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Potential impact of the main benthic amphipods on the eastern Weddell Sea shelf ecosystem (Antarctica)

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Abstract As they represent one of the most diversified taxonomic groups on Antarctic bottoms, amphipods are likely to play a complex role in biogeochemical fluxes that occur within benthic ecosystems. The aim of this paper is to present, using both digestive tract analyses and relative species abundance data, the impact of amphipod feeding on different potential preys of the Weddell Sea. The study is based on data obtained for 29 representative amphipod species collected at 130 stations distributed along the eastern shelf of the Weddell Sea (depth range: 60–2,000 m) during three summer cruises, from 1989 to 1998. Sedimenting plankton particles (10–27%), crustaceans (22–32%) and fish carrion (5–18%) are the main food resources. Other abundant potential preys, such as molluscs or tunicates, do not seem to be consumed. Variations in the proportions of the different preyed food items are observed, mainly related to differences in relative amphipod species composition in samples. Presented results will help in refining ecological models of the prospected area, but also underline the need for accurate and reliable measurements of the feeding rates of Antarctic benthic organisms.

Introduction

In a recent attempt to model the organic matter flows within the benthic communities of the Weddell Sea continental shelf (Jarre-Teichmann et al. 1997), biologists of the Alfred-Wegener Institute (Bremerhaven,

Germany) underlined the need for a better understanding and for an accurate measurement of several key processes that govern biogeochemical fluxes in these ecosystems. Among these processes, those related to nutrition of benthic organisms (like food intake or assimilation rates) are of primary interest.

Within the Southern Ocean benthic ecosystems, crustaceans are by far the most speciose taxon (Arntz et al. 1997) and, among crustaceans, amphipods represent the richest group, with more than 820 recorded species (De Broyer and Jazdzewski 1993, 1996), about 320 of which inhabit Weddell Sea waters. These peracarids have colonised a wide variety of ecological niches, from epontic to below-ground biotopes. They achieved a successful eco-ethological diversification, occupying apparently almost all the possible micro-habitats and developing various feeding strategies, from suspension-feeding to scavenging on vertebrate carcasses. Indeed, in a recent study (Dauby et al. 2001), we showed that at least eight different feeding types occurred among Weddell Sea gammaridean amphipods (despite the absence of macro-herbivory owing to the lack of benthic macroalgae in that area), including some specialised modes such as micro-predatory browsing on invertebrate colonies.

In this study, we try to answer the questions: what do amphipods eat (what is the share of every potential food in their diet), and also, what is their impact on the different available food sources? We then analyse the role of the Weddell Sea amphipod taxocoenosis in consuming these food sources, taking into account their food preferences and their in situ relative occurrence. The presented results are, however, limited to the austral summer season and are thus not likely to represent a year-round situation.

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Materials and methods

Amphipods were collected from benthic and suprabenthic samples taken in the eastern Weddell Sea during three Antarctic summer RV “Polarstern” cruises: EPOS leg 3 (1989; Arntz et al. 1990),

Table 1 Mean relative proportions (in %) of the different food items in the digestive tract of the most common amphipod species from the eastern Weddell Sea. Corresponding trophic types from Dauby et al. (2001)

Species	n	Family	Inorganic matter	Unidentified organic matter	Sedimenting plankton	Porifera	Cnidaria	Polychaeta	Crustacea	Bryozoa	Ophiuroidea	Holo-thuroidea	Pisces	Feeding type
<i>Ampelisca richardsoni</i>	20	Ampeliscidae		36	54	7			3					Suspension feeder
<i>Epimeria georgiana</i>	31	Epimeriidae	13	18	30	7	14	10	26					Deposit feeder
<i>Epimeria macrodonta</i>	10	Epimeriidae	5	18	8	14	30		15			10		Opportunistic predator
<i>Epimeria robusta</i>	10	Epimeriidae	7	25	8	12	19	7	19			3		Opportunistic predator
<i>Epimeria rubriques</i>	12	Epimeriidae		8	18	7	18	8	27			14		Opportunistic predator
<i>Epimeria similis</i>	27	Epimeriidae		5	9	14	63	9						Micropredatory browser
<i>Epimeriella walkeri</i>	17	Epimeriidae			20	10	6		2		36	1	25	Macropredator/scavenger
<i>Eusirus perdentatus</i>	20	Eusiridae	27	25				4	44					Macropredator/scavenger
<i>Rhachotropis antarctica</i>	12	Eusiridae			17		9	11	63					Macropredator/scavenger
<i>Antamelita</i> sp. nov.	27	Melitidae	10	18	1	4	1	3	57	1	4	1		Deposit feeder
<i>Paraceradocus gibber</i>	20	<i>Ceradocus</i> group	18	39	7	12		6	14		4			Deposit feeder
<i>Echiniphimedia hodgsoni</i>	20	Iphimediidae	8	20	9	62						2		Micropredatory browser
<i>Gnathiphimedia mandibularis</i>	15	Iphimediidae		5	2	15				78				Micropredatory browser
<i>Iphimediella cyclogena</i>	31	Iphimediidae			10			20				70		Micropredatory browser
<i>Maxilliphimedia longipes</i>	6	Iphimediidae		6	6	12	73	9						Micropredatory browser
<i>Jassa goniamera</i>	10	Isehyroceridae			50									Suspension feeder
<i>Liljeborgia georgiana</i>	22	Liljeborgiidae		13		13	13	24	37					Deposit feeder/predator
<i>Abyssorhynchone nodimanus</i>	14	Lysianassoidea		5									95	Carrion feeder
<i>Abyssorhynchone rossi</i>	21	Lysianassoidea		5	5	5			5				80	Opportunistic carrion feeder
<i>Hirondellea antarctica</i>	18	Lysianassoidea					50		25				25	Micropredatory browser
<i>Orchomenella pinguides</i>	16	Lysianassoidea			50				50					Deposit feeder macrophage

<i>Tryphosella murrayi</i>	35	Lysianassoidea	5		5	43	47	Opportunistic carrion feeder
<i>Uristes gigas</i>	42	Lysianassoidea	14	13		27	35	Deposit feeder/ carrion feeder
<i>Waldeckia obesa</i>	30	Lysianassoidea	5	5			85	Carrion feeder
<i>Melphidippa antarctica</i>	10	Melphidippidae	71	6	2	21		Suspension feeder
<i>Oediceroides calmani</i>	24	Oedicerotidae	22	8		26		Deposit feeder/ predator
<i>Oediceroides emarginatus</i>	26	Oedicerotidae	25	7		51		Deposit feeder/ predator
<i>Heterophoxus videns</i>	17	Phoxocephalidae	16	8		19		Macro predator/ scavenger
<i>Bathypanoploea schellenbergii</i>	12	Stilipedidae	9		81	5	4	Micro predatory browser

EASIZ I (1996; Arntz and Gutt 1997) and EASIZ II (1998; Arntz and Gutt 1999). In total, 130 catches provided amphipod material in water depths from 60 m down to 2,000 m. Gears used included Agassiz, benthopelagic and bottom trawls, dredges, epibenthic sledges, TV grabs, giant and multibox corers, and baited traps.

Ethological observations (food detection and capture, mobility patterns) were performed with living specimens of about 40 species kept in cool containers on board and afterwards in a cool laboratory at IRScNB, Brussels. Amphipods (between 25 and > 100 individuals, depending on species) were maintained at a temperature of -1°C ($\pm 1^{\circ}\text{C}$) in 2- to 30-l aquaria. Feeding experiments were performed in these aquaria, using as potential food source different living organisms (like crustaceans, echinoderms or plankton) or dead material (such as pieces of amphipods, fishes or squid) laid on the bottom or offered with forceps. These experiments were usually conducted over periods of 6–8 weeks.

Amphipod gut content analyses were done mainly on specimens fixed just after sampling in 4% formaldehyde. The amount of food in the stomach (C_s) and gut (C_g), respectively, was coded with arbitrary scores (4, more than 75% of the volume is filled; 3, from 50 up to 75%; 2, from 25 up to 50%; 1, less than 25%). Every item present in the digestive tract was determined to the group or species level when possible, and their proportion was coded using a similar coefficient (P_s , $P_g = 1, 2, 3$ or 4). A semi-quantitative approach, inspired from the “percentage points” method (Hynes 1950; Williams 1981), was used, with the following equations:

$$I(i) = \sum_{n=1}^x C_s(n) * P_s(n) + C_g(n) * P_g(n) \quad (1)$$

where $I(i)$, dimensionless, is the importance of item i in the diet of a given species, and x the number of specimens dissected;

$$R(i) = \frac{I(i)}{\sum_{n=1}^y I(n)} * 100 \quad (2)$$

where $R(i)$, in %, represents the relative importance of item i in the total diet of a given species, and y the number of different items.

The trophic impact of these amphipod species on Weddell Sea ecosystems has been evaluated by coupling feeding preferences and relative species abundances with the basic formula:

$$T(i) = \sum_{sp=1}^x \frac{\bar{N}_{sp}}{\bar{N}_{tot}} * R(i)_{sp} \quad (3)$$

where $T(i)$ is the trophic impact on food item i (in %), x the number of analysed species, and \bar{N} the mean number of individuals of a defined species (sp) and of all the x analysed species (tot) for all the samples of a cruise. Only classical benthic sampling devices (trawls and box corers) were taken into account for evaluating \bar{N} , as baited traps, for instance, do not reflect the actual instantaneous abundance of a species in a defined sampling area.

Results

The mean relative abundance [$R(i)$, in %] of the different food items in the digestive tract of the most important Weddell Sea amphipod species is presented in Table 1, with information about their principal feeding types. The latter, determined from both digestive tract analyses and behavioural observations, are extensively described in Dauby et al. (2001).

The 29 amphipod species selected for the present evaluation were chosen on the basis of their relative abundance, each one representing at least 0.4%, on average, of the total amphipod population collected during each cruise. For the EPOS cruise (1989), these 29

species represent 52.8% of total amphipods (58% of all the samples were analysed) while, for the EASIZ I cruise (1996), they represent 70.9% of total amphipods (82% of the samples were investigated).

The amphipod trophic impact on the different available food items [$T(i)$] of the Weddell sea is presented in Table 2, for the EPOS and the EASIZ I cruises, respectively.

For the EPOS samples, crustaceans appear to be the most frequently consumed items (32%), followed by fish carcasses (18%). If we do not take into account the unidentified organic matter (unrecognisable organic bodies without any specific features like cnidocysts, or without any hard structures like chitinous plates or spicules), particles of planktonic origin represent the third most common item. Sponges, cnidarians and worms (polychaetes and nematodes) are about equally consumed (5–7%), while bryozoans and echinoderms represent only a tiny fraction of the amphipod diet.

Results from the EASIZ I cruise are rather different. Plankton-originating cells (together with the unidentified matter) are the main dietary component (27%), before crustaceans (22%). Fish flesh constitutes only a small fraction (5%), and is of the same order of occurrence as worms, bryozoans or holothuroids. Sponges, with 7%, are the third item in importance in the amphipod diet.

Discussion

In their recent effort to summarise into a conceptual flow diagram the trophic interactions that occur on Weddell Sea bottoms, Jarre-Teichmann et al. (1997) admitted that crustaceans form a “very heterogenous box”. Literature on high-Antarctic amphipod feeding strategies is indeed scarce (Oliver and Slattery 1985; Slattery and Oliver 1986; Coleman 1989a, b, c, 1990a, b; Klages and Gutt 1990a, b), and is concerned with less than 5% of known species. Owing to this lack of knowledge, Jarre-Teichmann et al. (1997) arbitrarily attributed the following predation impacts to crustaceans in their model:

Table 2 Mean relative trophic impacts [$T(i)$] (in %) of the eastern Weddell Sea benthic amphipod community on different potential food sources, during the EPOS (1989) and EASIZ I (1996) cruises. Inorganic material (sediment grains) were omitted from calculations

	EPOS	EASIZ I
Unidentified organic matter	17	25
Sedimenting plankton	10	27
Porifera	7	7
Cnidaria	7	3
Worms	5	4
Crustacea	32	22
Bryozoa	2	3
Ophiuroidea	1	1
Holothuroidea	1	3
Pisces	18	5

10% polychaetes, 3% crustaceans, 4% echinoderms, 1% bryozoans and 82% detritus. From Tables 1 and 2, it clearly appears that such a $T(i)$ distribution is inappropriate. “Detritus”-feeders represent only one-half of the Weddell Sea amphipod species (Dauby et al. 2001) even when gathering together the deposit-feeders and all the occasional opportunistic scavengers of all types from micro-feeders to necrophages. The species used in Jarre-Teichmann et al.’s (1997) paper (*Paraceradocus gibber*, *Gnathiphimedia mandibularis*, *Epimeria robusta*, (*Abyss-*) *Orchomene plebs* and *Bovallia gigantea*) are not at all representative of the whole benthic amphipod community, and thus induce a bias in the model.

The present study shows that, when averaging over site and year variations, crustaceans, planktonic particles and carcasses form the bulk of the Weddell Sea amphipod diet. The other sources of feeding (worms, echinoderms, bryozoans or sponges) count for a minor part and are mainly consumed by some specialised predatory feeders.

The share between living and non-living food items is, however, sometimes difficult to establish. If it is relatively evident for, for example, fish muscles (although we have in very few cases observed cohorts of Lysianassoidea species attacking living fishes in the aquarium), it is not so obvious for items such as crustaceans. The presence of euphausiid remains in amphipod digestive tracts, for instance, would suggest a scavenging deposit-feeding mode, but the occurrence of amphipod remains can be attributed to both a predatory and a scavenging feeding mode. Complementary in vivo observations of feeding behaviour are thus necessary.

Two groups of benthic animals which are well represented in the high Antarctic are apparently absent from the diet of amphipods: molluscs (in terms of biodiversity, the second phylum after crustaceans; Arntz et al. 1997) and ascidians. The absence of these items could be related to their “protective” shell (although it is not much calcified in cold waters) or tunic. Such an argument is, however, not consistent, as some amphipod species are able to browse on holothuroid podia, on sponges or on bryozoan colonies. Some molluscs and ascidians may have been consumed, and may form part of the unidentified organic matter, which represents about one-fifth of the total ingested food, but no radula was found in amphipod digestive tracts.

The difference between the $T(i)$ distributions for the two cruises (Table 2) is likely to be attributed to differences in sampling areas, and concurrently in the sampled amphipod communities (De Broyer et al., *in press*). For instance, in the EPOS cruise, *Uristes gigas*, a scavenging lysianassoid, was abundant (>7% of total amphipods) in the samples, while in EASIZ I, one *Ampelisca richardsoni*, a typical suspension-feeder, was dominant (22%). Such differences emphasise the need for multiple sampling with devices that give a better overview of the benthic community composition, such as corers.

In the same way, the results presented in Table 2 should be regarded cautiously, as the analysed amphi-

pod species, albeit dominant in samples, are not necessarily the dominant species of the prospected areas. Indeed, owing to the gears used, larger species are significantly more numerous in the samples. Except for one species (*Heterophoxus videns*), all the amphipods we analysed are longer than the mean size (17 mm) for all known East Antarctic species. Moreover, all of them were adult specimens, and the diet of juveniles may be different.

The conversion of the measured trophic impacts into actual food consumptions requires knowledge of both biomass and feeding rate of the amphipods. Reliable biomass data (based on multibox corer sampling effort) for eastern Weddell Sea amphipods were only published by Gerdes et al. (1992) for cruises performed from 1987 to 1989. The authors found a mean biomass of 669 mg WW m⁻², with values ranging from 8 to 6,396 mg WW m⁻² depending on the sampling station. Amphipods counted for about 5‰ of total benthic animal biomass. Feeding rate measurements, however, were never published for high-Antarctic amphipods, maybe because of the experimental complexity in feeding most of these crustaceans in culture conditions. Some attempts, however, have been made to indirectly estimate this feeding rate (for example, using P/B ratios; Brey and Clarke 1993; Jarre-Teichmann et al. 1997), but these should be cautiously regarded. We have carried out some experimental series in aquaria on different necrophagous Lysianassoidea (De Broyer and Klages 1990; Y. Scaillieur, G. Chapelle, C. De Broyer, unpublished work), and measured feeding rate values ranging from 14 to 40 mg g⁻¹ day⁻¹, depending on species and prey. These values, however, are likely not applicable to the whole amphipod community, as necrophages are known to display a discrete method of feeding, depending greatly on food availability.

The present paper, hopefully shedding better light on the role of the amphipod taxocoenosis within the trophic flows which occur on the Weddell Sea bottoms, emphasises the necessity to amplify the research effort in at least two directions: a better knowledge of the benthic community structure (mainly species biomass estimates), and the development of techniques to accurately measure the organic matter fluxes at the individual (or population) level. Without such additional information, the elaboration of consistent ecosystem models, such as those presented, for example, by Rakusa-Suszczewski (1993) or Knox (1994), may remain at a standstill for a long time.

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