

## **CHAPTER 6: AMPHIPODS AS FOOD SOURCES FOR HIGHER TROPHIC LEVELS IN THE SOUTHERN OCEAN: A SYNTHESIS**

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## ABSTRACT

With more than 820 different species, among which about 75% endemics, the amphipod crustaceans form one of the richest animal group of the Southern Ocean. They have colonized most habitats and exhibit very diverse life styles and trophic types. They moreover show a broad size spectrum, with numerous giant species. Despite their importance in terms of biodiversity, very few is known about the role of amphipods in Antarctic trophodynamics. Based on an exhaustive literature survey (more than 300 references), we tried to delineate their importance as potential food for higher trophic levels. About 200 different predators were recorded: 33 invertebrates (from 12 orders), 101 fishes (19 families), 48 birds (11 families) and 10 mammals. Using this vast dataset (total amount of citations close to 1500) and published values about predators' standing stocks and feeding rates, an attempt was made to build up a small model, distinguishing between benthic and pelagic species of both amphipods and predators. The total amount of consumed amphipods was estimated to 60 millions of tons per year for the whole Southern Ocean, *i.e.* the second animal group in importance after euphausiids.

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## 6.1. INTRODUCTION

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Recent reviews on the knowledge about marine biodiversity in the Southern Ocean (e.g. Arntz et al. 1997) have stressed for instance the relative importance of some zoological groups, like molluscs and polychaetes, and the predominance of crustaceans. Among the latter, amphipods form obviously the richest group with more than 820 species recorded in the Antarctic and Subantarctic regions (De Broyer & Jazdzewski 1993, 1996). These peracarids have colonised a wide variety of ecological niches, in benthic habitats as well as in the water column (De Broyer et al. 2001), and have developed a large range of feeding strategies, from suspension-feeding to scavenging on big carrion and specialised modes like micro-predatory browsing on invertebrate colonies (Dauby et al. 2001a; Nyssen et al. 2002).

The important faunal diversity of amphipod taxocoenoses is likely to indicate a worthwhile significance of these crustaceans in total benthic or pelagic biomasses, and thus their major role in the trophodynamics of Antarctic ecosystems, as well as consumers than as preys. Total biomass data, and *a fortiori* relative data on amphipods are more than scarce, only available for some restricted areas like the eastern Weddell Sea shelf where amphipods should count for about 5% of the benthic biomass (Gerdes et al. 1992). In the same area, their impact as predators on benthic material has been arbitrarily estimated by Jarre-Teichmann et al. (1997) who supposed they feed for about 80% on detritus. This view was recently revised by Dauby et al. (2001b) who showed, from an extensive study of stomach contents of the most representative species, that their diet was far more complex, planktonic bodies and crustaceans forming the major part of it.

On another hand, the importance of amphipods, either benthic or pelagic, for Southern Ocean higher trophic levels has never been analysed in a global context. If numerous papers have been published on the diet composition of Antarctic top predators (some of which preying on amphipods to a more or

less large extent) very few (Duarte & Moreno 1981, Jazdzewski 1981, Jazdzewski & Konopacka 1999) took the "prey point of view" into account, i.e. the actual role of these crustaceans as food source. The present paper is the first attempt to summarize the available information about Amphipoda as preys. It is based on an exhaustive dataset collected from about 310 published articles wherein amphipods are mentioned to be included in the diet of Antarctic invertebrates, fishes, seabirds or marine mammals.

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## 6.2. RESULTS & DISCUSSION

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The bibliographic investigation covers a period running from 1905 till present and concerns the whole Southern Ocean *sensu lato* i.e. including the Sub-Antarctic islands (south of the Sub-Tropical Convergence) but excluding the Magellanic Region. All the collected papers cannot be used in the same way as the included information is not comparable. Old documents were purely qualitative but may be worthy as some amphipod species (such as *e.g. Waldeckia obesa*, Chevreux 1905) were first described from Antarctic fish stomach analyses. Papers since about the fifties were more informative as they contained data about the partition of the different faunal groups in the predator diet, usually as frequency of occurrence (O). More recently appeared more useful articles wherein prey breakdown was expressed in terms of number of items (N), volume (V) or mass (M) fractions. In the last years, finally, papers were published going into more details about prey species identification and their mass repartition in the predator diets. Owing to the editorial policy of the present volume, the set of 310 references will not be listed hereafter.

An amount of about 1500 "records" were registered in the whole dataset. A "record" is defined as the occurrence, in a reference, of a pair [predator species – amphipod species (or family, or sub-order, depending on how precisely preys were determined)]. Several records (up to 60 in *e.g.* Olaso et al. 2000) can thus be found in the same paper.

A total of 176 amphipod species were listed in top predator stomach contents, i.e. more than 20% of the species known for this area. The best represented (super-) families are: lysianassoids, eusirids and epimeriids for gammarideans, and hyperiids and vibiliids for hyperideans (Table 6.1). Curiously, some families well represented in the Antarctic Ocean, like iphimediids, are not commonly found, maybe because of their particular

spinose morphology which should protect them from a heavy predation (Brandt 2000).

**Table 6.1: Numbers of species in the different families of Gammaridea, Caprellidea and Hyperidea found in the digestive tract of the Southern Ocean amphipod predators, and corresponding 'records' (see text) in the literature. (+n.d.) indicates non-determined species.**

<b>FAMILY</b>	<b>n species</b>	<b>n records</b>
Ampeliscaidae	5 (+n.d.)	11
Amphilochidae	1	1
<i>Ceradocus</i> group	1 (+n.d.)	6
Colomastigidae	1	1
Corophiidae	2 (+n.d.)	6
Dexaminidae	2	10
Eophliantidae	0 (+n.d.)	2
Epimeriidae	8 (+n.d.)	32
Eusiridae	36 (+n.d.)	179
Gammarellidae	4 (+n.d.)	16
Hyalidae	2 (+n.d.)	7
Iphimediidae	2 (+n.d.)	10
Ischyroceridae	4 (+n.d.)	18
Leucothoidae	1 (+n.d.)	5
Liljeborgiidae	2 (+n.d.)	10
Lysianassoidea	29 (+n.d.)	200
Melphidipiidae	1	1
Oedicerotidae	3 (+n.d.)	12
Pardaliscidae	1	1
Phoxocephalidae	3 (+n.d.)	15
Podoceridae	1 (+n.d.)	4
Sebidae	1	1
Stenothoidae	5 (+n.d.)	17
Synopiidae	2 (+n.d.)	8
<i>undetermined</i>		155
<b>Total GAMMARIDEA</b>		<b>728</b>
Phtisicidae	1 (+n.d.)	4
<i>undetermined</i>		10
<b>Total CAPRELLIDEA</b>		<b>14</b>
Brachyscelidae	1	1
Hyperidae	13 (+n.d.)	315
Lanceolidae	1 (+n.d.)	2
Phrosinidae	2 (+n.d.)	28
Phronimidae	1 (+n.d.)	5
Platyscelidae	1	1
Proscinidae	0 (+n.d.)	2
Scinidae	1 (+n.d.)	1
Vibiliidae	6 (+n.d.)	102
<i>undetermined</i>		62
<b>Total HYPERIDEA</b>		<b>519</b>

Concurrently, 192 different predators were identified belonging to various zoological groups (Table 6.2). The most numerous records concern fishes

(101 species from 19 families, especially from the notothenioid ones) and seabirds (48 species from 12 families, mainly procellariids and penguins).

**Table 6.2: Numbers of species of amphipod predators in the different taxa (from classes to families, depending on groups), and corresponding 'records' (see text) in the literature.**

		n species	n records
ANNELIDA	Polychaeta	2	10
MOLLUSCA	Cephalopoda	6	9
CRUSTACEA	Amphipoda	5	8
	Decapoda	2	2
	Isopoda	4	6
	Mysidacea	1	1
ECHINODERMATA	Asteroidea	3	6
	Echinoidea	2	7
	Holothuroidea	4	4
	Ophiuroidea	4	13
CHAETOGNATHA		1	1
TUNICATA	Thaliacea		1
PISCES (101)	Achiropsettidae	1	1
	Artedidraconidae	14	124
	Bathydraconidae	10	43
	Bathylagidae	1	1
	Bovichthyidae	1	1
	Centrolophidae	1	1
	Channichthyidae	7	35
	Congiopodidae	1	6
	Cyclopteridae	4	5
	Gadidae	2	3
	Harpagiferidae	3	38
	Macrouridae	2	2
	Muraenolepidae	2	9
	Myctophidae	11	57
	Notacanthidae	1	1
	Nototheniidae	33	450
	Rajidae	4	7
	Scombridae	1	6
	Zoarcidae	2	8
AVES (48)	Anatidae	2	5
	Chionidae	2	3
	Diomedidae	4	30
	Laridae	5	33
	Muscicapidae	1	1
	Oceanitidae	2	15
	Pelecanoididae	2	30
	Phalacrocoracidae	3	7
	Procellariidae	17	164
	Spheniscidae	8	241
	Stercorariidae	2	9
	<i>undetermined</i>		7
MAMMALIA (10)	Cetacea	5	22
	Pinnipeda	5	17

Amongst invertebrates, the more important amphipod predators are species of polychaetes and echinoderms (starfishes, urchins and brittle stars) in the benthos, and several species of squids in the water column. Very few informative data (Table 6.3) are however available in order to estimate their impact on amphipod populations.

**Table 6.3: Examples of predation percentages on amphipods by some selected predators. Amphipod types: Gb: benthic Gammaridea; Gp: pelagic Gammaridea; H: Hyperiidea. Diet estimations: V: per volume; O: per occurrence; N: per number; M: per mass (see text).**

Taxa		Predator species	Amphi type	% in diet
ANNELIDA	Polychaeta	<i>Harmothoe spinosa</i>	Gb	99 V
MOLLUSCA	Cephalopoda	<i>Alluroteuthis antarcticus</i>	H	50 O
		<i>Galiteuthis glacialis</i>	H	100 O
ECHINODERMATA	Asteroidea	<i>Labidiaster rupicola</i>	Gb	38 N
	Echinoidea	<i>Sterechninus neumayeri</i>	Gb	4 V
PISCES	Bathyracidae	<i>Gerlachea australis</i>	Gb	13 M
		<i>Cygnodraco mawsoni</i>	Gb	1-12 M
	Artedidraconidae	<i>Artedidracon mirus</i>	Gb	4-72 M
		<i>Artedidracon orianae</i>	Gb	2-80 M
	Harpagiferidae	<i>Pogonophryne marmorata</i>	Gb	3-81 M
		<i>Harpagifer bispinis</i>	Gb	2-96 M
	Nototheniidae	<i>Harpagifer antarcticus</i>	Gb	2-82 M
		<i>Gobionotothen gibberifrons</i>	Gb-H	0-38 M
	Channichthyidae	<i>Notothenia coriiceps</i>	Gb-H	0-88 M
		<i>Lepidonotothen nudifrons</i>	Gb-H	3-38 M
	Myctophidae	<i>Champsocephalus gunnari</i>	H	5-83 M
		<i>Electrona carlsbergi</i>	H	4-27 M
AVES	Diomedidae	<i>Protomyctophum choriodon</i>	H	0-11 M
		<i>Diomedea chrysostoma</i>	H	3-17 O
	Laridae	<i>Sterna vittata</i>	Gb-Gp	3-30 M
		<i>Larus dominicanus</i>	Gp-H	1-38 O
	Oceanitidae	<i>Oceanites oceanicus</i>	Gp-H	1-45 M
	Pelecanoididae	<i>Pelecanoides urinatrix</i>	H	0-17 M
	Procellariidae	<i>Fulmarus glacioides</i>	Gp-H	0-5 M
		<i>Pachiptila desolata</i>	H	0-16 M
	Spheniscidae	<i>Pterodroma spp</i>	Gp-H	0-5 M
		<i>Eudyptes chrysocome</i>	H	0-3 M
		<i>Eudyptes chrysolophus</i>	Gp-H	2-67 M
		<i>Pygoscelis papua</i>	Gb-Gp	0-4 M
MAMMALIA	Cetacea	<i>Balaenoptera borealis</i>	H	→45 M
	Pinnipeda	<i>Leptonychotes weddelli</i>	Gb	3-29 O



Many species of the different notothenioid families feed on amphipods to a more or less broad range (Table 6.3). Bottom species such as dragonfishes (bathydraconids) and plunderfishes (artetidraconids and harpagiferids) actively prey upon benthic amphipods, sometimes to a very large extent (up to 96% of diet mass). Most of the species that feed in the water column, like icefishes (channichthyids), consume rather few amphipods, mainly hyperiids. Finally, members of the family Nototheniidae (rockcods) show a more complex behaviour, feeding on both benthic and pelagic animals; gammarideans as well as hyperideans are usual preys, forming up to 88% of diet mass in *e.g.* *Notothenia coriiceps*. Beside notothenioids, many other fish families were reported to consume amphipods, the most important one being the myctophids (lanternfishes). These small-sized, meso- or bathypelagic fish prey to a relatively small extent on different hyperidean families but, owing to their abundance and to their peculiar swarming behaviour, maybe represent the largest group of amphipod consumers in the Southern Ocean (see below).

All the Antarctic and Sub-Antarctic seabird families have been reported to feed on (pelagic) amphipods. If the latter constitute only a small fraction in the diet of albatrosses and gulls, they may form up to 30% of diet mass in terns, which forage closer to the shores. Diving and storm petrels (pelecanoidids and oceanitids) feed at a minor extent too on amphipods, except the Wilson's storm petrel (*Oceanites oceanicus*) for which these crustaceans can form up to 45% of food bulk. Most of the procellariids (petrels, prions and shearwaters) also feed occasionally on amphipods which usually constitute less than 5% of their diet mass. Finally, all the Southern Ocean penguins (sphenicids) have been reported to prey on hyperiids and pelagic gammariids, but to a very small extent (about 1% in mass); macaroni penguins (*Eudyptes chrysolophus*), however, seem to feed more frequently on amphipods (up to 67% in mass); typically benthic amphipod species are

also found in the diet of gentoo penguins (*Pygoscelis papua*), denoting that these birds feed near to the shorelines.

Among marine mammals, 10 species —4 baleen whales, 1 dolphin and 5 seals— have been found with amphipods in their stomach. The presence of these crustaceans in the diet of plankton-feeding cetaceans is not surprising as hyperiids like *Themisto gaudichaudii* are known to swim often at the vicinity of krill swarms (Pakhomov & Perissinotto 1996). The sei whale (*Balaenoptera borealis*) in particular seems to feed preferentially on this hyperiid which can form up to 45% of its diet mass (Kawamura 1974), while for the other whales the occurrence of amphipods is more anecdotal. Amphipods are also found in the diet of many Antarctic seal species, where they form only a few ‰ in mass, but most of the authors claim it should be an artifact, amphipods coming from the stomach of ingested fish.

To synthesize the dataset, a tentative 'box-model' was built up which shows the relative importance of both pelagic and benthic amphipods in the diet of the Southern Ocean top predators. To construct this model, various published data were used: (i) the mean quantitative values of amphipod mass fractions in predators' diet, (ii) the standing stocks of the main groups of predators in the Southern Ocean, (iii) the feeding rates of these predators. Available data are presented in Table 4; for some groups, namely both benthic and pelagic (squids) invertebrates, consistent biomass values are lacking, causing the total amount of preyed amphipods to be underestimated. The diagram (Fig. 1) shows the estimates of the different predation fluxes, expressed in millions of tons per year ( $\text{Mt.yr}^{-1}$ ). It clearly appears that pelagic fishes (myctophids) are responsible for the biggest flux ( $50 \text{ Mt.yr}^{-1}$ ), which can easily be understood when considering the area and depth ratios of the oceanic vs neritic zones. The second group in importance is represented by benthic and benthopelagic fish (notothenioids mainly), whose predation on pelagic amphipods was not estimated but is likely at least one order of magnitude smaller than on benthic ones ( $8.6 \text{ Mt.yr}^{-1}$ ). The other predator groups (birds and mammals) consume

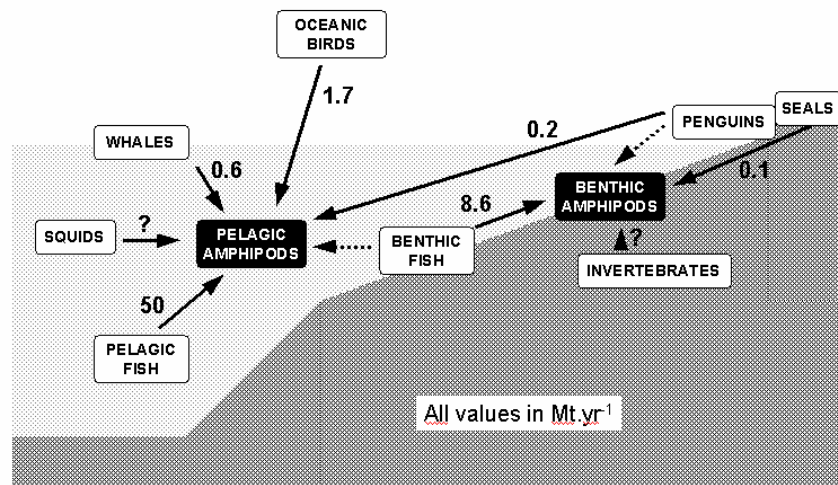
a lower amount of amphipods (from 0.1 to 1.7 Mt.yr<sup>-1</sup>) as their relative biomass is far weaker than that of fish. The total amphipod mass ingested per year is thus estimated at roughly 60 Mt. These values must however be cautiously regarded as they are tainted with biases and approximations for several reasons: (i) predator biomass data are usually widely scattered, available only either for areas of intensive scientific research or for species of commercial significance; (ii) just a few (characteristic) fish families were taken into account, while other ones (such as *e.g.* zoarcids or muraenolepids) are also well represented in the Southern Ocean but less studied; (iii) seasonal variations in either predator standing stocks or feeding rates are likely to occur, the importance of which can hardly be weighed; (iv) the proportion of amphipods in predators' diet may considerably vary with respect to several parameters like *e.g.* age, sex or geographical location; (v) some maybe significant groups (*i.e.* benthic and pelagic invertebrates) were totally omitted; (vi) the circumscription of what is the 'Southern Ocean' (south of the Antarctic Convergence, south of the Sub-Tropical Front, including or not the Sub-Antarctic islands) is not clearly defined in the literature. This notwithstanding, values presented in Fig. 1 can be considered to represent a rather realistic working hypothesis about the importance of amphipods for Southern Ocean top predators.

**Table 6.4: Values of the different parameters used to estimate the predation rates on amphipods by the main Southern Ocean predator groups.**

Parameters	Values	References
Southern Ocean Area	37 10 <sup>6</sup> km <sup>2</sup>	Stonehouse 1989
Continental Shelf Area (Continent)	2 10 <sup>6</sup> km <sup>2</sup>	
Continental Shelf Area (Islands)	0.5 10 <sup>6</sup> km <sup>2</sup>	
Demersal Fish Biomass (Continent)	0.9 T.km <sup>-2</sup>	Kock 1992
Demersal Fish Biomass (Islands)	20 T.km <sup>-2</sup>	<i>estimated from</i> Kock 1992
Myctophid Biomass	140 MT	Lubimova <i>et al.</i> 1987 in Kock 1992
Fish Mean Daily Ingestion Rate	2 %.day <sup>-1</sup>	various authors in Kock 1992
Penguin Annual Ingestion Rate	17 MT.yr <sup>-1</sup>	various authors in Williams 1995

Parameters	Values	References
Other Seabirds' Annual Ingestion Rate	35 MT.yr <sup>-1</sup>	<i>extrapolated from</i> Croxall & Prince 1987
Sei Whale Antarctic Population	24000 ind.	<i>mean from various sources</i>
Sei Whale Feeding Period	130 days.yr <sup>-1</sup>	
Sei Whale Daily Ingestion	900 kg.day <sup>-1</sup>	Kawamura 1974
Seal Mean Daily Ingestion Rate	7 kg.km <sup>-2</sup> .day <sup>-1</sup>	Joiris 1991
Amphipods in Diet	Mean (%)	
Demersal Fish (Notothenioids)	10	<i>this study</i>
Pelagic Fish (Myctophids)	5	"
Penguins	1	"
Oceanic Seabirds	5	"
Whales	20	"
Seals	2	"

Fig. 6.1: Scheme of the different predation fluxes on amphipods (in MT.yr<sup>-1</sup>) by the main Southern Ocean predator groups.



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### 6.3. CONCLUSIONS

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The exhaustive analysis of the literature dedicated to the diet of Southern Ocean top predators revealed the importance of amphipods in the trophodynamics of the higher food web. The integration of available data with published values about predators' biomasses and feeding rates allowed to estimate that about 60 millions of tons of these crustaceans are consumed each year in the area, *i.e.* about  $1.6 \text{ t.km}^{-2}.\text{yr}^{-1}$ . By comparison, the consumption of krill by all its predators in the Southern Ocean has been estimated to about  $250 \text{ Mt.yr}^{-1}$  (Everson 1977, Miller & Hampton 1989), while annual fish consumption by warm-blooded predators has been estimated to be up to 15 Mt (Everson 1977, Laws 1985). Amphipods are thus likely to be the second group of animal prey in importance after euphausiids. The present review also emphasizes the major role of hyperiids (and especially of *Themisto gaudichaudii*) in Antarctic food webs.

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