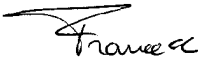


To Phil Pugh, my deep gratitude for your support
and friendship


THE GELATINOUS ZOOPLANKTON IN THE PELAGIC SYSTEM OF THE SOUTHERN OCEAN: A REVIEW

Francesc PAGES

Abstract

The classic view of the Antarctic planktonic system has suggested that food web dynamics are dominated by the phytoplankton-krill food web link. Recent observations, however, have indicated that this is an oversimplification and that the Antarctic food web is much more complicated. In contrast to crustaceans, gelatinous zooplankton (hydromedusae, siphonophores, scyphomedusae, ctenophores, gymnosomatous pteropods and tunicates such as salps, doliolids, pyrosomes and appendicularians) have received little attention among zooplanktologists in spite of the high biovolume that they contribute to the zooplankton communities. Gelatinous zooplankton comprises a quarter of the planktonic species number collected in the Southern Ocean although many additional species remain undescribed. This review considers the published information on spatial distribution, abundance, wet biomass, carbon and lipid content, feeding ecology and biological associations. The sparse but significant information collected suggests that the ecological role of gelatinous zooplankton is underestimated in the Antarctic pelagic system. Sampling methods and investigations that correctly evaluate the impact of gelatinous organisms are extremely necessary for properly placing this group in the Antarctic trophic web.

Key-words: Gelatinous zooplankton, abundance, biovolume, carbon content, feeding, predators, Antarctica.

Résumé

Le zooplancton gélatineux dans le système pélagique de l'océan Austral

Dans la vision classique du système planctonique de l'océan Antarctique, la dynamique du réseau trophique est dominée par le lien phytoplancton-Euphausiacés. Des observations récentes ont cependant souligné que c'est une simplification excessive et que le réseau trophique antarctique est beaucoup plus compliqué. À la différence des crustacés, le zooplancton gélatineux (hydroméduses, siphonophores, scyphoméduses, cténo-phores, ptéropodes gymnosomes et tuniciers tels que les salpes, les doliolés, les pyrosomes et les appendiculaires) a reçu peu d'attention de la part des zooplanctonologistes, en dépit de sa contribution élevée en biovolume aux communautés du zooplancton. Le plancton gélatineux renferme le quart des espèces planctoniques récoltées dans l'océan Austral, mais beaucoup d'autres espèces ne sont pas encore décrites. Cet article passe en revue l'information publiée sur la répartition spatiale, l'abondance, la biomasse, les teneurs en carbone et en lipides, l'écologie alimentaire, ainsi que les associations biologiques. L'information recueillie, clairesemée mais cependant significative, suggère que le rôle écologique du zooplancton gélatineux dans le système pélagique de l'Antarctique est sous-estimé. Un échantillonnage et des recherches appropriés pour évaluer l'impact des organismes gélatineux sont absolument nécessaires pour replacer correctement ce groupe dans le réseau trophique de l'Antarctique.

Mots-clés : Zooplancton gélatineux, abondance, biovolume, teneur en carbone, nutrition, prédateurs, Antarctique.

INTRODUCTION

Our knowledge of the ecology of the zooplankton communities in the Southern Ocean has considerably increased during the last few years. This has been mostly due to extensive recent studies on the biology of particular species that play key roles in the Antarctic trophic web. Crustaceans, particularly euphausiids and copepods, have been the main interest of most zooplanktologists due to their high abundance and biomass in Antarctic waters. In contrast, the gelatinous zooplankton (hydroidomedusae, siphonophores, scyphomedusae, ctenophores, gymnosomatous pteropods and tunicates such as salps, doliolids, pyrosomes and appendicularians) have received little attention. The sparse amount of information published on gelatinous zooplankton contrasts with the large aggregations of salps and medusae observed in recent years (HUNTLEY *et al.*, 1989; NISHIKAWA *et al.*, 1995; PAGÈS *et al.*, 1994) and has led some to believe that gelatinous zooplankton plays a much more important role than that acknowledged by several recent reviews on Antarctic zooplankton (SMITH & SCHNACK-SCHIEL, 1990; SCHNACK-SCHIEL & MUJICA, 1994; MARCHANT & MURPHY, 1994). Several questions come to mind when such reviews are considered in detail. For instance:

- How abundant is the gelatinous zooplankton (GZ) in the Southern Ocean in comparison with the non-gelati-

nous (NGZ) (crustaceans) and the semi-gelatinous (SGZ) (chaetognaths, polychaetes, heteropods and thecosomatous pteropods) populations?

- Is GZ less abundant in polar waters than in temperate or warm seas?
- Is GZ less abundant in the Antarctic than in the Arctic?
- What is the contribution of the GZ in terms of carbon to the biogeochemical flux of matter in the Southern Ocean?

The main objective of this review is to consider the presently published information regarding the gelatinous zooplankton from Antarctic waters. Recent individual studies are providing enumerations of many of the gelatinous species that are in direct conflict with the values (LONGHURST, 1985) given only a decade ago, and which imply that the GZ is of much more significance in driving the Antarctic pelagic ecosystem. These studies are considered here with the aim of being useful to scientists working on gelatinous zooplankton, but more particularly for bringing these fascinating creatures to the attention of those scientists already investigating other aspects of the Antarctic pelagic ecosystem.

THE LONGHURST DATA SET

It is difficult to estimate the average contribution in different seas and oceans of each taxonomic group in terms of abundance, wet weight, dry weight and carbon. To my knowledge, the best estimates were published by LONGHURST (1985) based on counts of individuals per taxa from 1500 zooplankton samples collected in all the world's oceans. The intention of that study was to analyze structure within ecosystems rather than to describe geographic differences in absolute abundance within taxonomic groups, since all data and transformations were expressed in relative terms as percentage composition. As such, they require care in interpretation. Nonetheless, the singularity of Longhurst's paper makes it useful in trying to find the answers to the above mentioned questions. These data are presented in *Tables I, II, III, and IV*.

Table I shows the zooplankton abundance, as percentages of total of individuals counted, for 17 important tax-

onomic groups in the main seas and marine ecosystems of the world. Each GZ taxon shows a low abundance in all seas and ecosystems. Overall their global abundance is low (7.78 %), as is that for the SGZ (6.83 %) and both are considerably less than that of NGZ (85.32 %). However, these percentages are probably biased in favour of crustaceans because their enumeration in preserved samples is easier than that of gelatinous organisms. This is due to the extreme fragility and morphological complexity of the latter. LONGHURST (1985) admitted that ctenophores, which are almost unrecognizable in plankton samples collected by nets, were underestimated. Also scyphomedusae were deliberately neglected; unfortunately this is a quite widespread practice among zooplanktologists who often removed all large medusae at the time of collection. Further, there may be doubts about the systematics when the identifications have been made by people unfamiliar

with GZ, particularly those organisms that form colonies (e.g. siphonophores and salps).

Latitudinally, the Longhurst's data reveals that the percentage abundance of GZ is highest in tropical waters (10.07 %) and lower in polar regions (3.55 %), where copepods are much more abundant (89.87 %) (Table I). However, an underestimation for GZ taxons is possible due to the small number of polar samples considered in comparison with those from tropical and temperate regions. Longhurst observed a trend towards a higher biomass percentage of predators in warm seas due to an increase in the relative abundance of coelenterates, despite the fact that his data did not include the high abundances of large coelenterates that swarm in neritic waters.

The GZ biomass, in units of organic carbon, also is much lower in comparison with the NGZ (Table II). Globally, the former contributes 5.69 %, the SGZ 11.5 %, while the NGZ makes up the remaining 82.87 %. Longhurst assumed "... there is an approximately constant relationship between the average sizes of individuals in all major taxonomic groups in all parts of the ocean." However, this statement is quite debatable. Copepods (approx. 2200 species in the world seas, OMORI & IKEDA, 1984) measure 0.4-10 mm in size and their average size is

easy to estimate in comparison with siphonophores (approx. 180 species, F. Pagès unpublished data), which measure 1 mm-10 metres in total length. Most part of the body of siphonophores is formed by the siphosome (stem). However, this part of the colony is rarely considered in estimating carbon content as, due to its extreme fragility, it is usually lost during sampling by nets. For instance, the carbon content of the siphosome of the common epipelagic species *Diphyes antarctica* Moser (10.6 % DW) is similar to that of the nectophores (11.5 % DW) (IKEDA & BRUCE, 1986), yet is not included in carbon measurements from plankton samples. Anyway, in polar waters the carbon content contribution of GZ (1.19 %) is apparently less than in temperate (5.92 %) and tropical waters (13.49 %) (LONGHURST, 1985).

The abundance of GZ is reported to be higher in the Arctic (4.78 %) than in the Antarctic (2.33 %) (Table III). However, the carbon content due to GZ is lower in the Arctic (0.37 % versus 2.00 %) (Table IV) indicating that the carbon content of Antarctic gelatinous organisms is higher than Arctic ones. Apparently, there are some inaccuracies in these tables due to the general lack of data on the abundance and carbon content of gelatinous organisms in polar seas at the time of publication.

TABLE I.— Global means for zooplankton numbers as percentages of total numbers of organisms counted for 17 principal taxonomic groups (modified from LONGHURST, 1985).

TABLEAU I.— Moyennes, pour différentes zones de l'océan mondial, du nombre d'individus de 17 groupes du zooplancton en pourcentage du nombre total d'organismes dans les comptages (modifié d'après LONGHURST, 1985).

	HYDR	SCYP	SIPH	CTEN	APPE	SALP	DOLI	MOL	CHAE	POLY	CLAD	OSTR	COPE	AMPH	MYSI	EUPH	DECA
Oceans																	
Polar	0.06	?	0.15	?	3.32	0.02	0.00	2.44	3.88	0.23	0.00	2.45	86.32	0.56	0.00	0.52	0.02
Temperate	1.39	?	0.45	?	2.79	0.52	0.12	1.76	3.99	0.54	0.47	3.12	80.45	0.81	0.02	2.77	0.33
Tropical	0.85	?	2.61	?	3.85	2.10	0.66	1.70	6.38	0.85	0.14	3.39	72.31	0.54	0.15	3.02	1.30
Continental shelves																	
Temperate	0.22	?	0.59	?	3.51	0.46	0.05	1.50	3.32	0.39	7.07	0.31	80.10	0.78	0.07	1.02	0.27
Tropical	0.67	?	2.11	?	5.45	5.15	0.10	0.60	5.83	0.43	6.46	5.72	62.95	0.82	0.02	1.17	3.15
Bays																	
Temperate	0.00	?	0.00	?	0.05	0.01	0.00	0.55	0.84	0.84	4.60	0.00	86.69	0.84	1.71	0.66	0.02
Tropical	0.00	?	0.00	?	1.89	0.00	0.00	0.00	7.74	0.00	2.21	0.00	84.38	0.88	0.73	0.00	2.54
Reefs																	
Tropical	0.22	?	1.48	?	0.74	1.07	0.00	0.73	5.66	0.58	0.10	2.63	71.41	0.71	0.04	1.10	13.35
Totals	0.54	?	1.47	?	4.07	1.29	0.41	1.28	4.96	0.59	2.33	2.37	76.55	0.67	0.17	1.98	1.25
				7.78					6.83					85.32			
	Gelatinous							Semi-gelatinous			Non-gelatinous						

TABLE II. — Global means for zooplankton biomass, in terms of relative organic carbon, as percentages for 17 principal taxonomic groups (modified from LONGHURST, 1985).

TABLEAU II. — Moyennes, pour différentes zones de l'océan mondial, de la biomasse, en termes de carbone organique, exprimée en pourcentage pour 17 groupes du zooplancton (modifié d'après LONGHURST, 1985).

	HYDR	SCYP	SIPH	CTEN	APPE	SALP	DOLI	MOL	CHAE	POLY	CLAD	OSTR	COPE	AMPH	MYSI	EUPH	DECA
Oceans																	
Polar	0.23	?	0.75	?	0.18	0.03	0.00	6.73	8.62	0.47	0.00	3.05	67.58	4.57	0.00	7.66	0.13
Temperate	3.28	?	1.78	?	0.08	0.78	0.00	2.95	6.17	0.74	0.03	2.52	42.54	4.43	0.00	33.27	1.44
Tropical	1.98	?	8.51	?	0.10	2.89	0.01	2.66	9.00	1.10	0.01	2.61	33.13	2.58	0.00	30.21	5.02
Continental shelves																	
Temperate	0.62	?	2.66	?	0.17	0.80	0.00	4.83	6.51	0.79	0.78	0.28	64.46	5.22	0.00	11.79	1.11
Tropical	1.39	?	7.88	?	0.18	5.80	0.00	1.15	9.81	0.64	0.48	4.98	37.51	4.25	0.00	10.67	15.26
Bays																	
Temperate	0.00	?	0.00	?	0.00	0.02	0.00	1.73	1.79	1.75	0.49	0.00	69.90	6.99	8.78	8.03	0.15
Tropical	1.14	?	0.00	?	0.09	0.46	0.01	0.37	15.10	0.00	0.27	0.80	48.89	7.08	0.00	0.00	25.79
Reefs																	
Tropical	0.37	?	3.92	?	0.02	0.98	0.00	1.57	7.24	0.69	0.00	1.27	36.83	2.68	0.00	11.38	33.05
Totals	0.98	?	3.15	?	0.10	1.45	0.01	2.75	7.96	0.80	0.25	1.91	50.70	4.68	1.08	14.00	10.25
				5.69					11.51					82.87			
	Gelatinous							Semi-gelatinous			Non-gelatinous						

TABLE III. — Means for zooplankton numbers in the Polar oceans as percentages of total numbers of organisms counted for 17 principal taxonomic groups (modified from LONGHURST, 1985).

TABLEAU III. — Moyennes du nombre d'individus de 17 groupes du zooplancton des océans polaires, en pourcentage du nombre total d'organismes dans les comptages (modifié d'après LONGHURST, 1985).

	HYDR	SCYP	SIPH	CTEN	APPE	SALP	DOLI	MOL	CHAE	POLY	CLAD	OSTR	COPE	AMPH	MYSI	EUPH	DECA
Polar Oceans																	
Antarctic	0.12	?	0.29	?	1.88	0.04	0.00	1.22	3.86	0.42	0.00	2.15	88.87	0.24	0.00	1.04	0.00
Total				2.33				5.50						92.30			
Arctic	0.01	?	0.00	?	4.77	0.00	0.00	3.67	3.91	0.04	0.00	2.75	83.78	0.88	0.00	0.00	0.04
Total				4.78				7.62						87.45			
	Gelatinous							Semi-gelatinous			Non-gelatinous						

TABLE IV. — Mean biomass, in terms of relative organic carbon, and as percentages for 17 principal taxonomic groups in the Polar oceans (modified from LONGHURST, 1985).

TABLEAU IV. — Biomasse moyenne du zooplancton des océans polaires, en termes de carbone organique, exprimée en pourcentage pour 17 groupes (modifié d'après LONGHURST, 1985).

	HYDR	SCYP	SIPH	CTEN	APPE	SALP	DOLI	MOL	CHAE	POLY	CLAD	OSTR	COPE	AMPH	MYSI	EUPH	DECA
Polar Oceans																	
Antarctic	0.39	?	1.49	?	0.06	0.06	0.00	3.38	8.08	0.82	0.00	2.79	65.86	1.78	0.00	15.29	0.00
Total				2.00				12.28						85.72			
Arctic	0.07	?	0.00	?	0.30	0.00	0.00	10.08	9.15	0.13	0.00	3.30	69.31	7.37	0.00	0.04	0.25
Total				0.37				19.36						80.27			
	Gelatinous							Semi-gelatinous			Non-gelatinous						

WHAT ELSE BESIDES CRUSTACEANS IS IMPORTANT?

For a long time, the krill, *Euphausia superba* Dana, was believed to be the key organism of the Antarctic trophic chain because it constituted the basic diet for many fish, penguins, seals and whales (KOCK & SHIMADZU, 1994). Krill is not homogeneously distributed in the Southern Ocean, but is generally concentrated near the ice-edge and the shelf break (LUBIMOVA *et al.*, 1982). In areas with low abundance or absence of krill, other filter-feeders predominate, particularly those like copepods and salps that compete with krill for food resources. A recent review (MARCHANT & MURPHY, 1994) presented trophic interactions in the lower levels of the Antarctic pelagic ecosystem where the types of new, regenerative and secondary production were shown based on the size and lifespan of organisms. Copepods and krill as well as salps stand out in this scheme, but also noteworthy is the presence of an "odds and ends box" called "other zooplankton", which includes the gelatinous carnivores among other groups.

Table V shows the approximate number of species for each marine zooplankton taxon in Antarctic waters based on recent guides and checklists. Copepods are the most diverse taxon followed by hyperiid amphipods and hydroidomedusae. Noteworthy is the low diversity for salps and doliolids and the total absence of cladocerans, heteropods and pyrosomes. GZ comprise 26 % of the total number, SGZ species 6 % and NGZ species 68 %. However, these percentages will most certainly change in the future, particularly as new species of medusae and siphonophores are described (Pagès unpublished data) and because of a substantial number of deep-water copepods that remain undescribed (E. Mizdalski pers. comm.).

TABLEAU V.— Estimated number of species of major zooplanktonic taxa in the Southern Ocean..

TABLE V.— Estimation du nombre d'espèces des principaux groupes du zooplancton de l'océan Austral.

<i>Taxa</i>	<i>Species number</i>	<i>Main reference</i>
Hydroidomedusae	> 71	O'Sullivan, 1982; Pagès unpubl. data
Scyphomedusae	18	Larson, 1986a
Siphonophorae	> 30	Pagès, unpubl. data
Ctenophora	9	O'Sullivan, 1986
Appendicularia	26	O'Sullivan, 1983
Pyrosomida	0	O'Sullivan, 1983
Salpida	5	O'Sullivan, 1983
Doliolida	1	O'Sullivan, 1983
Pteropoda	5	Lalli & Gilmer, 1989
Gelatinous	> 165	This study
Chaetognatha	19	O'Sullivan, 1982a
Polychaeta	18	O'Sullivan, 1982b
Heteropoda	0	Lalli & Gilmer, 1989
Semi-gelatinous	37	This study
Cladocera	0	Longhurst, 1985
Ostracoda	12	Kock, 1992
Copepoda	312	Razouls, 1994
Amphipoda	73	Hurley, 1969
Mysidacea	18	Kirkwood, 1983b
Euphausiacea	8	Kirkwood, 1982
Decapoda	11	Kirkwood, 1983a
Non-gelatinous	434	This study
TOTAL	> 636	

SAMPLING METHODS

There is a wide size spectrum for gelatinous zooplankton, ranging from 1 mm in tiny medusae to lengths of several meters in salp chains and physonect siphonophores. Many methods are used for collecting these organisms. Remoted operated vehicles (ROVs) have been used for filming the planktonic communities living below the sea ice as well as benthic communities. There are some surprising features with regard to gelatinous organisms in the benthos, which will be discussed in a later section. To date, manned submersibles for *in situ* obser-

vations have not been reported in the Southern Ocean. Scuba diving techniques require special training and logistics are widely used for activities in ice-covered waters, but its use for observations on the gelatinous zooplankton are few (*e.g.* HARBISON, 1988; LARSON & HARBISON, 1990). Pumping is sometimes used to collect zooplankton living beneath the ice (Pagès pers. obs.), but such a system is inadequate for collecting fragile gelatinous organisms. Consequently, nets are the most frequently used tools for collection of GZ.

SALPS

Salps constitute a predominant and conspicuous component of the zooplankton communities in ice-free waters. Salp diversity is low and the communities or blooms are often comprised of only a single species, *Salpa thompsoni* (FOXTON). Most studies of this species have dealt only with abundance and distribution, and little is known about its biology (FOXTON, 1966; HUNTLEY *et al.*, 1989). However, REINKE (1987) studied the biometrics and locomotion physiology of this species in the laboratory.

The large aggregations of Antarctic salps recorded during recent years (PIATKOWSKI, 1985; NAST, 1986; PARK & WORMUTH, 1993; NISHIKAWA *et al.*, 1995) seem to have had an effect on the distribution and recruitment of krill. This is probably the result of competition for the same food source (FOXTON, 1966), as salps are very efficient filter-feeders, retaining 2-5 μm bacterioplankton with 50-100 % efficiency (MADIN & PURCELL, 1992). For instance, NISHIKAWA *et al.* (1995) estimated that *Salpa thompsoni* could clear 100 % of the upper 100 m within 1.3-4.8 days. HUNTLEY *et al.* (1989) estimated that grazing by this species may have removed a majority of the primary production of the Antarctic Peninsula in March 1984, but less than 1 % in January of the same year. Filtration rates vary because they are highly dependent on water temperature, particle concentration and length of the salps (REINKE, 1987). Thus, clearance rates for *S. thompsoni* are significantly lower than those for salps in warmer waters (HUNTLEY *et al.*, 1989).

The rapid increase in salp abundance in spring/summer is probably dependent on sufficient food resources being available during early spring, thus allowing a quick early reproduction and prolonged period of population growth. A dense and prolonged ice cover, however, may cause a delayed seasonal peak of phytoplankton production (EL-SAYED, 1988) and then conditions for the rapid growth of salps are suboptimal, favouring instead the early spawning and recruitment of krill (SIEGEL & LOEB, 1995).

Salp abundance decreases from open waters to pack ice (SIEGEL *et al.*, 1992) and salps rarely occur at the ice-edge, where krill is abundant and are known to be the major grazers of phytoplankton. However, *Salpa thompsoni* specimens examined from shallow waters (0-50 m) within the pack ice, contained tishid harpacticoids copepods in their guts, which are dominant in ice-pore water (LANCRAFT *et al.*, 1991). In addition, salps are not present in areas with high particle concentration, thereby avoiding the clogging of their feeding apparatus (HARBISON *et al.*, 1986). They are non-selective filter-feeders (MADIN, 1974) and the

examination of salp gut contents has occasionally found krill to be present (HOPKINS *et al.*, 1993). It is suspected that salps, beside being competitors for the phytoplankton food, may exert a substantial trophic impact on the larvae and eggs of krill and other crustaceans. However, such observations are rather limited and further studies are required to quantify this potential impact.

An important aspect of the role that salps play in the biogeochemical cycle is their contribution to the transport of matter, as faecal pellets, towards the sea bed. No data have been published on the morphology, composition and sinking rates of *Salpa thompsoni* faecal pellets. However, those of *S. fusiformis* Cuvier and *S. maxima* Forsskål, a very similar species, sink extraordinarily rapidly, up to 2700 m and 2470 m per day respectively (BRULAND & SILVER, 1981; CARON *et al.*, 1989). These velocities are three times higher than those reported for euphausiid faecal pellets and an order of magnitude greater than the rates for copepod pellets (ALLDREDGE & MADIN, 1982). This indicates that the contribution made by tunicates to the flux of biogenic materials may be highly important during periods when large aggregations are present. *Salpa thompsoni* also undertakes diel vertical migrations to a depth of about 500 m (REINKE, 1987), which also could substantially accelerate the particle flux, as well as the vertical movement of biomass. REINKE (1987) estimated that *S. thompsoni* would be able to swim 500 m in 10 hr. The rate at which micro-organisms colonize the surface membrane that packages the faecal pellets is related to temperature, so biodegradation of faecal pellets may be insignificant in waters < 5° C (HONJO & ROMAN, 1978). Oceanic salps like *Salpa thompsoni* occur in great numbers and produce the largest, fastest sinking, richest in carbon and perhaps slowest-degrading fecal pellets and therefore, they are potentially the main contributors to the deep faecal carbon flux (PFANKUCHE & LOCHTE, 1993; FORTIER *et al.*, 1994).

The second most abundant salp in the Southern Ocean is *Ihleia racovitzai* (van Beneden). FOXTON (1971) reinstated *I. racovitzai* and the subantarctic *I. magalhanica* as valid species based on body shape, muscle arrangement, muscle structure and their geographical distribution. Further evidence of the validity of this species has come from observations showing differences in stolon development, musculature and embryological development (ESNAL & DAPONTE, 1990; DAPONTE & ESNAL, 1994). The distribution of *I. racovitzai* is restricted to waters south of the Polar Front and its southern limit lies at the continental ice edge (FOXTON, 1971). This distribution range overlaps with

that of *Salpa thompsoni* and sometimes they co-occur (NISHIKAWA *et al.*, 1995). CASARETO and NEMOTO (1986) observed that, in the Australian sector during summer 1983-84, *I. racovitzai* was restricted to high latitude waters whereas *S. thompsoni* was most abundant in middle latitudes. The vertical distribution of *I. racovitzai* ranged from 30 to 600 m by day, and 0 to 600 m at night. Higher abundances were found at night (up to 1500 ind. \cdot 1000 m⁻³ in surface waters), with the aggregate form predominating in the upper 50 m, and a steadily increasing number of the solitary form towards deeper depths.

In the region of the Antarctic Peninsula, ESNAI & DAPONTE (1990) found that *Ihleia racovitzai* was more abundant than *Salpa thompsoni* in February 1986, although no density values were given. This trend also occurred in May 1986 (Pagès unpublished data), when large numbers of *I. racovitzai* were concentrated in the upper 300 m (up to 18.6 ind. \cdot m⁻³), while only a few *S. thompsoni* occurred between 500 and 1000 m depth (up to 0.09 ind. \cdot m⁻³). In

the Bransfield Strait, in the summer of 1989-90, *I. racovitzai* occurred in the greatest number of Bongo samples (65 %) and had the second highest abundance (350 ind. \cdot 10 m⁻² in the upper 300 m) of all species captured (KIM *et al.*, 1991). *S. thompsoni* ranked only ninth. In the same area, in December 1990 - early January 1991, *S. thompsoni* had a mean density (0.17 ind. \cdot m⁻³) slightly greater than that for *I. racovitzai* (0.14 ind. \cdot m⁻³) although the carbon biomass was higher for the latter species. Density values for both species strongly decreased in late January (NISHIKAWA *et al.*, 1995).

Lastly, there can be no question that salps are at least as common and important as krill in the Antarctic at some times and in some places. Future "salp years" cannot be qualified as adverse events for research in Antarctic waters but they should be considered as excellent opportunities to investigate more about the significance of this group in the Antarctic ecosystem.

MACROPLANKTONIC CNIDARIANS AND CTENOPHORES

High abundances of large cnidarians and ctenophores have been recorded in recent years. For instance, in the environs of the Antarctic Polar Frontal Zone (APFZ), in the South Georgia sector in summer 1994, gelatinous carnivores were the most abundant nektonic organisms together with myctophid fish (PAGÈS *et al.*, 1996). Twenty seven species of gelatinous organisms were collected: 13 hydroidomedusae (3 anthomedusae, 3 leptomedusae, 5 trachymedusae and 2 narcomedusae), 6 siphonophores, 3 scyphomedusae, 3 ctenophores, 1 salp and 1 nemertean. Scyphomedusae were the most conspicuous component because of their size and biovolume, contributing more than 50 % of the biovolume to 1/3 of the RMT25 hauls. In total, gelatinous carnivores constituted 69.3 % of total biovolume. Salps were very sparse and krill abundance was very low (BRIERLEY & WATKINS, 1996), such that there were profound repercussions on the rest of the trophic web because starvation were observed among numerous birds and sea lion juveniles in South Georgia (F. Pagès, pers. obs.).

At the Weddell Sea ice edge in autumn (March) 1986, salps, medusae and ctenophores were responsible for over three quarters (17876 mg WW \cdot m⁻²) of the wet weight estimates and one third (475 mg DW \cdot m⁻²) of dry weight of the micronekton/macrozooplankton in the upper 200 m

(LANCRAFT *et al.*, 1989). Despite these values, no conclusions about their significance were reached.

In the Weddell-Scotia Confluence in winter (June-August) 1988, when salps were sparse (2 % DW), cnidarians (mainly *Atolla wyvillei* Haeckel) and ctenophores (*Beroë* sp.) had a greater wet weight biomass than fish and euphausiids together in both the 200-0 and 1000-0 m depth ranges (LANCRAFT *et al.*, 1991). Coelenterate dry weight contributed one quarter (389 mg DW \cdot m⁻²) of the total in the 0-200 m depth range, and also in the 0-1000 m depth range (755 mg DW \cdot m⁻²). LARSON (1986a) estimated that the standing stock of scyphomedusae in the Southern Ocean range from about 0.5 to 1.5 g DW \cdot m⁻² for the upper 2500 m. These dry weight values are relatively high and are comparable to total zooplankton biomass in some oceans (HOPKINS, 1971), indicating that scyphomedusae are sometimes a significant part of the total zooplankton biomass.

The high wet biovolumes and relatively high dry weights reached by cnidarians and more particularly scyphomedusae greatly contrast with the conclusions drawn by LONGHURST (1985). The values mentioned above clearly reflect that large gelatinous carnivores are a predominant, and at times the main, component of the oceanic macroplankton/nekton community in the Southern Ocean.

CO-OCCURRENCE OF SALPS, CNIDARIANS AND CTENOPHORES

Occasionally high abundance and biomass of both salps and cnidarians have been observed during research cruises. For instance, in the oceanic waters of the APFZ in summer 1991, *Salpa thompsoni* dominated the wet weight of samples, particularly in the upper 200 m (28632 mg WW · m⁻²) while gelatinous carnivores (*Calycopsis borchgrevinki* (Browne), *Halicreas minimum*, *Atolla wyvillei* and *Periphylla periphylla*) were abundant in the 200-1000 m depth range (27871 mg WW · m⁻²) (PIATKOWSKI *et al.*, 1994). On the continental slope of South Georgia, however, *S. thompsoni* was virtually absent and the majority of the wet weight was contributed by cnidarians (mainly *Periphylla periphylla*), particularly below 200 m (14401 mg WW · m⁻²) while euphausiids (mainly *Euphausia triacantha*) dominated (1197 mg WW · m⁻²) in the upper 200 m. In addition, RODHOUSE *et al.*, (1994) converted wet biomass to dry biomass using data from the literature. Although values were not given, they concluded that oceanic biomass was dominated in order of importance by cnidarians, salps and fishes whereas fishes, cnidarians and crustaceans dominated in South Georgia.

Also in the APFZ but to the east (0°-10° E), PAKHOMOV *et al.* (1994a) observed in January-February 1993 that the macroplankton/micronekton in the top 300 m was characterized by a high abundance of *S. thompsoni* (mean abundance 7.2 ind. · m⁻², 83.5 % of total abundance; mean biomass 94.6 mg DW · m⁻², 51.3 % of total), whereas medusae, siphonophores and ctenophores only totaled 0.7 %. Abundance and biomass of salps decreased sharply south and north of the front, coincident with an increase in the occurrence of euphausiids and other zooplankton, respectively.

In the Lazarev Sea (January-February 1990), *Salpa thompsoni* dominated the macroplankton community with an average of 62 % of the total biomass, although its mean abundance (110.4 ind. · 1000 m⁻³) was only just over 3 % of the total (PAKHOMOV *et al.*, 1994b). The remainder of the mean biomass was due to the siphonophore *Diphyes antarctica* (8.5 %), other siphonophores (5.3 %) and the hydroidomedusa *Calycopsis borchgrevinki* (3.1 %). However, numerical abundances were dominated by the chaetognath *Eukrohnia hamata* (47 %), the euphausiid *Thysanoessa macrura* (19 %), the appendicularian

Oikopleura sp. (9 %) and the polychaete *Pelagobia longicirrata* (7 %).

In the oceanic waters of the Weddell Sea in February-March 1983, *Salpa thompsoni* was the dominant single species with 1.6 mg DW · m⁻³ (0.5 g DW · m⁻²) in the top 300 m of oceanic waters (BOYSEN-ENNEEN *et al.*, 1991). Siphonophores (mainly *Dimophyes arctica* (Chun) and *Diphyes antarctica*) reached 0.8 mg DW · m⁻³. Unfortunately, ctenophores and scyphomedusae were excluded from these calculations although they were known to be present and abundant. In the northeastern shelf, *S. thompsoni* and cnidarians accounted for 0.5 mg DW · m⁻³ and 0.06 mg DW · m⁻³, respectively, whereas in the southern shelf region they reached values of 0.87 mg DW · m⁻³ and 0.25 mg DW · m⁻³ respectively. Copepod biomass predominated in open waters (4.5 mg DW · m⁻³) and on the northeastern shelf (6.3 mg DW · m⁻³), while euphausiids, mainly *Euphausia crystallorophias*, contributed the greatest biomass in the south eastern shelf region (0.9 mg DW · m⁻³).

Despite these studies, data on the spatio-temporal distribution of Antarctic gelatinous zooplankton are very sparse, particularly away from the Atlantic sector. These observations do not denote a new phenomenon since high abundances and diversity were reported from the eastern part of the Weddell Gyre in summer 1979, a region with scarce krill, where 43 species of medusae and siphonophores were collected (PAGES *et al.*, 1994). Antarctic siphonophores of small to medium size were abundant there in the upper 500 m, larger siphonophore species were more frequently found in the 1000-2000 m depth range whereas medusae were concentrated between 500 and 1000 m depth. The displacement volume of cnidarians in the samples averaged 52.6 % of the total although the range was wide (5.0-93.1 %).

This set of results is more reflective of the occasional knowledge that is available on the distribution and abundance of GZ rather than the sporadic presence of these organisms in Antarctic waters. These recent results indicate that apart from salp aggregations, the occurrence of high numbers of scyphomedusae is frequent in oceanic waters, although little else besides species composition and wet biomass is known.

VERTICAL DISTRIBUTION OF CNIDARIANS

Studies on the vertical distribution of gelatinous groups have been mainly centred on cnidarians. For instance, PUGH *et al.* (1997) investigated the vertical distribution of macroplanktonic cnidarians in the top 2800 m of the water column at a single station located in the Cold Regime of the eastern Weddell Sea. Hauls were made over approximately 100 m depth ranges in the top 1000 m and below this depth were carried out over approximately 200 m depth ranges. Siphonophores (up to 140 ind. $10^4 \cdot \text{m}^{-3}$ in the 400-500 m depth range) were more abundant than medusae (up to 54 ind. $10^4 \cdot \text{m}^{-3}$ in the 400-500 m depth range), particularly in the upper 800 m, and some individual species occurred at relatively discrete depth layers. The three commonest siphonophore species, *Diphyes antarctica*, *Dimophyes arctica* and *Muggiaea bargmannae* Totton, each reached a peak abundance in a different depth range within the epipelagic (0-500 m) depth range, while a fourth, *Crystalliphyes amygdalina* Moser, was found almost exclusively in the 400-600 m. Even deeper species were found to occur within restricted depth ranges. Thus, with one exception in each of the following species, the medusae *Atolla wyvillei* and *Halicreas minimum*, and the siphonophore *Chuniphyes moserae* Totton

were found in the 700-2200, 500-1800 and 1200-1800 m depth ranges, respectively. The largest concentrations of cnidarians were found in the 250-500 m depth range, with maxima between 400 and 500 m depth. Below this level, siphonophore numbers remained quite stable whereas those of medusae decreased gradually in number until becoming relatively unchanging below 800 m. Although a high abundance of siphonophores was expected in the upper 500 m, the occurrence of abundance peaks of medusae contrasted with conclusions drawn by PAGÈS *et al.* (1994) who observed that medusae were usually most abundant in the 500-1000 m depth range. This was because of the unexpected abundance of *Solmundella bitentaculata* (QUOY & GAIMARD) between 250 and 400 m. The highest zooplankton abundance was observed in the top 700 m, with a peak in 400-500 m, where a high number of euphausiids were concentrated. Chaetognaths were numerically the predominant taxon in the samples, reaching 50 % of the total number of specimens collected. Cnidarians averaged 15 % of the total number of specimens although below 2000 m, where overall abundance was low, they contributed up to 40 % of the specimens and >70 % to the biovolume. On average medusae contributed 45 % to the cnidarian totals.

GELATINOUS MESOZOOPLANKTON

Gelatinous mesozooplankton (1-20 mm in size) is abundant in the Southern Ocean although it is less well known than, for instance, the large scyphomedusae. In the Weddell Sea, the spatial distribution of mesoplanktonic cnidarians is related to temperature such that they concentrate in and below the thermocline, decreasing in number in the superficial cold waters (PAGÈS & KURBJEWIT, 1994; PAGÈS & SCHNACK-SCHIEL, 1996). When the oceanic thermocline deepens as the shelf is approached, creating the Antarctic Slope Front, it separates the oceanic community from a neritic one. The latter is comprised of a few Antarctic species, like the siphonophore *Pyrostephos vanhoffeni* Moser, well adapted to cold temperatures. Highest

abundances in particular depth ranges are reached by the trachymedusan *Pantachogon scotti* Browne (12500 ind. $\cdot 1000 \text{ m}^{-3}$ in the 130-90 m depth range), the narcomedusan *Solmundella bitentaculata* (2080 ind. $\cdot 1000 \text{ m}^{-3}$ in the 330-280 m depth range) and the siphonophore *Muggiaea bargmannae* (1360 eudoxids $\cdot 1000 \text{ m}^{-3}$ in the 280-180 m depth range) (PAGÈS & SCHNACK-SCHIEL, 1996). Highest mean abundances at standard depth ranges are 3133 ind. $\cdot 1000 \text{ m}^{-3}$ for *P. scotti*, and 515 nectophores $\cdot 1000 \text{ m}^{-3}$ for *M. bargmannae* both in the 200-100 m depth range (PAGÈS & KURBJEWIT, 1994). The biomass and carbon contribution of this size-range is unknown.

GELATINOUS ZOOPLANKTON BENEATH THE ICE

The gelatinous plankton populations living under the sea ice have been rarely reported. Most data have been obtained from examining samples collected through a hole in the ice or from open sea-ice edge transects. The latter have shown a progressive decrease of abundance towards the ice covered waters (SIEGEL *et al.*, 1992). Near Syowa Station (68°59'57"S-39°40'25"E) gelatinous mesozooplankton comprised less than 10 % of the community abundance from May to October 1982 in the upper 660 m of the fast ice area. Siphonophores and appendicularians were the most abundant taxa and both peaked in August with 600 and 400 ind. · 1000 m⁻³ respectively (FUKUCHI *et al.*, 1985). Zooplankton was also sampled monthly during the same year off Davis Station (68°35'S-77°58'E) (TUCKER & BURTON, 1990), where copepods were numerically dominant. Non-quantified hydromedusae, siphonophores and ctenophores were collected by net in April and November; the scyphomedusae *Desmonema gaudichaudi* was collected by divers in November and the larvacean *Oikopleura* sp. was sampled by pump and net in February-May and November-December (TUCKER & BURTON, 1990). Several unidentified coelenterates and appendicularians were collected in the same area in 1984-86 (KIRKWOOD & BURTON, 1987).

In McMurdo Sound, *Clione antarctica* (*limacina*) (Smith), siphonophores, *Oikopleura* sp., hydromedusae and ctenophores (ranked in order of frequency) were collected in the top 300 m (FOSTER, 1987) in spring 1985. A comparison with results from the upper 100 m, showed that

ctenophores (*Beroe* sp.) were more frequent and abundant within this depth range. *Clione antarctica* and its main prey *Limacina helicina* appeared to be evenly distributed throughout the top 300 m of the water column. The density of gelatinous organisms decreased in spring 1987 when compared with 1985 (FOSTER, 1989). The low density of gelatinous zooplankton beneath the ice at that time was observed *in situ* (HARBISON, 1988) when abundance was higher in open waters, although diversity was similar in comparison with ice edge and under ice waters. Seven species of medusae, two of them new to science (*Leuckartiara brownei* and *Benthocodon hyalinus*), were collected in 19 dives (HARBISON, 1988; LARSON & HARBISON, 1990). Three species of siphonophores, four species of ctenophores and *Salpa thompsoni* were also collected.

The physonect siphonophore *Pyrostephos vanhoeffeni* is a common species in the Ross Sea ice edge. It was ubiquitous throughout the southwest Ross Sea and along the Ross Ice Shelf in austral summer 1977-78 whereas hydromedusae, ctenophores, appendicularians and salps were only occasionally collected in open waters (BIGGS, 1982). *P. vanhoeffeni* also occurred in 97 % of the samples (34) collected through a hole, near the edge of the permanent McMurdo Ice Shelf in spring 1985 (FOSTER, 1987). PAGES & SCHNACK-SCHIEL (1996) reported it as the predominant cnidarian beneath the ice in the eastern Weddell Sea in autumn 1992. This species appears to be one of the most abundant gelatinous creatures beneath the ice.

WATER CONTENT, WET WEIGHT, DRY WEIGHT AND IMPLICATIONS ON METABOLISM RATES

CLARKE *et al.* (1992) estimated the wet mass, dry mass and ash content of several species of Antarctic gelatinous zooplankton. Excepting the polychaete *Tomopteris* that is a semi-gelatinous organism, the average dry weight of seven species (2 ctenophores, 3 medusae, 1 siphonophore and 1 salp) was 4.48 % WW, ranging from 4.01 to 4.92. This average is very similar to that given by LARSON (1986b) for hydromedusae from the northern Pacific (4.0 % WW). CLARKE *et al.* (1992) also estimated the percentage of carbon in relation to dry weight. Carbon values ranged from 4.11 to 15.57 % WW, averaging 9.51. This is quite similar to the 8.29 % DW given by LARSON (1986b) and 9.4 %

DW for 5 species given by DONNELLY *et al.* (1994) from the Scotia/Weddell Sea region.

A comparison of the carbon content between GZ and NGZ shows that crustaceans have 4-5 times higher carbon values per individual, around 40-50 % DW (IKEDA & BRUCE, 1986; DONNELLY *et al.*, 1994). On the contrary, wet weight of gelatinous organisms is higher when compared with non-gelatinous ones (IKEDA & BRUCE, 1986). However, the oxygen consumption and ammonia excretion is similar or less per individual and doubtless much less with regard to the DW, which can lead to the conclusion that GZ is metabolically less active.

CLARKE & PECK (1991) showed the low respiration rate on a dry weight basis of high latitude GZ when compared with that of herbivorous and/or omnivorous/carnivorous high latitude NGZ. They demonstrated that dry weight of polar gelatinous organisms has been overestimated by about 10 % because of residual water and therefore their respiration rates are underestimated. SCHNEIDER (1990) converted 560 data from the literature, from dry weight-specific ammonia excretion rates to carbon-specific values of both GZ and NGZ. He applied the same type of conversion to 470 data on dry-weight specific respiration rates (SCHNEIDER, 1992). The resulting carbon-specific excretion and respiration rates showed no significant differences between the two groups of zooplankton, indicating similar

nitrogen output and oxygen requirements per gram of carbon biomass. SCHNEIDER suggested that the differences in the rates of nutrient regeneration and oxygen consumption measured in the two types of zooplankton can be explained by their carbon-biomass ratio. Likewise the low rate of metabolism of gelatinous species compared with that of non-gelatinous forms of the same volume can be attributed to the relative low organic matter and high water content in the former. These factors are by no means detrimental to the GZ and LARSON (1986b) has suggested that transparency, neutral buoyancy and low carbon content may give an important selective advantage for life in the pelagic realm.

CARBON BIOMASS

Few studies report gelatinous zooplankton biomass in carbon units. NISHIKAWA *et al.* (1995) compiled the salp biomass and density near the Antarctic Peninsula during the last decade, where mean biomass ranged between 9.9 and 387.2 mg C · m⁻² (NISHIKAWA *et al.*, 1995; HUNTLEY *et al.*, 1989). The amount of carbon contributed by gelatinous carnivores to the total zooplankton/nekton carbon biomass is less known. PUGH *et al.* (1997) estimated that siphonophores and medusae averaged 25.3 % of the total carbon in the top 2800 m of the water column in the eastern Weddell Sea in summer 1979. Nevertheless, in two depth ranges (250-400 m and 1000-1200 m), where the bio-volume was dominated by large medusan specimens, values reached 0.34 mg C · m⁻³ and 0.28 mg C · m⁻³ respectively, and these organisms contributed over 50 % to the

total macroplankton/micronekton carbon. Likewise, gelatinous organisms, mainly medusae, averaged 30.3 % of the total carbon in the top 1000 m of the Antarctic Polar Frontal Zone in summer 1994 (PAGÈS *et al.*, 1996). Also in that study, they contributed substantially in three depth ranges (50-100 m, 375-400 m and 800-1000 m) where values reached 0.17, 0.21 and 0.21 mg C · m⁻³ respectively and contributed over 50 % to the total nekton carbon. It should be noted that even higher values would have been obtained from night pelagic trawls made in surface waters during the same sampling program, that collected many *Periphylla periphylla* Péron & Lesueur, but unfortunately accurate densities could not be provided from these pelagic trawls.

LIPID CONTENT

In polar waters, the herbivorous and carnivorous NGZ, particularly copepods and amphipods, synthesize lipids as energy stores for the winter, when food is scarce (HAGEN, 1988). In contrast, gelatinous carnivores have been reported to store only small quantities of lipids (<3 % WW) derived from their prey, and this is mainly used as energy reserve and possibly as an aid to buoyancy (LARSON & HARBISON,

1989). This minimum reserve reflects the independence of these organisms from the seasonal and unexpected food fluxes since carnivorous behaviour allows the capture of prey at any time and laboratory experiments have indicated a well-developed ability to reduce in size during periods of food shortage (HAMNER & JENSSEN, 1974).

FEEDING ECOLOGY

Investigations on the trophic ecology of gelatinous carnivores in the Antarctic food web have to date been few. The most studied species is the gymnosomatous pteropod *Clione antarctica*, a feeding specialist which preys exclusively on the shelled thecosomatous pteropod *Limacina helicina* (GILMER & LALLI, 1990). Both species are abundant in Antarctic waters and localized populations of *C. antarctica* in McMurdo Sound may reach as many as 300 ind. · m⁻³ in the top 20 meters (BRYAND *et al.*, 1995). This pteropod is rarely eaten by other predators because it contains a noxious compound, pteroenone (BRYAND *et al.*, 1995).

The few attempts to understand the feeding of cnidarians have been largely unsuccessful in assessing their trophic impact because of the poor state of the specimens collected by midwater hauls (HOPKINS & TORRES, 1989; LANCRAFT *et al.*, 1991). Data on diet are available for a few species of cnidarians. An analysis of contents of the gastrozooids of *Pyrostephos vanhoeffeni* showed the presence of a wide variety of prey, from diatoms to pteropods (PAGÈS & SCHNACK-SCHIEL, 1996). However, krill larvae, and the copepods *Calanus propinquus* and *Metridia gerlachei* were prominent because of their large size. The relatively high percentage of krill larvae found among the prey items (up to 90 %), suggested a substantial trophic impact when both organisms co-occur. Examination of the gut contents of 8 specimens of the scyphomedusa *Diplulmaris antarctica* Maas showed that they had ingested 13 specimens of the gymnosomatous pteropod *Clione antarctica* (LARSON & HARBISON, 1990). Two more medusae had eaten 12 specimens of the thecosome pteropod *Limacina helicina* while another specimen contained two *C. antarctica* specimens in its gut and four more were in its oral arms. The narcomedusa *Solmundella bitentaculata* also feeds upon *L. helicina* (LARSON & HARBISON, 1990).

Numerous observations have shown that salps and coelenterates are often consumed by birds (AINLEY *et al.*, 1991; FOXTON, 1966) and notothenioid fish (e.g. TARVERDIYEVA, 1972; PAKHOMOV 1993). KASHKINA (1986) recorded at least 6 species of Antarctic fish that fed to variable extent on salps. Because of the high water content of their tissues, much of the nutritional value of salps could reside in the phytoplankton and microzooplankton packed in their gut (FOXTON, 1966). Therefore much of the carbon exported to fish and birds is not digested in salp guts, shortening one trophic step (FORTIER *et al.*, 1994). In the same way, amphipods co-occur with their salp hosts in the gut of fish and birds and these symbionts could represent the

actual source of carbon targeted by the top predators when they feed on salps.

Table VI lists vertebrate and invertebrate animals from the Southern Ocean which feed on marine gelatinous zooplankton as indicated by examination of their stomach contents. Birds and fish, particularly nototheniids, stand out among predators while amphipods are the only invertebrates known to frequently consume gelatinous prey items. Nothing is known about the feeding habits of some medusae and ctenophores that are important consumers of gelatinous zooplankton in other ecosystems (PURCELL, 1991).

RODHOUSE & WHITE (1995) reported the trophic system of the Antarctic Polar Frontal Zone in the proximities of South Georgia in years of large squid and krill abundances. However, this trophic system substantially changes in years with high occurrence of medusae and ctenophores such as summer 1994, when gelatinous nekton was abundant in the area and albatrosses and nototheniid fish foraged on them (PAGÈS *et al.*, 1996). Figure 1 shows the trophic relationships in summer 1994 when a great number of specimens of *Notothenia rossi* collected on the South Georgia shelf had the stomachs plenty of ctenophores, the predominant zooplankters in the area, and albatrosses were observed foraging on large scyphomedusae, probably *Desmonema* or *Diplulmaris*. Moreover, gelatinous zooplankton was the predominant component of the nekton community in the APFZ, and the high abundance and biomass indicated that it was one of the main predators in the area (PAGÈS *et al.*, 1996).

The poor understanding of the diet of gelatinous carnivores is surprising taking into account the relative high number of species in the Antarctic (> 133 species, Table V). This point clearly reflects how little is known about the role of these organisms in the Antarctic pelagic ecosystem. The trophic impact exerted on zooplankton communities by medusae, siphonophores and ctenophores could be one of the most important parameters for evaluating their ecological importance. To maintain polar gelatinous zooplankton under laboratory conditions is very difficult, but estimation of the digestion time of some key species (e.g. *Calycopsis borchgrevinki*, *Dimophyes arctica*) together with information on the feeding habits of these important species by their abundance would allow a calculation of their potential predatory impact on the zooplankton communities and would doubtless confirm the importance of their role in the Antarctic pelagic ecosystem.

TABLE VI.— Predation on gelatinous zooplankton in the Southern Ocean based on stomach contents data; pr., prey number; pr.wt., prey weight; obs., stomachs in which gelatinous prey was observed; the number of specimens examined is between brackets.

TABLEAU VI.— Prédation exercée sur le zooplancton gélatineux dans l'océan Austral, basée sur des données de contenus stomacaux. pr., nombre de proies; pr.wt., poids des proies; obs., estomacs dans lesquels des proies gélatineuses ont été observées; le nombre de spécimens examinés est entre parenthèses.

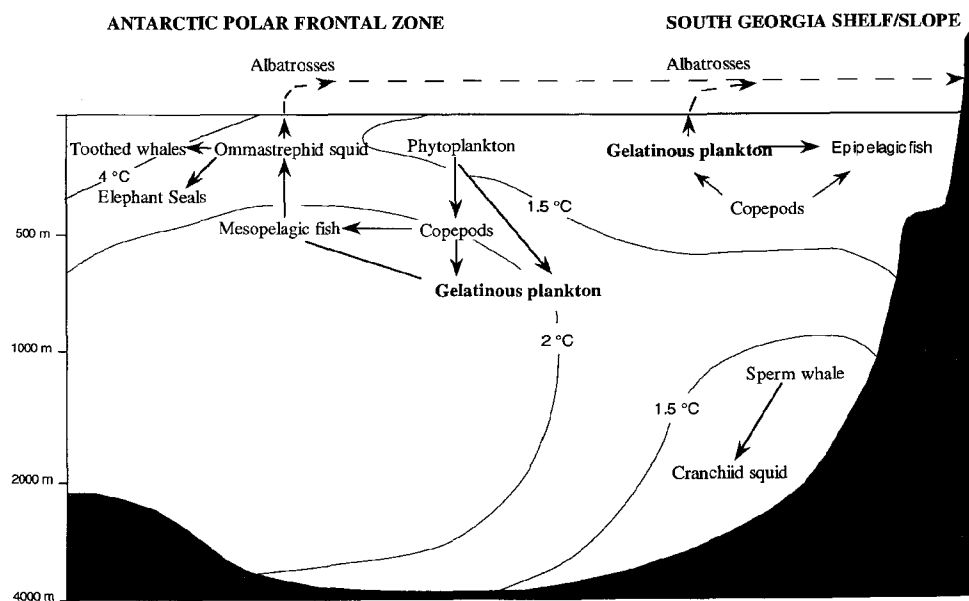
Predator	Prey	Consumption Rate	Time	Location	Reference
Birds					
Antarctic fulmar <i>Fulmarus antarcticus</i>	<i>S. thompsoni</i>	5.0 % pr.wt. (27)	Spring 1983	Scotia-Weddell Confl.	Ainley <i>et al.</i> , 1991
Blue petrel <i>Halobaena coerulea</i>	"	2.7 % pr.wt. (19)	"	"	Ainley <i>et al.</i> , 1991
Cape petrel <i>Daption capense</i>	"	14.9 % pr.wt. (39)	"	"	Ainley <i>et al.</i> , 1991
	"	1.0 % pr.wt. (16)	Autumn 1986	"	"
Antarctic prion <i>Pachiptila vittata</i>	"	3.2 % pr.wt. (40)	Spring 1983	"	Ainley <i>et al.</i> , 1991
Wilson's storm petrel <i>Oceanites oceanicus</i>	"	1.8 % pr.wt. (36)	Spring 1983	"	Ainley <i>et al.</i> , 1991
Grey-headed albatross <i>Diomedea chrysostoma</i>	Salps	71.6 % obs. (60)	Summer 1959	Bird Is., S. Georgia	Foxton, 1966
	"	17.6 % obs. (51)	Summer 1961	"	"
Black-browed albatross <i>Diomedea melanophrys</i>	Salps	18.5 % obs. (54)	Summer 1959	Bird Is., S. Georgia	Foxton, 1966
	"	14.5 % obs. (55)	Summer 1961	"	"
Fish					
Fam. Nototheniidae					
<i>Gobionotothen gibberifrons</i>	Ctenophora	7.9 % pr. (1160)	Sum. 65-69	South Georgia	Permitin & Tarverdiyeva, 1972
	Jellyfishes	0.1 % pr. (1160)		"	"
	Salps	0.2 % pr. (1160)		"	"
	Salps	4.3 % pr. (45)		"	"
<i>Notothenia rossii rossii</i>	Cnidaria	13.7 % pr. (254)	Sum. 79-80	Kerguelen Is.	Duhamel, 1981
		42.4 % pr. (71)	August 1981	"	Duhamel & Hureau, 1985
		4.5 % pr. (1137)	June 1983	"	"
	Ctenophora	6.6 % pr. (254)	Sum. 79-80	Kerguelen Is.	Duhamel, 1981
		13.4 % pr. (1137)	"	"	Duhamel & Hureau, 1985
	Salps	4.4 % pr. (254)	Sum. 79-80	Kerguelen Is.	Duhamel, 1981
		18.4 % pr. (1137)	"	"	Duhamel & Hureau, 1985
<i>N. rossii marmorata</i>	Ctenophora	61.6 % obs. (469)	"	Scotia Sea	Tarverdiyeva, 1972
		8 % pr.wt. (?)	Spring	South Georgia	Chekunova & Naumov, 1982
		11 % pr.wt. (?)	Summer	"	"
		35 % pr.wt. (?)	Autumn	"	"
		30 % pr.wt. (?)	Winter	"	"
<i>Lepidonotothen larseni</i>	Ctenophora	34.8 % pr. (49)	Feb. 1982	Crozet Is.	Duhamel & Pletikoscic, 1983

TABLE VI.— *Continued*TABLEAU VI.— *suite*

<i>Predator</i>	<i>Prey</i>	<i>Consumption Rate</i>	<i>Time</i>	<i>Location</i>	<i>Reference</i>
<i>L. kempi</i>	Ctenophora	7.1 % obs. (45)	Sum. 65-69	South Georgia	Permitin & Tarverdiyeva, 1972
	Jellyfishes	1.4 % obs. (45)		"	"
<i>L. nudifrons</i>	Salps	1.4 % pr. (102)		South Georgia	Permitin & Tarverdiyeva, 1972
<i>L. squamifrons</i>	Ctenophora	13.8 % pr. (2880)			Duhamel, 1981
		6.5 % pr. (441)	Feb. 1982	Crozet Is.	Duhamel & Pletikosic, 1983
		12.9 % pr. (417)			Duhamel & Hureau, 1985
	Salps	35.8 % pr. (2880)	Sum. 79-80	Kerguelen Is.	Duhamel, 1981
		2.7 % pr. (441)	Feb. 1982	Crozet Is.	Duhamel & Pletikosic, 1983
		34.4 % pr. (75)	May 1983	Crozet Is.	Duhamel & Hureau, 1985
		39.5 % pr. (417)	June 1983	Kerguelen Is.	"
	Cnidaria	23.5 pr. (2880)	Sum. 79-80	Kerguelen Is.	Duhamel, 1981
		0.5 % pr. (441)	Feb. 1982	Crozet Is.	Duhamel & Pletikosic, 1983
		3.0 % pr. (75)	May 1983	Crozet Is.	Duhamel & Hureau, 1985
		9.4 % pr. (417)	June 1983	Kerguelen Is.	"
<i>L. squamifrons s</i>	Salps	30.6 % pr.wt. (14319)	Spring	Indian sector	Pakhomov, 1993
		25.7 % pr.wt. (15062)	Summer	"	"
	Ctenophora	17.7 % pr.wt. (14319)	Spring	"	Pakhomov, 1993
		28.8 % pr.wt. (15062)	Summer	"	"
		3.2 % pr.wt. (14319)	Fall	"	"
	Medusae	27.6 % pr.wt. (15062)	Winter	"	Pakhomov, 1993
Fam. Rajidae					
<i>Raja georgiana</i>	Ctenophora	1.0 % pr. (38)	Sum. 65-69	South Georgia	Permitin & Tarverdiyeva, 1972
Fam. Channichthyidae					
<i>Champscephalus gunnari</i>	Ctenophora	0.2 % pr. (1149)	Sum. 65-69	South Georgia	Permitin & Tarverdiyeva, 1972
Fam. Bathylagidae					
<i>Bathylagus antarcticus</i>	Appendicularia	4 st. (35)	Fall 1986	west. Weddell Sea	Hopkins & Torres, 1989
	Coelenterata	20 st. (35)	"	west. Weddell Sea	Hopkins & Torres, 1989
	<i>S. thompsoni</i>	1 st. (35)	"	west. Weddell Sea	Hopkins & Torres, 1989
	Salps	14 % st. (28)	"	Weddell-Scotia Confl.	Lancraft <i>et al.</i> , 1991
	Siphonophora	50 % st. (28)	Winter 1988	Weddell-Scotia Confl.	Lancraft <i>et al.</i> , 1991
<i>B. gracilis</i>	Appendicularia	38.7 % pr. (48)	Feb.-March	Lazarev Sea	Gorelova & Kobylansky, 1985
	Jellyfish	2 % pr. (48)	"	"	"
Fam. Myctophidae					
<i>Electrona antarctica</i>	Appendicularia	13 % st (60)	Fall 1986	west. Weddell Sea	Hopkins & Torres, 1989
	<i>Oikopleura</i>	6.4 % st. (109)	Winter 1988	Weddell-Scotia Confl.	Lancraft <i>et al.</i> , 1991
	<i>S. thompsoni</i>	1 st. (60)	Fall 1986	west. Weddell Sea	Hopkins & Torres, 1989
		0.5 % prey (52)	Spring 94-95	Lazarev Sea	Pakhomov <i>et al.</i> , 1996
	Siphonophora	3 % st. (109)	Winter 1988	Weddell-Scotia Confl.	Lancraft <i>et al.</i> , 1991
<i>Gymnoscopelus braueri</i>	Appendicularia	3 st. (9)	Fall 1986	west. Weddell Sea	Hopkins & Torres, 1989
	<i>Oikopleura</i>	11.3 % st. (53)	Winter 1988	Weddell-Scotia Confl.	Lancraft <i>et al.</i> , 1991
<i>G. opisthopterus</i>	Appendicularia	3 st. (12)	Fall 1986	west. Weddell Sea	Hopkins & Torres, 1989
	<i>S. thompsoni</i>	11.1 % (32)	March 1985	Prydz Bay	Pakhomov <i>et al.</i> , 1996
<i>Notolepis coatsi</i>	Appendicularia	2 st. (27)	Fall 1986	west. Weddell Sea	Hopkins & Torres, 1989

TABLE VI.— *Continued*TABLEAU VI.— *suite*

<i>Predator</i>	<i>Prey</i>	<i>Consumption Rate</i>	<i>Time</i>	<i>Location</i>	<i>Reference</i>
Amphipoda					
<i>Cylopus lucasi</i>	Coelenterate	10 st. (36)	Fall 1986	west. Weddell Sea	Hopkins & Torres, 1989
	Siphonophora	46 % st. (26)	Winter 1988	Weddell-Scotia Confl.	Lancraft <i>et al.</i> , 1991
	<i>S. thompsoni</i>	7 st. (36)	Fall 1986	west. Weddell Sea	Hopkins & Torres, 1989
<i>Hyperiella dilatata</i>	Coelenterata	29 st. (30)	Fall 1986	west. Weddell Sea	Hopkins & Torres, 1989
		66 % pr. (30)	Fall 1983	Gerlache Strait	Hopkins, 1985
<i>H. macronyx</i>	Coelenterata	16% pr. (5)	Fall 1983	Gerlache Strait	Hopkins, 1985
<i>Themisto gaudichaudi</i>	Coelenterata	6 % pr. (51)	Fall 1983	Gerlache Strait	Hopkins, 1985
<i>Parandania boeckii</i>	Coelenterata	575 pr. (16)	Fall 1983	Gerlache Strait	Hopkins, 1985
Chaetognatha					
<i>Eukrohnia hamata</i>	Appendicularia	35 % pr. (8860)	Summer 1987	Gerlache Strait	Øresland 1990

FIG. 1. — Antarctic trophic web in February-March 1994 from observations collected during JR 06 cruise (PAGÈS *et al.*, 1996) (modified from RODHOUSE & WHITE, 1995).FIG. 1. — Réseau trophique de l'Antarctique en février-mars 1994, d'après les observations recueillies au cours de la campagne JR 06 (PAGÈS *et al.*, 1996) (modifié d'après RODHOUSE & WHITE, 1995).

BIOLOGICAL ASSOCIATIONS WITH GELATINOUS PLANKTON

LARSON (1986a) speculated about the possible biotic associations with Antarctic scyphozoans, taking into account associations recorded in the North Atlantic. Few more observations have been made recently. Several species of the scyphomedusan genus *Desmonema* occur in South Georgia (WARD, 1989) and sometimes are foraged on by albatrosses (PAGÈS *et al.*, 1996). These scyphomedusae also occur in New Zealand waters where *in situ* observations have shown how swarms of juvenile fish aggregate around them looking for food and shelter (KINGSFORD, 1993). It is probable that such associations also occur in Antarctic waters.

In situ observations made from manned submersibles in temperate waters (AUSTER *et al.*, 1992) have shown that myctophid fish aggregate close to several pelagic organisms, including medusae and ctenophores. These fish are abundant in mesopelagic depths of the Southern Ocean (LANCRAFT *et al.*, 1989) where they co-occur in the same depth layers as large cnidarians (PAGÈS *et al.*, 1996). However, these fish probably seek protection from rather than feed on these medusae and ctenophores, whilst feeding on prey like copepods.

Pycnogonids (Pagès, unpublished data) as well as stromateid fish and amphipods have been found in association with Antarctic scyphomedusae (PAGÈS *et al.*, 1996). *Diplumaris antarctica* is usually infested by the hyperiid amphipod *Hyperiella dilatata* Stebbing. The amphipods were always found sitting with their dorsal surfaces against the exumbrellar surface of the medusa. Superb photos taken by Ron Gilmer illustrate this association (HODGSON, 1990; LARSON & HARBISON, 1990). This hyperiid also attaches to

the exumbrella of *Solmundella bitentaculata* (LARSON & HARBISON, 1990). Likewise, *H. dilatata* can capture and carry live individuals of *Clione antarctica* as a chemical protection against predation by the notothenid *Pagothenia borchgrevinki* (Boulenger) (MCCLINTOCK & JANSSEN, 1990). Juveniles of *Hyperia macrocephala* (Dana) live in the gastrovascular system of the scyphomedusa *Desmonema glaciale* Larson, while the adults are ectoparasites, living on and feeding on the epidermis (WHITE & BONE, 1975; CURTSINGER, 1986 as *Desmonema gaudichaudi*).

Benthic communities are very diverse in the Southern Ocean, being mainly composed of echinoderms, polychaetes and sponges (JARRE-TEICHMANN *et al.*, 1997). However, the Antarctic benthos is also the habitat for some gelatinous organisms. The platyctenean *Lyrocteis flavopalidus* Robilliard & Dayton is a large ctenophore (up to 110 mm tall) usually found on top of sponges or other elevated surfaces (ROBILLIARD & DAYTON, 1972). It was described from specimens collected in McMurdo Sound (36-55 m depth) and since then has been observed in King George Island (H. Klöser, pers. comm.) and in the Lazarev Sea where it reaches a mean abundance of 0.7 specimens per 100 m² at 429 m depth (GUTT & STARMANS, in press).

The species of the physonect family Rhodaliidae have an unusual morphology and, uniquely amongst the siphonophores, are benthic organisms (PUGH, 1983). *In situ* observations from ROVs have shown the presence of several colonies of these rare organisms in the Weddell Sea in 300-350 m depth (mean abundance 1.6 specimens per 100 m², GUTT & STARMANS, in press).

CONCLUSIONS

Certainly, this review does not satisfactorily answer the questions framed in the Introduction as appropriate data are still not available in the literature. Although gelatinous organisms are abundant in the plankton and nekton communities of the Southern Ocean, apparently only the salp populations reach top abundances in comparison with other taxa. Presently, the most compelling argument for the importance of GZ in the Antarctic pelagic system is their biovolume. These organisms are seemingly as plentiful and active in Antarctic waters as they are in lower-latitude marine systems. Although carbon content per individual is

low, the high wet biomass and consequently, the relative high carbon content of gelatinous zooplankton in pelagic communities, clearly indicates their potential role in the trophodynamics of the Southern Ocean. The relative contribution of GZ to biomass, and the wide size range shown by these animals suggest that more organisms than those showed in *Table VI* must feed upon them. In contrast, the diet and trophic impact of both herbivorous and gelatinous carnivores still remain some of the principal gaps in our understanding of the pelagic trophic web. Examining the recent literature, one can expect a continued interest in

Antarctic investigations focused on food web dynamics and carbon and nutrient cycling.

It is hoped that this review has helped to make apparent that the activity of herbivorous and carnivorous GZ may be important in these processes and cannot continued to be ignored. Systematic and distribution studies are doubtless necessary, particularly from areas other than the Atlantic sector. Such studies will require the use of sampling methods that correctly evaluate the abundance of gelatinous organisms as well as specialists familiar with these organisms in order to make accurate comparisons between species and areas. This review will have served its

purpose if more studies on Antarctic gelatinous zooplankton are carried out in the future and, of course, if gelatinous organisms are not disregarded in future studies on zooplankton communities.

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