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Salp distribution and grazing in a saline intrusion off NW Spain

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Abstract

Salp distribution and grazing were studied along three transects (19 stations) and a Lagrangian phase (7 stations) off Galician coast (NW Spain) in November 1999 during GIGOVI 99 cruise. A poleward saline intrusion was detected at the shelf-break, reaching salinity values above 35.90 u.p.s. at 100-m depth. The salp community was dominated by *Salpa fusiformis*, although *Cyclosalpa bakeri*, *Thalia democratica* and *Iasis zonaria* were also found in the study area. Total salp abundance ranged from 4 to 4500 ind m^{-2}, representing biomass values between 0.2 and 2750 mg C m^{-2}. Maximum densities were located in the frontal area separating the saline body from coastal waters. *S. fusiformis* pigment ingestion was estimated using the gut fluorescence method. Gut contents were linearly related to salp body size. Total pigment ingestion ranged from 0.001 to 15 mg Chl-*a* m^{-2} d^{-1}, with maximum values at the coastal edge of the saline body. Estimated ingestion translates into an average daily grazing impact of 7% of chlorophyll standing stock, ranging from < 1% to 77%.

Keywords: Salp distribution; *Salpa fusiformis*; Saline intrusion; Grazing; Gut content; Galicia; NW Spain

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1. Introduction

Salps are among the biggest of the planktonic animals (individual body sizes as large as 20 cm in some species) and are widely distributed in oceanic waters. In spite of their importance in marine ecosystems, relatively little attention has been paid to these organisms when compared with other zooplanktonic groups (e.g. copepods). Their high growth rates, among the fastest within the metazoans (Bone, 1998), and the occurrence of asexual budding in their life cycle enable them to develop, under favourable conditions, extremely dense populations in the form of swarms of several kilometres of diameter (Bathmann, 1988 and references therein). On these occasions, salps can dominate planktonic biomass, compete with other filter feeders (such as copepods) and exclude other zooplankton groups (Aldredge and Madin, 1982) by removing all available food.

Salps obtain their food by filtering a current of water (originated by muscular action) through a continuously produced internal mucus net. Their filtration rates are high relative to most other herbivores (Madin and Purcell, 1992) and can feed efficiently on particles of a wide size range, from bacteria to large diatoms and microzooplankton (Silver and Bruland, 1981; Caron et al., 1989; Kremer and Madin, 1992). Ingesting small particles and serving as prey for fish and other marine animals, salps could play an important role in the transfer of energy from ultraplankton to higher trophic levels (Deibel, 1985). Their ability to ingest small particles also suggests the potential importance of salps as

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grazers in areas dominated by small producers, preventing the build up of phytoplankton blooms (Fortier et al., 1994). During mass occurrences of salps, their grazing pressure can also influence the seasonal development of copepod populations (Makarov and Solyankin, 1990; Dubischar and Bathmann, 1997; Paffenhofer et al., 1995) and the structure of the whole pelagic community (Bathmann, 1988). Besides this, their large fast-sinking fecal pellets contribute to the downward flux of materials in the ocean (Bathmann, 1988 and references therein) and provide food for bathypelagic and benthic organisms (Pomeroy and Deibel, 1980).

The Galician coast (NW Iberian Peninsula) can be defined as a typical temperate region, where winter mixing of the water column is followed by thermal stratification on summer. This alternation of oceanographic regimes determines plankton dynamics in a seasonal scale, but different hydrographic features introduce important sources of variability in the region. Cold coastal upwelling (Bode et al., 1996) of nutrient-rich waters has made this area a productive fisheries region. However, the most remarkable feature is probably the episodic intrusion of high-salinity (≈ 0.2 u.p.s. higher than surrounding areas) water during periods of vertical mixing, driven by wind-induced onshore Ekman transport (Frouin et al., 1990). This current flows poleward along the Portuguese and Galician coast (Frouin et al., 1990) and extends to the Cantabrian slope (Botas et al., 1988; Bode et al., 1990). Sharp thermohaline fronts related to this current have been suggested to largely alter the structure of the pelagic community (Fernández et al., 1993).

Galician shelf has been the subject of many oceanographic studies, both physical (see references in Valdés et al., 1990a) and biological (Bode et al., 1994, 1996) including zooplankton (Álvarez-Ossorio, 1984; Valdés et al., 1990b; Barquero et al., 1998; Bode et al., 1998), but no attention has been paid to gelatinous zooplankton. The main objective of this study is to describe salp distribution and grazing in a poleward high-salinity slope current off Galician coast.

2. Methods

Sampling was carried out onboard R/V *Thalassa* at 27 stations off NW Spain in November 1999 (GIGOVI 99 cruise). Stations were distributed (Fig. 1) in three main transects perpendicular to the coast (stations 77 to 96) and a Lagrangian phase following a drifting biplane deployed to 100-m depth (stations 97 to 105). At every station, vertical profiles of temperature and salinity were obtained with a Neil Brown Mark-III CTD. Sampling depth was 200 m at oceanic stations, 150 m at shelf-break stations (81, 84 and 93) and 95 m at coastal stations (82, 83 and 94). Chlorophyll concentration was estimated from CTD fluorometer (calibrated with extracted chlorophyll *a* assayed by HPLC) and expressed as integrated value in the photic layer.

Salps were collected by a treble-ring WP2 net (60 cm ∅, 200 μm mesh), towed vertically at 0.5 m s^{-1} from 200 m (150 and 95 m at shelf and coastal stations) to surface. Sampling was carried out between 8:30 AM and 23:00 PM. Contents of one cod end were devoted to determination of salp abundance and taxonomic composition. Samples were fixed with 4% buffered formaldehyde and determined in an Olympus SZ-40 stereomicroscope. Body length of every salp was measured as the distance from oral to atrial cavities, using an image-analysis system attached to the stereomicroscope. Individual carbon weight for the different

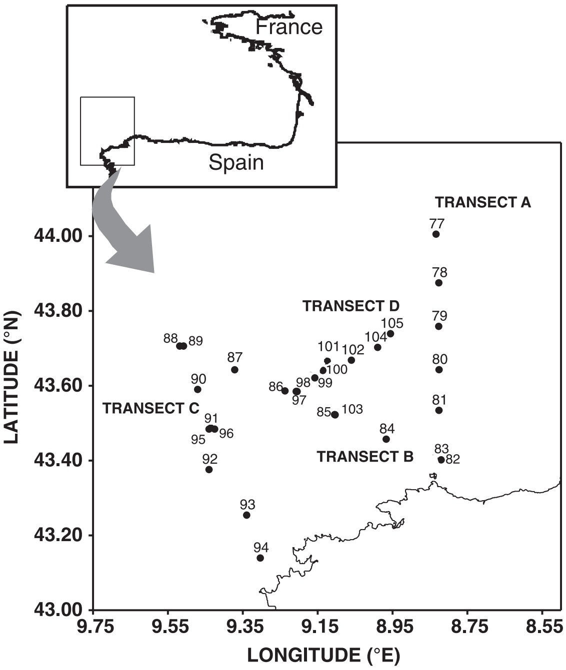

Fig. 1. Stations sampled during GIGOVI 99 cruise.

salp species was estimated from body length, using equations summarised in Madin and Deibel (1998, Table 5.3). No correction for shrinkage due to preservation was applied.

Salpa fusiformis grazing rates were estimated at stations 77, 78, 79, 85, 86, 88, 90, 93, 98 and 104, using the gut fluorescence technique (Mackas and Bohrer, 1976). Each individual animal obtained from the second cod end at these stations was isolated in a Petri dish, its body length was measured as above and the tunica was removed to avoid interference with the pigment analysis. Guts were removed surgically with the help of tweezers and knife blades, placed into Petri dishes and frozen at − 60 °C for later pigment analysis. Frozen guts were placed in 20-ml glass vials with 7 ml of acetone (90%) and extracted for 24 h at 4 °C in the dark. The fluorescence of the acetone extracts was measured using a Turner Design II fluorometer before and after acidification with two drops of 1N HCl and expressed as ng chlorophyll *a* equivalents (Chl-*a* + phaeopigments). Gut contents of every analysed salp were plotted against body length. The equation

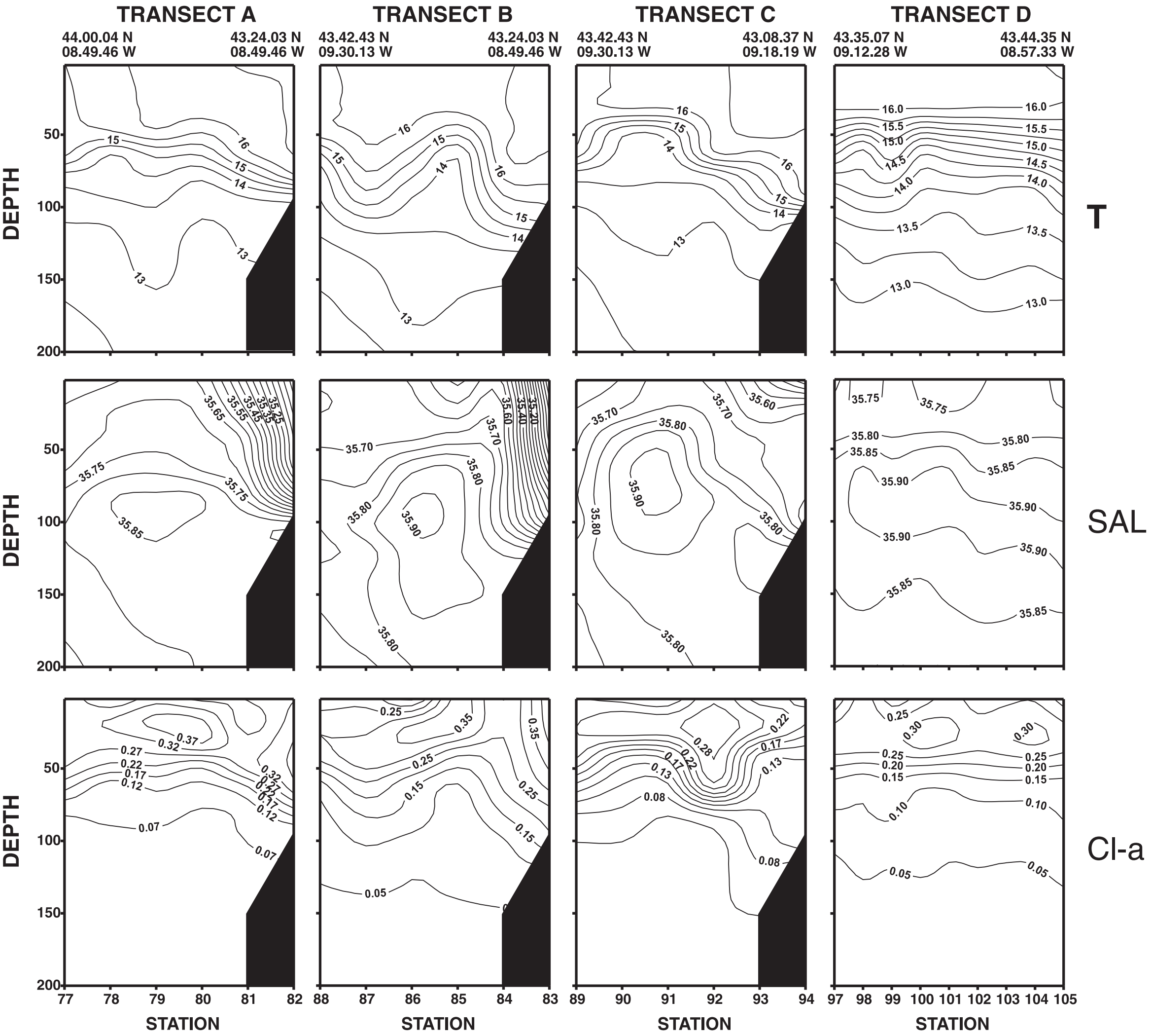

Fig. 2. Vertical profiles of temperature, salinity and chlorophyll concentration (mg m^{-3}) along the four transects sampled during GIGOVI 99 cruise.

Table 1
Integrated abundance and biomass of the different salp species

Station	Abundance (ind m^{-2})				Total	% Aggregate form	Average size (mm)	Biomass (mg C m^{-2})				Total
	S. fusiformis	*C. bakeri*	*T. democratica*	*I. zonaria*				*S. fusiformis*	*C. bakeri*	*T. democratica*	*I. zonaria*	
77	1282	–	–	–	1282	99	10.34	384.9	–	–	–	384.9
78	796	29	–	–	825	99	6.14	82.6	11.1	–	–	83.8
79	2768	–	–	–	2768	99	4.09	94.3	–	–	–	94.3
80	218	–	–	–	218	81	11.58	109.1	–	–	–	109.1
81	2307	–	89	–	2396	87	7.61	405	–	4	–	409
83	29	–	–	–	29	86	15.63	25.5	–	–	–	25.5
84	914	–	–	–	914	91	7.62	180.3	–	–	–	180.3
85	4507	–	–	–	4507	63	8.02	2748.1	–	–	–	2748.1
86	761	–	–	–	761	67	12.56	327.7	–	–	–	327.7
87	300	–	14	–	314	75	13.43	115.1	–	0.8	–	115.9
88	200	14	4	–	218	100	11.65	184.8	12.2	0.5	–	197.5
89	7	–	–	–	7	100	3.85	0.2	–	–	–	0.2
90	2836	–	–	–	2836	99	3.62	61.7	–	–	–	61.7
92	979	–	25	–	1004	97	4.36	24.1	–	4.6	–	28.7
93	157	–	–	–	157	98	3.60	3.6	–	–	–	3.6
94	4	–	–	–	4	100	8.2	0.6	–	–	–	0.6
95	75	–	–	–	75	95	8.03	19.2	–	–	–	19.2
96	4	–	–	7	11	100	19.6	0.1	–	–	12.8	12.9
103	2186	–	4	–	2190	99	4.84	207.5	–	0.4	–	207.8
Lagrangian phase												
97	982	–	–	–	982	7	5.79	179.4	–	–	–	179.4
98	196	–	–	–	196	99	6.26	26.3	–	–	–	26.3
100	796	–	–	–	796	99	5.85	89	–	–	–	89
101	686	–	–	–	686	99	9.29	139.1	–	–	–	139.1
102	257	57	–	4	318	99	6.44	12	17.2	–	30.6	59.7
104	46	–	–	–	46	92	7.11	10.4	–	–	–	10.4
105	254	–	–	–	254	97	6.69	81.4	–	–	–	81.4

obtained after fitting data to a linear model (see Results) was used to estimate contents at stations where only abundance and size of salps were available.

Gut evacuation rates were calculated using the empirical relationship with body length proposed by Madin and Cetta (1984). Individual ingestion rates were obtained by multiplying the gut content by the gut evacuation rate. Community ingestion rates were calculated summing individual rates at each station and were combined with integrated Chl-*a* standing stock and primary production to estimate grazing impact. A C/Chl index of 60 was used.

3. Results

3.1. Hydrographic conditions and chlorophyll

Vertical profiles of temperature, salinity and Chl-
concentration along the four transects sampled
cruise are shown in Fig. 2. Surface t
increased from oceanic to coastal wate
15.4 to 16.6 °C, while surface s
≈ 34.65 at coastal to 35.7 at
main hydrographic feature
the presence of a high-sa
the shelf-break, separat
by an uplifting of isoth
this structure was lo
A), 85–86 (transect
ing salinity values
temperature and sa
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Spatial distributio
hydrographic structure
concentrations were found with
maximum values above 0.37 0 m.

3.2. Salp abundance an

Four different sp p were found: *Salpa fusiformis*, *Cyclo* ri, *Thalia democratica* and *Iasis zona* iformis was present at all the stations s nd was always the most abundant specie eri, *T. democratica* and *I. zonaria* were on d at three, five and two stations, respect always in low densities (Table 1). Total salp dance ranged from 4 to 4500 ind m^{-2},

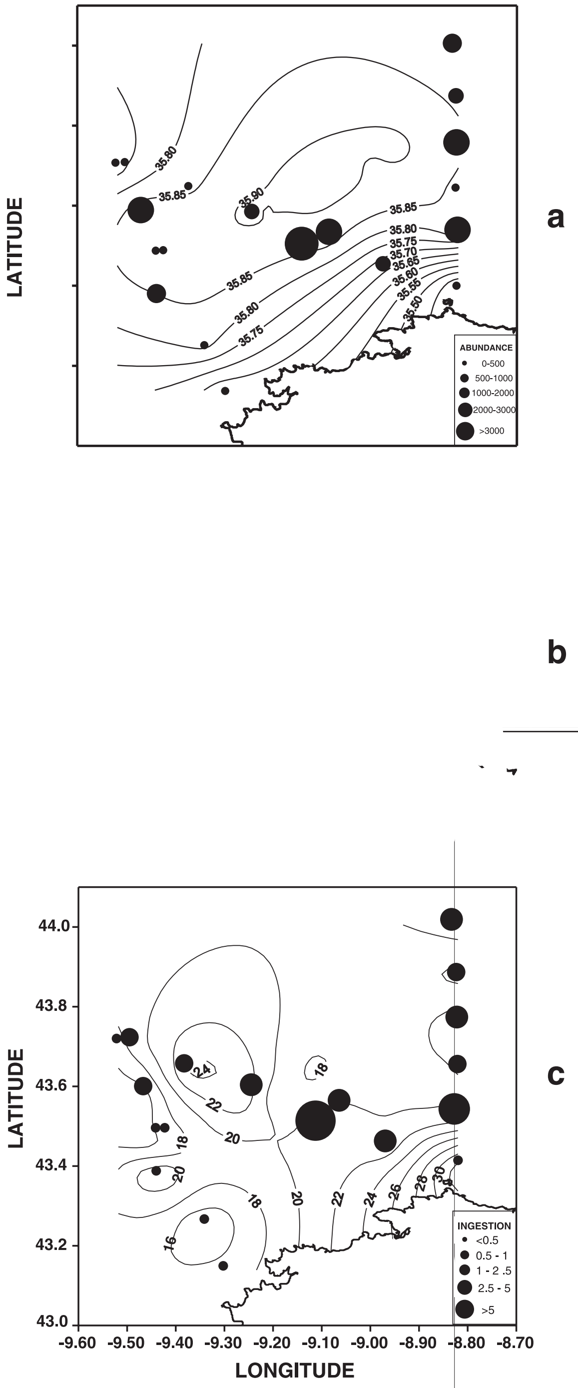

Fig. 3. Integrated salp abundance (ind m^{-2}) (a), biomass (mg C m^{-2}) (b) and ingestion (mg Chl-*a* m^{-2} day^{-1}) (c) in transects A, B and C. Isolines represent salinity at 100-m depth [(a) and (b)] and integrated chlorophyll concentration (mg m^{-2}) (c).

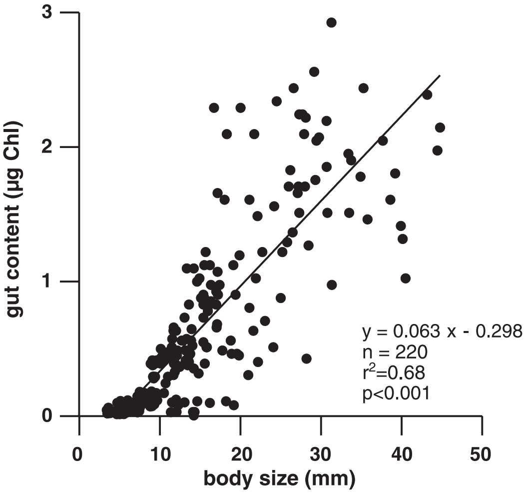

Fig. 4. Relationship between salp gut content and body size.

translating into biomass values ranging from 0.2 to 2750 mg C m^{-2}. Aggregated forms represented 85% of total individuals sampled. Maximum contribution of solitary forms to total abundance was found in stations 85, 86 and 87 (>25%). Average size of salps ranged from 3.62 mm at station 90 to 15.63 mm at station 83 (Table 1).

Fig. 3a and b shows spatial distribution of total salp abundance and biomass in transects A, B and C. Both variables presented a high degree of spatial heterogeneity. The density and biomass of salps reached the maximum values at stations located in the frontal area separating the saline body from coastal waters at transects A and B (stations 81, 85 and 103) and at two stations inside the saline core (stations 79 and 90). Minimum values of both variables were found at coastal stations (83, 93 and 94) and also inside the saline body (stations 89 and 96).

3.3. Ingestion

S. fusiformis gut contents were linearly related with body size (Fig. 4). No differences in gut content–body size relationship were found between stations (ANCOVA $p>0.1$). Pigment ingestion (Table 2) averaged 1.38 ± 0.59 (S.E.) mg Chl-*a* m^{-2} day^{-1}, ranging between 0.001 and 15.43 mg Chl-*a* m^{-2} day^{-1}. Ingestion was higher at transects A and B (Fig. 3c), especially at stations separating the saline body from coastal waters (stations 81, 85 and 103). Minimum ingestion values were found at transect C and at transect A coastal station (station 83).

Estimated pigment ingestion translates into an average daily grazing impact (Table 2) of 6.9 ± 2.9% of Chl-*a* standing stock, with a maximum value of 77% (station 85) and a minimum one of 0.01% (station 89). *S. fusiformis* consumed daily 1.3% and 5.2% of primary production at the two stations where this measurement is available (stations 95 and 88, respectively).

3.4. Lagrangian phase

During the Lagrangian phase of the cruise (transect D), the buoy displaced northeastwards from 43°35′N, 9°12′W to 43°44′N, 8°57′W in 67 h. This translates into an estimated current velocity of 13 cm s^{-1}. Fig. 5 shows temporal variation of salp abundance and bio-

Table 2
Integrated *S. fusiformis* ingestion and grazing impact on chlorophyll standing stock and primary production

Station	Ingestion (mg Chl-*a* m^{-2} day^{-1})	% Chl	% PP
77	2.18	10.35	
78	0.53	3.07	
79	1.28	6.03	
80	0.51	2.57	
81	3.6	18.36	
83	0.14	0.41	
84	1.91	9.32	
85	15.43	77.4	
86	1.9	7.86	
87	0.74	3.03	
88	0.53	2.88	5.23
89	0.001	0.01	
90	0.77	5.21	
92	0.37	1.68	
93	0.05	0.34	
94	0.01	0.03	
95	0.13	0.85	1.29
96	0.06	0.29	
103	2.34	10.65	
Lagrangian phase			
97	1.08	6.16	
98	0.22	1.20	
100	0.85	4.83	
101	0.51	2.9	
102	0.27	1.49	
104	0.06	0.29	
105	0.3	1.57	

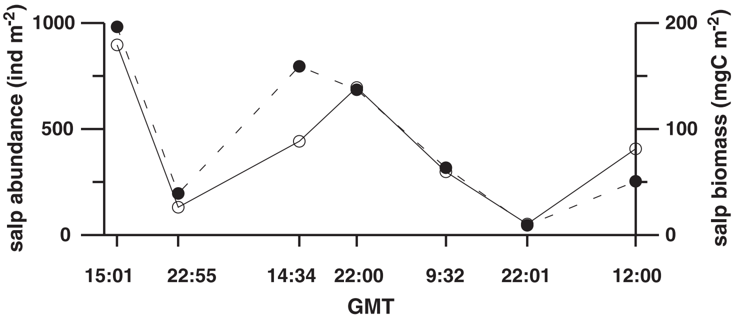

Fig. 5. Salp abundance (closed circle) and biomass (open circle) during the Lagrangian phase of GIGOVI 99 cruise.

mass along the transect of the buoy. Salp abundance ranged between 46 and 982 ind m^{-2}, while biomass varied from 10.5 to 179 mg C m^{-2}. Results are not consistent with any clear pattern of vertical migration out of the upper 200 m of the water column, with nighttime (≈ 22:00 PM) presenting high and low values of both parameters. *S. fusiformis* pigment ingestion varied between 0.05 and 1.08 mg Chl-*a* m^{-2} day^{-1}, representing 0.29–6.16% of chlorophyll standing stock (Table 2).

4. Discussion

Since Mackas and Bohrer (1976), gut fluorescence measurements, combined with estimations of gut passage time, have been one of the most popular methods to study zooplankton feeding, although its accuracy has been questioned due to methodological limitations (see review in Bamstedt et al., 2000). The technique has been widely applied with copepods (e.g. Dagg and Wyman, 1983; Peterson et al., 1990; Morales et al., 1991; Bautista and Harris, 1992; Huskin et al., 2001), but also with other zooplanktonic groups such as euphausiids (Perissinotto and Pakhomov, 1996) or appendicularians (Acuña, 1999). The main advantages and disadvantages of employing this method in the particular case of salps are summarised in Madin and Kremer (1995). It is a simple, rapid and mostly in situ method, which eliminates animal confinement and unnatural diet, but on the other hand, measurement of gut passage time is not as easy as in copepods and pigments could be degraded to nonfluorescent components during digestion.

We have used gut passage times calculated from Madin and Cetta (1984) relationship with body length. We are aware of the uncertainty in assuming rates calculated for different salp species (*Pegea confoederata*) and different temperature ranges, but direct estimations of *S. fusiformis* gut passage time are not available in the literature. In fact, few authors have directly measured gut passage time in salps (Madin and Cetta, 1984; Drits and Semenova, 1989; Drits et al., 1993; Perissinotto and Pakhomov, 1998). However, the gut passage times used in our study are in the range found by Madin and Kremer (unpublished) for *S. fusiformis* at ≈ 25 °C (2–4 h in 10-mm animals, 3.5 h in 25 mm, and ≈ 7 h in 35-mm individuals). We have not applied any correction factor to consider background fluorescence of salps with cleared guts. However, if we assume the values found by Madin and Kremer (unpublished) for *S. fusiformis*, ranging from 0.02 μg of pigment in 15-mm salps to ≈ 0.4 μg in 40-mm individuals, our results would be overestimating ingestion by a factor of 1.25. Finally, we have assumed no degradation of chlorophyll to nondetectable by-products within the guts of salps. Although pigment destruction has been widely investigated in copepods (ranging from 0% to 100% of ingested pigments), the only measurements referred to salps are those of Madin and Purcell (1992), Madin (unpublished, in Madin and Deibel, 1998) and Perissinotto and Pakhomov (1998) reporting losses of 50%, 34% and < 10%, respectively. Gut fluorescence has been suggested to provide accurate measurements of salp ingestion when compared with alternative methods, even if pigment destruction is not considered (Madin and Kremer, 1995). In any case, due to mentioned uncertainties, our results must be considered as only approximate estimations of ingestion.

We found salp abundance to be much less than maximum values reported in the literature (see summary table in Andersen, 1998), up to 1000 ind m^{-3}. However, results are not always comparable because most of published values pertain only to surface waters where salp swarms are usually restricted, while our data are integrated in the upper 200 m. In this sense, maximum abundance reported in this study (≈ 22 ind m^{-3}) is similar to that of Nival et al. (1985) for the same depth interval in the NW Mediterranean (19 ind m^{-3}). We must also consider that standard nets used in our study could be underestimating salp abundance in stations with high salp density (e.g. station 85) due to clogging of the net. To our knowledge, there is no previous information concerning oceanic salp distribution or abundance in Galician waters. All the studies available in this region are referred to coastal waters (Álvarez-Ossorio, 1984; Braun et al., 1990; Valdés et al., 1990a,b; Valdés and Álvarez-Ossorio, 1994), always reporting absence or extremely low abundance of salps. Huskin et al. (submitted for publication) did not find any salps along an annual cycle analysed in a shelf-break station located in the adjacent Central Cantabrian Sea, except in early autumn when salps were present in numbers similar to maximum ones found in this study (≈ 5000 m^{-2}).

Due to their feeding mechanism, salps are not able to modify filtration rates in response to changes in food concentration, so clogging of the filtering system may explain exclusion from particle-rich coastal waters (Deibel, 1982; Harbison et al., 1986). Although coastal stations presented low values of both abundance and biomass, low numbers were also found in several oceanic stations. This high spatial heterogeneity in salp distribution is confirmed by the differences in salp abundance found during the Lagrangian phase. This spatial heterogeneity could be masking any pattern of vertical migration out of the upper 200 m. We must also consider that the movement of one single buoy deployed to 100 m does not necessarily represent the movements of the entire salp population. Maximum densities were related to the front which separates the saline body from coastal waters. The effect of oceanic fronts in accumulating planktonic organisms has been widely reported in the literature, including high concentrations of salps associated to thermohaline fronts (see references in Deibel, 1982). Fernández et al. (1993) reported significant increases in zooplankton densities related to thermohaline fronts associated with a poleward slope current in the Cantabrian Sea. This kind of hydrographic feature could represent an important mechanism in the transport of salps into our study region, as transport processes (Gili et al., 1991) easily affect gelatinous zooplankton.

Environmental conditions inside the saline body could also be facilitating the development of salp populations. Poleward currents detected in this domain originate in the oligotrophic subtropical Atlantic (Frouin et al., 1990), characterised by small phytoplankton cells. During GIGOVI 99 cruise, cryptomonas and small flagellates dominate phytoplankton populations (Varela, personal communication), as reported in previous studies carried out in similar poleward currents (Botas et al., 1988; Bode et al., 1990; Fernández et al., 1993; Varela, 1996). Although other zooplankton groups, such as copepods, do not feed efficiently on particles smaller than 5 μm (Nival and Nival, 1976), salps have been found to feed on particles as small as 1 μm (Kremer and Madin, 1992), which may adapt these animals to survive in oligotrophic regions or stratified phases in temperate mid-latitudes (Acuña, 2001).

Zooplankton grazing has been suggested to play a key role in the control of phytoplankton populations (Banse, 1995). Although copepods and microzooplankton are considered to be the main consumers of phytoplankton in marine ecosystems, when abundant, salps can also exert a strong grazing pressure on phytoplankton. Harbison and Gilmer (1976) estimated that one 50-mm-long blastozooid of *P. confoederata* could exert the grazing impact of 450 large calanoid copepods. Moreover, salps have the potential to be important in grazing mediated carbon fluxes (Fortier et al., 1994) because they feed on smaller particles and produce larger fast-sinking pellets than crustacean zooplankton.

Although some studies (Huntley et al., 1989; Nishikawa et al., 1995) found low grazing impact (<9% of primary production) of salps on phytoplankton communities, when abundant, salps can present high grazing rates ($\approx 100\%$ of primary production) (Dubischar and Bathmann, 1997; Huntley et al., 1989; Bathmann, 1988) which can prevent the development of phytoplankton blooms or end blooms before nutrient depletion. We report ingestion rates averaging 1.4 mg C m^{-2} day^{-1}, which represents 6.9% of chlorophyll standing stock. These values decrease to 0.8 mg C m^{-2} day^{-1} and 4% if we do not consider the extremely high ingestion found in station 85. Combining our pigment ingestion estimations with Chl-*a* standing stock, we obtained weight-specific filtration rates ranging between 95 and 2012 ml mg C^{-1} h^{-1}. These values are 0.5 to 10 times higher than predicted from Andersen (1985) relationship between filtration rate and body size, pointing to a possible overestimation in our pigment-based estimations, specially in the smallest animals, which showed higher differences between calculated and predicted rates. Due to the patchily distribution of salps, their grazing impact is not horizontally homogeneous, as suggested by Bathmann (1988), being maximum at one station located in the frontal region separating the saline body from very coastal waters. At station 85, salps were calculated to consume 15 mg C m^{-2} daily, equivalent to 77% of chlorophyll standing stock. We observed a lower effect of the front at stations 81 and 103, where *S. fusiformis* was calculated to consume 18% and 10% of chlorophyll standing stock, respectively. We only have direct estimations of impact on phytoplankton production ($<6\%$) at two stations, both characterised by low salp abundance. However, if we assume the ratio production/Chl-*a* to be constant in the region, salps would consume 31%, 18% and >100% of this production at frontal stations (stations 81, 103 and 85, respectively). For comparison, Barquero et al. (1998) found copepods to ingest only 0.2% of phytoplankton stock or less than 3% of primary production during spring in the study area, while Isla (personal communication) also reports low grazing impact (0.2–5% of chlorophyll standing stock) of copepods in the same saline body 15 days before our study. This points to the importance of salps grazing in the control of phytoplankton production for the area when compared with crustacean mesozooplankton, at least in some stations close to the frontal system linked to the saline intrusion. According to this, Fernández et al. (1993) concluded that poleward currents and associated fronts are essential in the control of primary production, grazers activity and trophic structure of the region.

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