m^{-3}) at the entrance of the GC in February. Similarly, Esnal (Esnal, 1976) reported that abundance of *T. rhomboides* surpassed that of the congener species during the February–March cruise from EASTROPAC expedition. She also showed that salps were more abundant near the coast in a broad area south and west of Manzanillo ($\sim$12°–18° N, 100°–112° W).

The abundance of the remaining species was low and only *M. hexagona* and an unidentified *Cyclosalpa* attained numbers >3 per 10 m^3 in November. Salp abundance in the study area was low compared with the maximum values reported in the adjacent areas of the northern and the tropical Pacific. Within the CC System off Baja California, maximum abundance of up to 200 salps m^{-3} in the upper 200 m depth was reported during the ENSO of 1997–1999 (Hereu *et al.*, 2006) and up to 1059 salps m^{-3} in the upper 76 m within Vizcaino Bay (Angeles Reyes *et al.*, 2002). Both patches were swarms of *Thalia*.

From this study, it was evident that simple vertical/oblique tows through the column water undersampled the species present in the area. The horizontal tows in February were longer than those in November and collected six species not detected by the vertical tow, whereas in November two species absent from oblique tows appeared in surface samples. This could be the result of several factors, such as the larger volume of water filtered during horizontal tows and a possible aggregation of some species of salps in the upper few meters of the column water at night (Madin *et al.*, 1996, 1997). Other factors that affect salp collection are their patchy distribution and the presence of bridles in the mouth of the net that can interfere with the collection of salps due to disruption and dispersion of chains (Madin and Kremer, 1995; Ohman and Lavaniegos, 2002). Ohman and Lavaniegos (Ohman and Lavaniegos, 2002) concluded that the bridleless Bongo net (0.71 m diameter) collected up to 2.7 times more salps in the upper 0–200 m than the 1 m diameter net similar to the one used in this study.

Grazing impact

Gut pigment concentrations of salps observed as part of this study were within the range of values determined for the same or related species collected in other areas (Madin and Cetta, 1984; Madin and Kremer, 1995; Huskin *et al.*, 2003). Our estimates of grazing impact, considered here as the percentage of phytoplankton and PP consumed by the salp assemblage, were generally low. Salp community ingestion at most of the stations was <0.1 mg Chl *a* m^{-2} day^{-1}, mainly due to the dominance of the small species *Thalia*, which had the lowest GPCs and ingestion rates. However, at some stations, large salps were also present. Even when their numbers

were not large, their consumption resulted in a higher impact compared with other co-occurring smaller species. For example, at station 8 during November, a population of *Thalia* ingested <1 μg Chl *a* m^{-2} day^{-1}. In contrast, *M. hexagona*, *Cyclosalpa* sp. and *P. confoederata* ingested $\sim$816 mg m^{-2} day^{-1}, representing a consumption of 3.5% of the phytoplankton biomass or 24.5% of the average PP (if the upper estimations of ingestion rates are taken, Table VI). In the present study, gut contents of solitaries of *M. hexagona* were among the highest values. Esnal (Esnal, 1976) reported that this species is present most of the year north of 10°N. In this area, it is the main food source of the sea turtle *Lepidochelys olivacea* during the reproductive season (Montenegro Silva *et al.*, 1984), suggesting an important ecological role for this species. *Pegea confoederata* has also been observed in large numbers in the ETNP (Esnal, 1976). This species as well as *P. socia* occasionally form swarms in neighboring CC System waters (Berner, 1967; Durazo *et al.*, 2005). Similarly, *S. aspera*, *S. maxima* and *S. younti*, with feeding rates in the order of *M. hexagona* (Fig. 8), also contribute considerably to community grazing. The remarkably large amount of pigment (17 μg Chl *a* equivalents) determined from the gut of a 140 mm *C. polae* (Fig. 6) indicates the potential grazing impact of salp assemblages in the study area. If a GPT similar to that of the congener *C. bakeri* (Table II) is assumed, the ingestion rate of this individual would be 104 μg Chl *a* day^{-1}, comparable to feeding rates of large *Salpa thompsoni* (>50 mm) in the southern hemisphere (Perissinotto and Pakhomov, 1998).

Although the gut pigment method is relatively quick and simple, it has certain disadvantages due to potential sources of error influencing the estimation of ingestion rates. For example, the variable distribution of the food in the environment, the variability in the evacuation rates and the pigment destruction in the gut, all can be affected by the confinement of individuals in containers (Madin and Kremer, 1995; Phillips *et al.*, 2009). Some gut evacuation may also take place during the collection and handling of the salps. If this material is not recovered and measured with the stomach content, the total gut pigment would be underestimated. Another source of error is the assumption that the salps are feeding homogenously at the depth range where they were captured. The salps for gut content analysis were collected from a subsurface layer ($\sim$10–20 m depth) and community ingestion was extrapolated for the salps distributed in the upper (0–70 and 0–150 m) layer. Ingestion rates of salps would be underestimated if in fact salps are preferentially feeding at depths other than the depth of collection for gut pigment analysis (Madin and Kremer, 1995). We have also considered a constant daily pattern of feeding which may be the case for *Thalia* (Gibbons, 1997) and other salps in oligotrophic environments (Madin and Deibel, 1998) but not for some species inhabiting different systems such as *Cyclosalpa bakeri* in the subarctic Pacific (Purcell and Madin, 1991) and species that undergo extensive diel vertical migration such as *S. aspera* and *S. thompsoni* (Madin *et al.*, 2006; Pakhomov *et al.*, 2006).

The pigment degradation to non-fluorescent compounds is also an important and controversial factor in the application of the gut pigment method (Conover *et al.*, 1986; Madin and Kremer, 1995; Goericke *et al.*, 2000b). The degradation of pigments will lead to an underestimate of gut content and hence, to an underestimation of the ingestion rates. Pigment destruction has been widely studied in copepods and varies between 8% and 100% (Conover *et al.*, 1986; Dagg and Walser, 1987) with an average of 10–30% (Båmstedt *et al.*, 2000) whereas in salps it can be up to 50% (Madin and Purcell, 1992). We determined in this study the pigment destruction for two species, *Thalia* and *M. hexagona*. For the former, the pigment destruction of replicates in one experiment varied between 16% and 36% and for *M. hexagona* between 20% and 45%, with an average of 27% for both experiments. This correction was applied to all species to estimate pigment ingestion. Although pigment degradation can vary among species and as a function of diet and season (Madin and Cetta, 1984; Landry *et al.*, 1994b), the values we obtained are within the range reported for other salp species (Madin and Kremer, 1995; Perissinotto and Pakhomov, 1998). Nevertheless, the effect of underestimating the pigment destruction is less severe than that produced due to variability in the estimate of GPT (Madin and Kremer, 1995).

We could only determine GPT for two species, *T. democratica* and *M. hexagona*. Values obtained for the former species were within the range expected (Gibbons, 1997) whereas for *M. hexagona*, which is an active swimmer, we obtained a slow GPT compared with other species (Madin and Cetta, 1984) if we extrapolate the GPT obtained for a limited size range (14–30 mm) to larger individuals. Therefore, in order to evaluate the possible range of ingestion rates for *M. hexagona*, we took values from *S. maxima* held experimentally at temperature conditions similar to ambient temperature in the study area. In any case, even when applying correction factors due to possible source of errors and uncertainties, the grazing impact obtained here should be considered as approximate estimates.

Most studies comparing the grazing impact of different herbivores have focused on individual species, different size fractions of the mesozooplankton community (Dam *et al.*, 1995; Zhang *et al.*, 1995; Slaughter *et al.*, 2006), or a taxonomically defined subset of the

grazer assemblage (Landry *et al.*, 1994a; González *et al.*, 2000). Studies in temperate systems, where more eutrophic conditions prevail and swarming by salp populations may be favored, showed that although salps are more episodic than other herbivores, their grazing impact can be similar to or even surpass that of the crustacean zooplankton community (Landry *et al.*, 1994a; González *et al.*, 2000; Huskin *et al.*, 2003). The main grazers in tropical waters are microzooplankton (<200 μm) (Landry *et al.*, 1995; Le Borgne and Landry, 2003) whereas mesozooplankton (200–20 000 μm) contribute moderately to grazing (Calbet, 2001). The salps collected in the ETNP fall into the meso to macrozooplankton size categories. Our estimates of grazing by the salp community, when dominated by *Thalia* and other small species, were generally low (<1% of the chlorophyll standing stock and PP). However, when larger salps were present, grazing on phytoplankton approached values reported for the whole mesozooplankton community (Zhang *et al.*, 1995; Le Borgne and Landry, 2003) and at times surpassed reported averages.

To estimate how these grazing rates translate into carbon flux through fecal pellets sedimentation, we performed the following calculation. Madin and Deibel (Madin and Deibel, 1998) reported that the average defecation rates for different salp species generally ranges from 10% to 30% of body carbon on a daily basis, though *P. confoederata* defecation rates may be even higher. If we apply the lower rates (10%) to the salp biomass present (Table IV), defecation rates would range between <0.01 and 19.3 mg C m^{-2} day^{-1}. Conversely, if an assimilation efficiency of 70% is applied to the ingestion estimates in Tables V and VI (Madin and Deibel, 1998), maximum egestion rates for salp species would range between 0.01 and 1.31 mg C m^{-2} day^{-1} in February and between 0.1 and 14.6 mg C m^{-2} day^{-1} in November, which falls within estimates from salp biomass. Small *et al.* (Small *et al.*, 1983) cited unpublished data for a total C flux of 38 mg C m^{-2} day^{-1} from a sediment trap at 120 m depth for our study area (18°N, 108°W). According to Small *et al.* (Small *et al.*, 1983), the total pellet-derived removal of carbon by zooplankton (>300 μm) would not surpass 10% of daily PP and would average ~5%. Consequently, the egestion-derived fecal pellet production by salps present in ETNP waters could account for <1 to 38% of the average C flux below the mixed layer, in agreement with previous estimates of fecal matter derived flux from our study area. In our study, higher salp biomass was due to the presence of larger salps (i.e. *M. hexagona*, *P. confoederata*), which produce larger, fast-sinking fecal pellets than small salps (i.e. *Thalia* and *S. cylindrica*) and other mesozooplankton (Pomeroy and Deibel, 1980; Andersen, 1998). Large pellets have shorter residence times within the mixed layer than smaller ones and their chemical composition remains almost intact during downward sinking (Caron *et al.*, 1989). Our data indicate that pellet-derived carbon flux from salps could at times be high and could surpass 5% of PP (Small *et al.*, 1983) when the salp assemblage is dominated by larger species.

To conclude, salps in the ETNP off Mexico during the study period were not major contributors to grazing on phytoplankton. Salp grazing impact is strongly influenced by species composition and abundance. Grazing by the salp assemblage is low when the community is dominated by small salps, but it can be higher when grazing is dominated by moderate aggregations of large sized salps. It is expected that salp grazing impact changes considerably during times of favorable environmental conditions that enhance phytoplankton biomass production. Such conditions may be induced seasonally in the area by the offshore export of enriched coastally upwelled waters through filaments (Torres-Orozco *et al.*, 2005) or other mesoscale process (Lavín *et al.*, 2006; Pennington *et al.*, 2006; Zamudio *et al.*, 2007) as well as throughout the year promoted by local topography (Salas *et al.*, 2006).

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