

CHAPTER 5: THE CRUSTACEAN SCAVENGER GUILD IN ANTARCTIC SHELF, BATHYAL AND ABYSSAL COMMUNITIES

After De Broyer C, Nyssen F, Dauby P (2004) Deep-Sea Research,
Part II: 51: 1733-1752

Abstract

Peracarid crustaceans form a significant part of the macrobenthic community which is responsible for scavenging on large food falls onto the sea floor. Although several studies are available about scavengers from tropical and temperate seas, very little information has been published about such species living in Antarctic waters, particularly at greater depths. The present paper is based on a collection of 31 baited trap sets deployed in the Weddell Sea, Scotia Sea and off the South Shetland Islands, and presents results on the geographical and bathymetric distribution of the different taxa and on the ecofunctional role of scavengers.

Some 68,000 peracarid crustaceans from 62 species were collected. About 98% of individuals belonged to the amphipod superfamily Lysianassoidea, and 2% to the isopod family Cirolanidae. Of these species, 31, including 26 lysianassoids (1,400 individuals), were collected deeper than 1000 m.

High species richness was discerned for the eastern Weddell Sea shelf compared with other Antarctic areas. The Antarctic slope also seems to be richer in species than other areas investigated in the world, while in the abyss, scavenger species richness appears to be lower in Antarctica. A richness gradient was thus observed from the shelf to the deep. For amphipods, a number of species extend their distribution from the shelf to the slope and only one to the abyssal zone.

Amphipod species showed degrees of adaptation to necrophagy. The functional adaptations of the mandible and the storage function of the gut are discussed. Feeding experiments conducted on lysianassoid species collected at great depths and maintained in aquaria showed a mean feeding rate of about 1.4 to 4.1 % dry body weight.day⁻¹, which is consistent with data obtained from other species.

5.1. Introduction

The scavenger guild plays a key role in deep-sea benthic communities by rapid recycling and dispersing organic falls of all sizes, from small plankters to whales (e.g. Gage and Tyler 1991, Britton and Morton 1994).

In the Antarctic seas, the existence of an abundant and active scavenger fauna was noticed by early Antarctic marine investigators. Observing the large catch of lysianassid amphipods attracted quickly to baited nets at Cape Adare during the National Antarctic Expedition 1901-1904, Hodgson (in Walker 1907) wrote: "*The trap contained about 10,000 of these amphipods.... Four fish were in the trap, one of them had been reduced to an absolute skeleton; on another the amphipods hung by their 'teeth' in a compact mass, completely concealing their victim. Its skin had disappeared, and I judged also a millimetre of flesh.... the other two fish were presumably waiting their turn.*"

These early collections were mostly opportunistic. With the establishment of permanent coastal Antarctic stations, baited traps have been used more systematically to collect necrophagous invertebrates (e.g. Hurley 1965, Arnaud 1970, Bruchhausen et al. 1979, Rakusa-Suszczewski 1982, Nagata 1986, Presler 1986, Slattery and Oliver 1986, Moore 1994). These catches have provided data on the composition, ecology and biology of scavengers, as well as the discovery of species new to science (e.g. Hurley 1965, De Broyer 1985a, Nagata 1986). Most of this sampling was done at depths shallower than 150 m. Attempts to collect scavengers on the deep Antarctic continental shelf, which extends to an average depth of 450 m and, in places, to over 1000 m depth (Clarke and Johnston, 2003), have been relatively few (Arnaud 1970, De Broyer and Klages 1990, De Broyer et al. 1997, 1999, Takeuchi et al. 2001).

Baited trap sampling led to the discovery of an unexpected vagile benthic fauna of fish and crustaceans under the Ross Ice Shelf at a distance of 400

km from the sea, under ice 415 m thick (Bruchhausen et al. 1979, Lipps et al. 1979, Stockton 1982).

In the deep sea, bathyal and abyssal trap sampling was initiated by the Prince of Monaco as early as 1888 and provided new, and sometimes giant, species of crustaceans and fishes (Richard 1934, Chevreux 1935, De Broyer and Thurston 1987). Much later, baited cameras revealed the existence of a very active guild of mobile necrophages in the deep sea which attracted much interest (e.g. Isaacs and Schwartzlose 1975, Hessler et al. 1978, Gage and Tyler 1991, Britton and Morton 1994). In the Antarctic deep sea, attempts at baited trap collecting have, so far, been extremely few: two operations were reported by Bowman and Manning (1972) from north of Amundsen Sea at depths of 4930 and 5045 m and one single operation at 3186 m off Queen Maud Land was undertaken by Takeuchi et al. (2001).

During the *Polarstern* EASIZ campaigns (1996 & 1998) in the Weddell Sea baited traps were used systematically to complement the catches made by other gears in order to obtain a more complete representation of the shelf and slope assemblages at the so-called “integrated stations” (Arntz and Gutt 1997, 1999, De Broyer et al. 1997, 1999). These trap operations collected mobile scavengers (sometimes in large number) that were not, or only rarely, sampled by other gears such as trawls, dredges, epibenthic sledges, box-corers and deep plankton nets.

In addition, investigations of the Antarctic deep sea have recently been conducted during the *Polarstern* ANDEEP cruises in 2002 in the Scotia Sea, the western Weddell Sea and the South Sandwich Trench (Brandt et al. 2003, De Broyer et al. 2003). These bathyal and abyssal investigations involved a series of successful deep-sea trapping operations.

The results of these *Polarstern* campaigns in terms of composition and bathymetric distribution of the crustacean scavenger guild are reported herein and Antarctic shelf and deep sea faunules are compared. In addition, to investigate the role of the scavenger guild in Antarctic shelf communities and

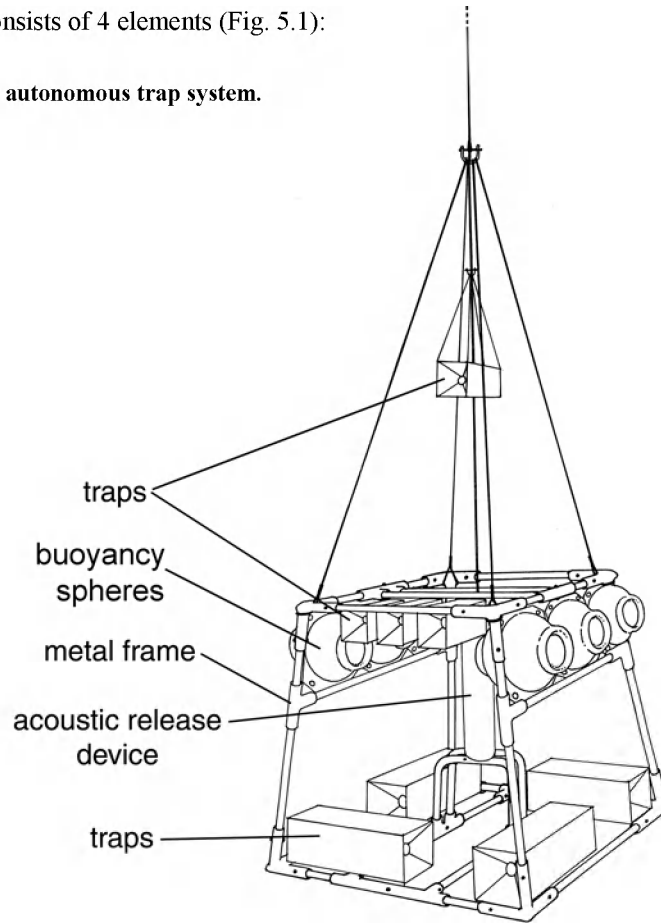
to complement data previously obtained from gut content analyses (Dauby et al. 2001a, b), results of feeding experiments on necrophagous amphipods are presented.

5.2. Material and Methods

5.2.1. THE AUTONOMOUS TRAP SYSTEM

All scavengers were sampled using an 'autonomous trap system' (ATS), based on the system developed at IFREMER, Brest (Guennegan and Martin 1985). It consists of 4 elements (Fig. 5.1):

Fig. 5.1. The autonomous trap system.



1. A brass trapezoidal frame (about 1 m³) on which are fixed various baited traps, either in direct contact with bottom or held one metre above. "Box traps" are metal rectangular frames of different sizes (7 or 22 l), covered with nylon gauze of 500 µm, with two inverse conical openings (diameter: 2 or 4 cm). Their upper side can be opened for rapid retrieval of collected animals.
2. A buoyancy package made of sets of high pressure 10" or 17" glass balls (50 and 260 N buoyancy, respectively) attached directly to the frame and a few metres above it.
3. A deep-sea acoustic release (Ix-Sea Oceano Instruments, Brest, France).
4. Disposable ballast made of iron plate and anchor chains.

Traps were baited (preferably) with notothenioid fish when available, or with other fish or beef meat (from about 200 to 600 g, depending on trap size). Bait was usually wrapped in nets (5 mm mesh) in order to prevent too rapid consumption and so increase the time over which it remained attractive. The system was deployed and retrieved after 1 to 5 days (preferably 48 h) on the bottom (Table 5.1). A low-frequency acoustic signal sent from the ship activated release of the ballast and the ATS was returned to the surface by the buoyancy.

The ATS has provided healthy individuals of necrophagous species that could be reared in aquaria and kept alive for as long as two years.

5.2.2. SAMPLING SITES

The material was collected with the ATS during several cruises of the German icebreaker *Polarstern* in the Southern Ocean:

2 operations (using classical line mooring traps) during the EPOS leg 3 cruise, January-February 1989, in the eastern Weddell Sea (De Broyer and Klages, 1990);

6 operations during the EASIZ I cruise, January-March 1996, in the eastern Weddell Sea (De Broyer et al. 1997);

15 operations during the EASIZ II cruise, January-March 1998, in the eastern Weddell Sea and off South Shetland Islands (De Broyer et al. 1999). In addition to ATS catches, two samples were collected from a classical fish trap, at stations 152 and 266.

6 operations during the cruises ANDEEP 1 and ANDEEP 2, January-March 2002, in the southern Drake Passage, the western Weddell Sea and the Scotia Sea (De Broyer et al. 2003).

Sampling data are presented in Table 5.1. and sampling locations are shown in Fig. 5. 2.

Fig.5.2. Location of the 29 trap deployments. Circles and triangles indicate stations lower and deeper than 1000 m, respectively.

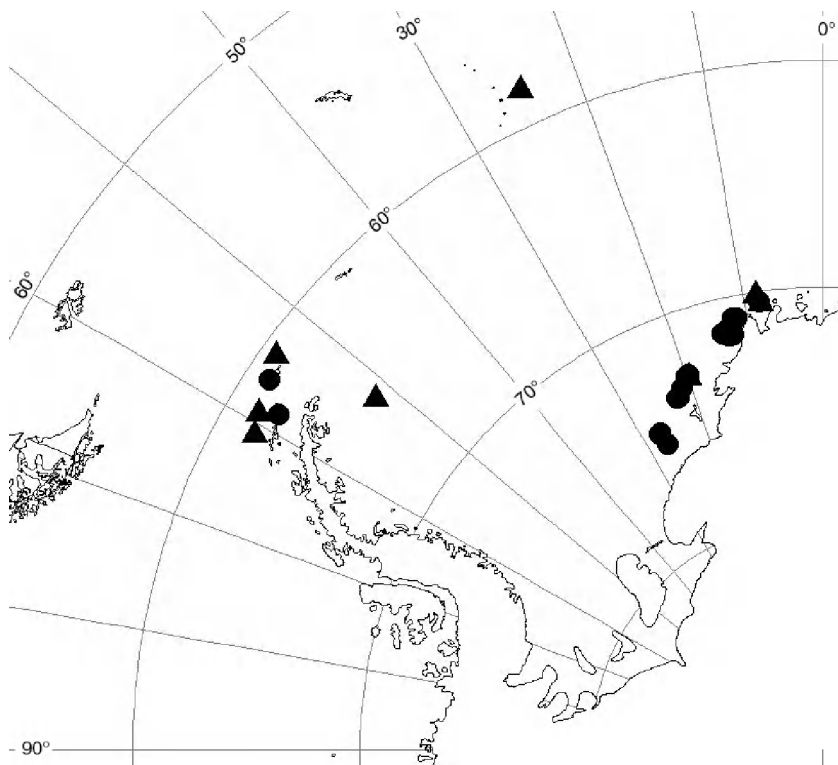


Table 5.1.
Station data for 29 autonomous trap system operations and two fish traps. Italic rows correspond to stations deeper than 1000 m.

Cruise	Station	Date	Area	Location		Depth (m)	Soak Time (h)	Number of specimens
				°S	°W			
EPOS	228 (T2)	28.01.89	Halley Bay	75°14.4'	26°42.1'	399	70	3500
	275 (T4)	15.02.89	Kapp Norvegia	71°39.5'	12°04.4'	236	50	
EASIZ I	04 (T4)	20.02.96	Kapp Norvegia	71°40.6'	12°31.0'	421	132	2924
	05 (T1)	06.02.96	Kapp Norvegia	71°40.2'	12°45.3'	223	23	576
	06 (T2)	07.02.96	Kapp Norvegia	71°31.5'	13°31.4'	234	74	2619
	12 (T3)	13.02.96	Vestkapp	73°15.7'	21°04.8'	791	65	769
	28 (T5)	26.02.96	Kapp Norvegia	71°29.6'	12°21.2'	219	74	2848
	30 (T6)	01.03.96	<i>Atka Bay</i>	<i>70°01.0'</i>	<i>08°16.5'</i>	<i>2009</i>	<i>86</i>	<i>818</i>
EASIZ II	11/25 (T1)	26.01.98	Drescher Inlet	72°50.8'	19°55.5'	377	38	25365
	27/76 (T2)	28.01.98	Kapp Norvegia	71°19.0'	12°24.2'	171	103	10528
	38/75 (T3)	29.01.98	Kapp Norvegia	70°59.0	11°09.1	389	82	765
	094/119 (T4)	05.02.98	Vestkapp	73°35.7'	22°23.4'	813	50	788
	102/122 (T5)	05.02.98	Vestkapp	73°36.0'	22°00.5'	396	46	516
	138/155 (T6)	09.02.98	Halley Bay	74°39.8'	27°13.1'	798	39	3434
	152 (FT)	11.02.98	Halley Bay	74°36.8'	26°53.9'	597		
	160/179 (T7)	11.02.98	Halley Bay	74°40.0'	26°57.9'	403	38	4188
202/233 (T8)	18.02.98	Kapp Norvegia	70°57.0'	11°40.6'	808	58	401	

Cruise	Station	Date	Area	Location		Depth (m)	Soak Time (h)	Number of specimens
				°S	°W			
	203/234 (T9)	18.02.98	Kapp Norvegia	70°58.8'	11°39.4'	442	58	787
	251/267 T10)	22.02.98	Drescher Inlet	72°47.8'	19°31.4'	895	66	1820
	255/268 (T11)	23.02.98	<i>Drescher Inlet</i>	72°48.4'	19°39.6'	1453	58	1642
	266 (FT)	25.02.98	Drescher Inlet	72°50.5'	19°21.8'	419		
	279/283 (T12)	28.02.98	<i>Atka Bay</i>	70°24.1'	07°52.2'	1136	48	75
	280/284 (T13)	28.02.98	<i>Atka Bay</i>	70°27.4'	07°55.9'	550	48	2085
	291/312 (T14)	14.03.98	King George Isl.	62°16.6'	58°15.8'	798	57	451
	292/315 (T15)	14.03.98	King George Isl.	62°11.3'	58°20.2'	414	58	
ANDEEP 1	46	29.01.02	<i>Elephant Isl.</i>	60°39'	53°59'	2926	14	44
	83	07.02.02	Elephant Isl.	61°07'	56°09'	349	72	8597
	100	13.02.02	<i>King George Isl.</i>	61°25'	58°54'	2280	57	171
	114	17.02.02	<i>King George Isl.</i>	61°46'	60°45'	2754	54	36
ANDEEP 2	131	05.03.02	<i>N-W Weddell Sea</i>	65°19'	51°35'	3070	71	129
	139	19.03.02	<i>South Sandwich Trench</i>	58°18'	24°29'	3739	71	1000

5.2.3. FEEDING EXPERIMENTS

Directly after collection, animals were transferred to a cool laboratory (maintained at $-1 \pm 1^\circ\text{C}$), sorted by species and counted. They were then distributed, by groups of 40 to 150, among different aquaria (15 to 200 l) continuously provided with clean fresh sea water.

Several experiments were performed in order to evaluate the feeding rate of four common scavenging Antarctic amphipod species (all lysianassoids, see Table 6). Animals were starved for periods of 9 to 15 days to maximize foregut clearance (as checked from dissected individuals). During this fast, faeces and exuvia were removed daily. After starvation, weighted (and calibrated for dry vs wet weight) food items (pieces of squid or fish) were given *ad lib* every day during experiments lasting 7 to 29 days. Uneaten food was removed after 24 hours, oven-dried and weighed, enabling calculation of mean daily ingestion rates. At the end of last day of experiment, amphipods were sacrificed and oven-dried to obtain their mean individual weight. Results are expressed as $\text{g}_{\text{food-DW}} \cdot \text{g}_{\text{animal-DW}}^{-1} \cdot \text{day}^{-1} \times 100$ (or $\% \cdot \text{day}^{-1}$).

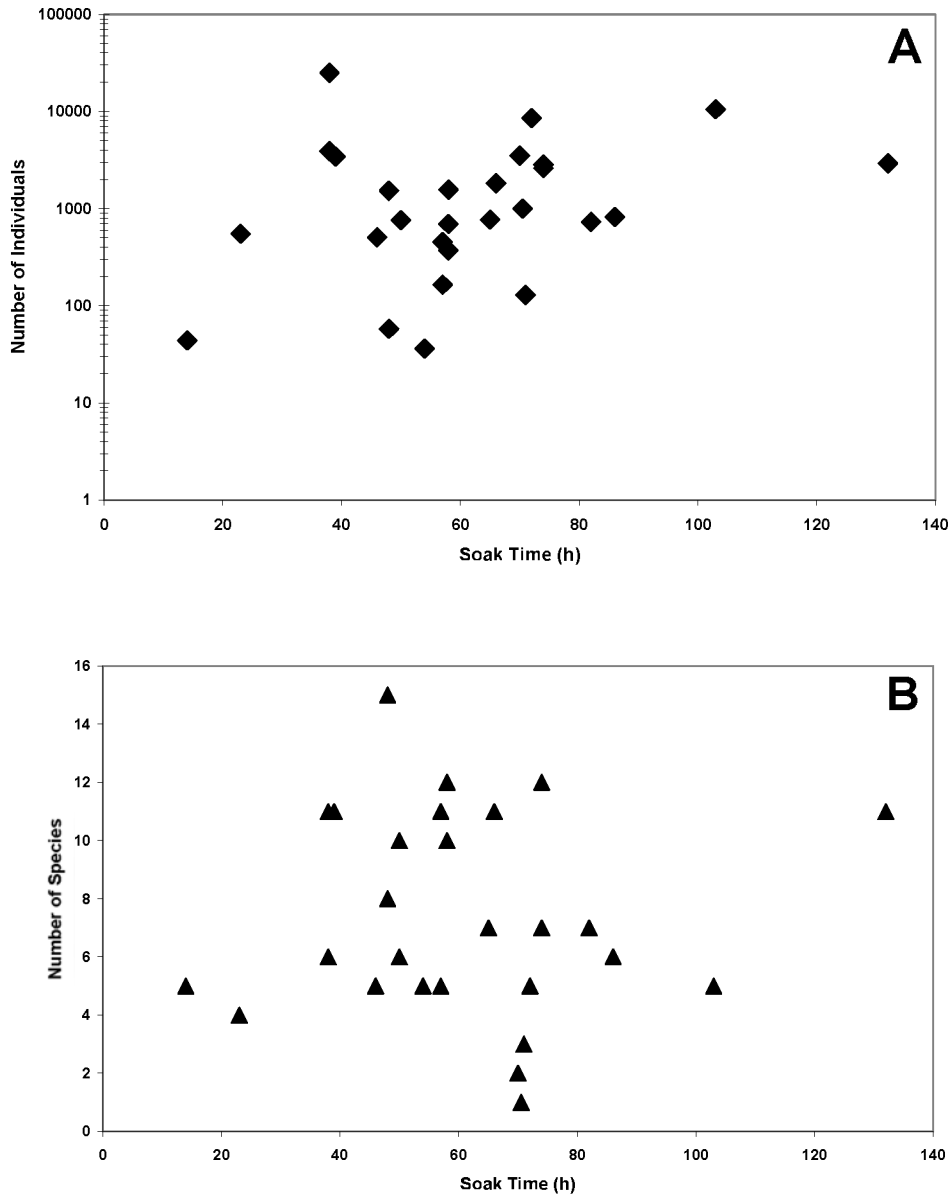
Egestion rates were estimated, in parallel to some feeding experiments, with *Waldeckia obesa* (Chevreux 1905). After a single 24 hour feeding period, a group of animals was placed in nylon gauze baskets (mesh size 2 mm) which allowed faecal pellets to pass through, so to avoid coprophagy. Animals were kept unfed for 5 to 9 days, and faeces were collected twice daily, dried and weighed as above.

5.3. Results and discussion

5.3.1. SAMPLING METHODOLOGY

The ATS is a sampling device which collects roughly "what is scavenging around", *i.e.* the necrophagous organisms able to detect and track the bait odour and living at a distance corresponding to the food odour plume in the water, itself influenced by the direction and velocity of the local bottom current (Sainte-Marie and Hargrave 1987). Several factors, such as bottom topography and related benthic biological community structure, are likely to affect the number and composition of the fauna attracted to bait. Sample size and composition not only depend on these environmental factors, but also on structural ones related to the trap design (mouth opening, mesh size) and relative position of the trap on or above the sea floor. Finally, bait quality and type may attract preferentially some species. The duration of trap deployment has been reported to influence the number of individuals caught, at least initially, when a positive correlation is found (Stockton 1982). However, in our study there was no relationship between the number of individuals or species and soak time for ATS deployments ranging from about 10 to 135 hours (Fig. 5.3.). Possible causes include escape from traps, bait exhaustion, interspecific predation or cannibalism inside the traps (behaviours we observed in restricted aquarium conditions), tidal effects, or simply the local density of the scavenging fauna. Thus the ATS can be considered at best only a semi-qualitative sampler.

Fig. 5.3. Numbers of collected individuals (A) and species (B) vs soak time of the autonomous trap system.



5.3.2. COMPOSITION OF THE SCAVENGER GUILD

The 31 trap sets reported here captured a total of about 70,000 invertebrates from 76 species and 10 specimens of fish from 4 species (Table 5.2).

Table 5.2. Comparison between the number of species and individuals of the different taxonomic groups collected by the autonomous trap system and fish traps at shelf and deep-sea depths.

	ANTARCTIC SHELF	ANTARCTIC DEEP SEA	
	(< 1000m)	(>1000m)	
		EASIZ	ANDEEP
		Eastern Weddell Sea	South Shetland Islands
Campaign	EPOS / EASIZ I & II	South Shetland	Scotia Sea
Locality	Eastern Weddell Sea	Islands	South Sandwich Trench
Depth range	171- 895 m	1139- 2009 m	2280- 3739 m
N trap operations	20	3	5
	N spp (N ind.)	N spp (N ind.)	
CRUSTACEA			
Amphipoda			
Lysianassoidea	37 (~ 65 000)	26 (1374)	
Iphimedioidea	2 (4)	2 (2)	
Eusiridae	2 (7)		
Melphidippidae	1 (1)		
Stegocephalidae		2 (3)	
Isopoda			
Cirolanidae	3 (1547)	1 (4)	
Leptostraca	2 (23)		
Ostracoda	2 (1500)		
Copepoda	2(4)	2 (2)	
Mysidacea	1 (13)		
Decapoda	1(1)		
MOLLUSCA			
Gastropoda		1 (1)	
ECHINODERMATA			
Asteroidea	1(1)		
Ophiuroidea	3(4)		
PISCES			
	3 (7)	3 (3)	

Twenty one trap sets at shelf depths (less than 1000 m) in the eastern Weddell Sea and around South Shetland Islands captured more than 68,000 specimens of crustaceans belonging to 53 benthic and benthopelagic species, 5 specimens of echinoderms and 7 specimens of 3 fish species.

In the deep sea, 8 trap operations on the slope of the eastern Weddell Sea and at bathyal and abyssal depths in the western Weddell Sea, the Scotia Sea and the South Sandwich Trench provided about 1400 crustaceans of 33 species, 1 specimen of a gastropod and 3 specimens of fish.

While the trap samples can be considered representative of the crustacean scavenger fauna, this is not the case for the fish as the traps were suboptimal in terms of size and entrance diameter for collecting them.

Both at shelf depth and in the deep sea (slope and abyssal plain) the bulk of the catches consisted of amphipod crustaceans, in particular lysianassoids. The second dominant group, the cirrolanid isopods, was not represented significantly in the deep-sea samples. A few representatives of other amphipod families (Epimeriidae, Iphimediidae, Eusiridae, Melphidippidae, Stegocephalidae) were collected as well as other crustacean groups, namely Leptostraca, Ostracoda, Copepoda, Mysidacea and Decapoda.

The detailed taxonomic composition of the amphipods collected is presented in Tables 5.3. and 5.4. Complete taxonomic references and zoogeographical characterization of the species can be found in De Broyer and Jazdzewski (1993). Within the very diverse superfamily Lysianassoidea, species have been allocated to the different family groups recognized by a recent cladistic analysis (Lowry pers. comm.). On the shelf, a total of 37 lysianassoid species have been collected belonging to 17 different genera. Lysianassoid amphipods are known to comprise a number of scavenger species (e.g. Thurston 1990, Lowry and Stoddart 1989, 1994). Representatives of *Adeliella* and *Allogaussia* were taken in traps for the first time but may be accidental (one unique specimen in each case). Part of the collected species remains to be precisely identified. One new species has been found in each of

the genera *Allogaussia*, *Paracallisoma*, *Pseudorchomene*, *Stephonyx* and *Tryphosella*.

Table 5.3. Amphipod species collected with the autonomous trap system and fish traps at depths shallower than 1000 metres; occurrence by station and depth ranges.

	EPOS	EASIZ I	EASIZ II	Depth range
LYSIANASSOIDEA				
Lysianassidae and Uristidae				
<i>Abyssorhomene charcoti</i> (Chevreux, 1912)		T2		234
<i>Abyssorhomene nodimanus</i> (Walker, 1903)	T4	T2-4-5	T2-4-13	171-813
<i>Abyssorhomene plebs</i> (Hurley, 1965)	T2		T1-5-7-13-14-15	377-798
<i>Abyssorhomene rossi</i> (Walker, 1903)		T4-5	T1-7-9-13	219-550
<i>Adeliella</i> sp.A			152	597
<i>Allogaussia</i> n.sp.1		²	T4	813
<i>Cheirimedon crenatipalmatus</i> Stebbing, 1888		T3	152	389-597
<i>Hippomedon</i> sp.A		T2-5	T6-7-8-9-10-13, 152	219-895
<i>Orchomenopsis cavimanus</i> (Stebbing, 1888) var.A		T4-5	T1 to 10, 13-14, 152	171-895
<i>Orchomenopsis kryptopinguides</i> (Andres, 1983)			T3	389
<i>Orchomenopsis pinguides</i> (Walker, 1903)	T4	T2-5	T2-7	171-403
<i>Parschisturella carinata</i> (Schellenberg, 1926)		T1-2-3-4-5	T3-4-5-6-8-10, 152	219-895
<i>Pseudorchomene coatsi</i> (Chilton, 1912)	T4	T4-5	T1-10,13-14-15, 266	171-895
<i>Pseudorchomene</i> n.sp.1			T4-6-10	798-895
<i>Stephonyx</i> n.sp.1		T3	T4-6-8-10-13	791-895
<i>Tryphosella cf analogica</i> K.H. Barnard, 1932		T3	T6-10	791-895
<i>Tryphosella bispinosa</i> (Schellenberg, 1931)		T2		234
<i>Tryphosella intermedia</i> (Schellenberg, 1926)			T6-7-8-9-10, 152	403-895
<i>Tryphosella longiseta</i> Ren, 1991			T8	808
<i>Tryphosella macropareia</i> (Schellenberg, 1926)		T4	T4-8	421-813
<i>Tryphosella murrayi</i> (Walker, 1903)	T4	T1-2-4	T1-3-7-9-10-13, 266	223-895
<i>Tryphosella</i> n.sp.1			T6	798
<i>Tryphosella</i> sp.A			T4	813
<i>Tryphosella</i> sp.B			T7	403
<i>Tryphosella</i> sp.C			T7	403

	EPOS	EASIZ I	EASIZ II	Depth range
<i>Tryphosella</i> sp.D			T9	442
<i>Tryphosella</i> sp.E		T2-3		234-791
<i>Tryphosella</i> sp.F		T4		421
<i>Tryphosella</i> sp.G		T4		421
" <i>Tryphosella</i> " <i>cicadopsis</i> Schellenberg, 1926			T7-9-13	403-550
" <i>Tryphosella</i> " n.sp.2			T6-13, 152	550-798
<i>Uristes gigas</i> Dana, 1849			T13, 152	550-597
<i>Uristes stebbingi</i> (Walker, 1903)	T4	T2	T2-4	171-813
<i>Waldeckia obesa</i> (Chevreux, 1905)	T2-4	T1-2-3-4-5	T1, 3 to 10, 13, 152	219-895
Eurytheneid family group				
<i>Eurythenes gryllus</i> (Lichtenstein, 1822)		T3	T13-14	550-798
Hirondelleid family group				
<i>Hirondellea antarctica</i> (Schellenberg, 1926)		T1-2-3	T8-13, 152	223-808
Scopelocheiridae				
<i>Paracallisoma</i> n.sp.1			T14	451
IPHIMEDIOIDEA				
Epimeriidae				
<i>Epimeria similis</i> Chevreux, 1912			T10-13, 152	550-895
Iphimediidae				
<i>Iphimediella bransfieldi</i> K.H. Barnard, 1932			266	419
EUSIROIDEA				
Eusiridae				
<i>Eusirus cf antarcticus</i> Thomson, 1880		T2-5	T3-9, 152	219-597
<i>Eusirus bouvieri</i> Chevreux, 1911		T4	T7	403-421
Melphidippidae				
<i>Melphidippa antarctica</i> Schellenberg, 1926			152	597

Table 5.4. Amphipod species collected with the autonomous trap system and fish traps at depths greater than 1000 metres; occurrence by station and depth ranges.

	EASIZ I	EASIZ II	ANDEEP	Depth range
LYSIANASSOIDEA				
Lysianassidae and Uristidae				
<i>Abyssorhomene rossi</i> (Walker, 1903)		T11		1453
<i>Abyssorhomene scotianensis</i> (Andres, T6 1983)		T11-12	100,114,131	1136-3070
<i>Abyssorhomene sp.A</i>			114	2754
<i>Hippomedon sp.A</i>	T6			2009
<i>Hippomedon sp.B</i>		T11		1453
<i>Orchomenopsis cavimanus</i> (Stebbing, 1888) var.A		T11-12	100,131	1136-3070
<i>Orchomenopsis n.sp.1</i>			46	2926
<i>Parschisturella carinata</i> (Schellenberg, 1926)		T11-12		1136-1453
<i>Pseudorhomene coatsi</i> (Chilton, 1912)		T11	100	1453-2280
<i>Pseudorhomene n.sp.1</i>		T11		1453
<i>Stephonyx n.sp.1</i>		T11-12		1136-1453
<i>Tryphosella cf analogica</i> K.H. Barnard, 1932		T11-12		1136-1453
<i>Tryphosella sp.C</i>		T12		1136
<i>Tryphosella sp.H</i>			100	2280
<i>Tryphosella sp.I</i>			100	2280
<i>Tryphosella sp.J</i>			100	2280
" <i>Tryphosella</i> " n.sp.2		T11		1453
<i>Tryphosinae gen. sp.A</i>		T11		1453
Alicellid family group				
<i>Alicella n.sp.1</i>			100	2280
<i>Paralicella cf caperesca</i> Shulenberger & Barnard, 1976			46	2926
<i>Paralicella n.sp.1</i>			100,114	2280-2754

	EASIZ I	EASIZ II	ANDEEP	Depth range
Eurytheneid family group				
<i>Eurythenes gryllus</i> (Lichtenstein, 1822)	T6	T11-12	46,100,114, 131,139	1453-3739
Hirondelleid family group				
<i>Hirondellea antarctica</i> (Schellenberg, 1926)		T12		1136
<i>Hirondellea n.sp.1</i>			100	2280
Scopelocheridae				
<i>Paracallisoma n.sp.1</i>			100	2280
<i>Scopelocheirus sp.A</i>			46,100,114	2280-2926
IPHIMEDIOIDEA				
Epimeriidae				
<i>Gen. sp.A</i>			46	2926
Iphimediidae				
<i>Iphimediella sp.A</i>	T6			2009
Stegocephalidae				
<i>Gen.sp.C</i>	T6			2009
<i>Gen.sp.D</i>	T6			2009

In the deep sea, 26 lysianassoid species from 15 genera were found, with one new species in each of the following genera: *Alicella*, *Hirondellea*, *Orchomenopsis*, *Paralicella* and “*Tryphosella*” in addition to the 4 new species occurring also in the shelf zone.

Single species of Epimeriidae and Iphimediidae have been found in each depth zone. There is no previous record of Epimeriidae in baited traps except for *Epimeria cf. cornigera* (Jones et al. 2003) and *Epimeria similis* (Dauby et al. 2001a). Stomach content analysis of the latter species by the same authors revealed the presence of various food items such as cnidocysts of hydrozoans and actiniids, sponge spicules, polychaete setae and planktonic cells (diatoms and foraminifers) but also of pieces of fish flesh in individuals captured in traps. Iphimediidae have never been taken in baited traps and their trophic ecology generally characterises them as being specialist micropredators (Coleman 1989a, 1989b, Dauby et al. 2001a). They were probably caught accidentally in traps.

Few Eusiridae are regular scavengers (e.g. Chevreux 1935, Vader 1972, Bowman 1974). Some *Eusirus* species have been recorded in traps in Admiralty Bay, King George Island (De Broyer unpubl.) and on the shelf off Enderby Land (Takeuchi et al. 2001). Examination of feeding behaviour and stomach contents showed that *E. cf. antarcticus*, for instance, is a selective macropredator able to feed partially on carrion (Dauby et al. 2001a).

Melphidippa antarctica is a passive suspension feeder (Dauby et al. 2001a) and the unique specimen was quite probably collected accidentally in trap.

Stegocephalidae are mostly micropredators associated with diverse benthic sessile invertebrates, while some species have been reported to be occasional scavengers (Berge and Vader 2003). They are, however, not taken commonly in traps except for some species of *Andaniotes* and *Austrocephaloides* (Berge and Vader 2001, Berge pers. comm.). Takeuchi et al. (2001) found *Parandania boeckii* (Stebbing 1888) and *Euandania gigantea* (Stebbing 1883) in their abyssal trap off Enderby Land. Both species are meso- or

bathypelagic and rarely if ever taken in baited traps. Some specimens of *Euandania* were also found by Thurston (*pers. comm.*) in bathyal and abyssal trap catches in the Atlantic Ocean.

Species diversity is high in the scavenger guild on the Antarctic shelf (eastern Weddell Sea), in particular in crustaceans, i.e. in comparison with catches at shallower depths, such as those reported by Presler (1986) in the sublittoral of King George Island, who found 5 species of amphipods and 2 of isopods. Nemerteans, gastropods, and echinoderms (asteroids, ophiuroids, echinoids and holothuroids) occur frequently in traps at depths of less than 100 m (*e.g.* Arnaud 1970, Presler 1986, De Broyer *unpubl.*). These groups were not represented in our catches at shelf, slope or abyssal depths except for five specimens of echinoderms and a single gastropod respectively found on the Weddell Sea shelf and slope.

The higher species richness seems also to hold true when eastern Weddell Sea shelf data are compared with other Antarctic catches at similar depths (*e.g.* Arnaud 1970, Stockton 1982, Nagata 1986, Takeuchi et al. 2001). Arnaud (1970), for instance, found only a few tens of amphipods of two species (*Abyssorchomene plebs* and *A. rossi*), one specimen of two species of pycnogonid and of one species of fish at a depth of 320 m off Terre Adélie. Stockton (1982) recorded five species of amphipods (among which four lysianassoids) and one mysid under the Ross Ice Shelf, while Nagata (1986) collected only four species of lysianassoids near Syowa Station (Lützow-Holm Bay, East Antarctica). Takeuchi et al. (2001) found 7 species of amphipods (6 lysianassoids, 1 eusirid), 2 of isopods (Cirolanidae, Gnathiidae), 1 mysid, 3 ostracods, 1 copepod, 1 leptostracan and 2 species of nototheniid fish in two trapsets on the shelf (171 and 353 m) off Enderby Land. The general composition of the scavenger fauna thus appears quite similar between the eastern Weddell Sea and Enderby Land but more amphipods have been recorded in the former, which may at least partly be due to the larger number of trapsets analysed from the Weddell Sea (18 vs 2).

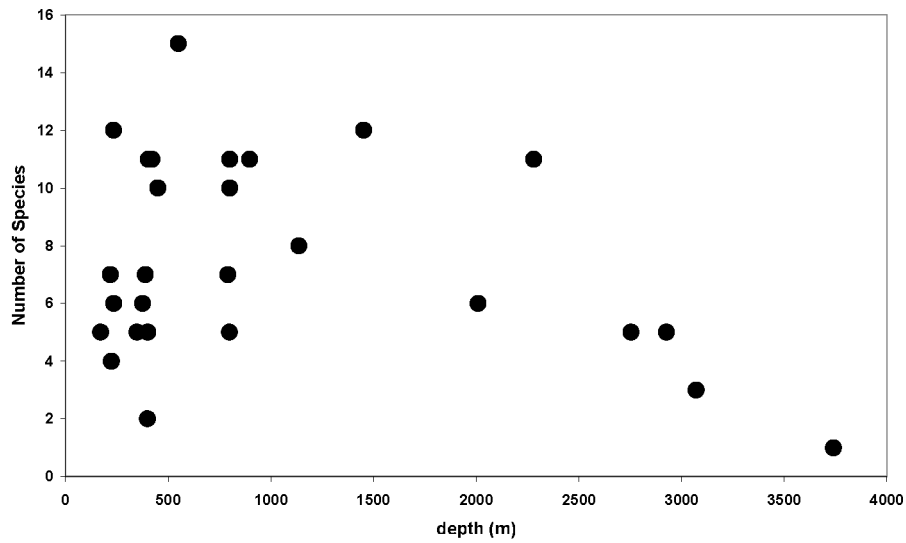
In the Antarctic abyssal waters (3000 m or deeper) the species richness of the scavenger guild appears to be less than documented from abyssal trap collections elsewhere in the world. The three ANDEEP trapsets close to or deeper than 3000 m provided only 5 species of necrophagous amphipods (Table 4) and Takeuchi et al. (2001) reported 5 amphipod and 1 isopod species. In comparison, the 44 trap-sets at 3144-5940 m in the northeastern and tropical Atlantic Ocean analysed by Thurston (1990) yielded 15 different species (13 lysianassids, 1 scopelocheirid, 1 valettiettid), which constitute the largest abyssal trap record. Thurston's record, however, concerned several distinct abyssal plains and a much wider bathymetric range, prospected with many more trap-sets.

On the other hand, the Antarctic slope (1000-3000 m) appears to be richer in scavenger species than elsewhere in the world at similar depth range. Thirty one amphipod species have been collected (18 in the eastern Weddell Sea) versus e.g. 6 amphipods species (all lysianassoids) on the Gulf of Biscay slope (200-1800 m depth; Desbruyères et al., 1985), 11 amphipod species (9 lysianassoids, 1 eusirid, 1 tironid) found in baited traps by Vinogradov (1997) on the slope of the Norwegian Sea (1690 m) or 5 amphipod species (4 lysianassoids, 1 epimeriid) collected by traps in the deep Cretan Sea (1511-2485 m depth; Jones et al. 2003).

It must be kept in mind in such comparisons that trap sampling is by no means quantitative, as remarked above, and that repeated sampling may yield more species.

The relation between species richness of necrophagous amphipods and depth is shown in Fig. 5.4. This figure clearly shows the variability of amphipod richness in coastal and shelf traps and its reduction from the shelf down-slope to the abyssal zone.

Fig. 5.4. Relation between species richness of necrophagous amphipods and depth.



A number of species occurred on both the shelf and the slope showing in some cases a quite extended level of bathymetry: *Abyssorchomene rossi* (219-1453 m), *Eurythenes gryllus* (550-3789 m), *Hippomedon* sp.A (389-2009 m), *Hirondellea antarctica* (223-1136 m), *Orchomenopsis cavimanus* var.A (171-3070 m), *Paracallisoma* n.sp.1 (451-2280 m), *Parschisturella carinata* (219-1453 m), *Pseudorchomene coatsi* (171-2280 m), *Pseudorchomene* n.sp.1 (798-1453 m), *Stephonyx* n.sp.1 (791-1453 m), *Tryphosella* cf *analogica* (791-1453 m), *Tryphosella* sp.C (403-1136 m), “*Tryphosella*” n.sp.2 (550-1453 m). In the Southern Ocean, *E. gryllus* is the only scavenger species found on the shelf, the slope and in the abyssal zone (see also Takeuchi et al. 2001). The latter species is a panoceanic bathyal (on seamounts, as shallow as 1440 m, Bucklin et al. 1987), abyssal and hadal stenotherm species which can occur far above the sea floor (Thurston 1990). It has been found in both polar regions at bathyal and abyssal depths (e.g.

Bowman and Manning 1972, Paul 1973, Hargrave et al. 1992, De Broyer et al. 1999) and in bird stomachs (see Rauschert 1985).

Arnaud (1970) observed some seasonality in the presence or abundance of several scavengers in the Terre Adélie catches (16 to 120 m): *Waldeckia obesa* was much more abundant in traps in winter than in summer and this could indicate a seasonal shift in diet or a migration. *W. obesa* was abundant in the Weddell Sea at shelf depths (171-895 m) during summer, suggesting migration or local movement as a most like cause (see Bregazzi 1972, Slattery and Oliver 1986).

5.3.3. MORPHOLOGICAL ADAPTATIONS TO NECROPHAGY

Morphological analysis of the amphipod species collected in traps (Tables 5.3. and 5.4.) has shown several types and degrees of adaptation to a necrophagous mode of life, thus confirming previous observations and interpretations (Dahl 1979, Thurston 1979, De Broyer 1983). The typical eco-functional adaptations to necrophagy are summarized briefly in Table 5.5. No attempt is made here to document detailed differences in chemosensory organs (in particular callynophores, see Lowry 1986, Meador 1981) or mechanoreceptors (Klages et al. 2002). The focus is on the morphology of the mandible and the digestive tract.

Table 5.5. Morphological and physiological adaptations of scavenging amphipods with respect to behavioural constraints.

<i>Typical behavioural sequence of scavengers</i>	<i>Morphological and physiological adaptations</i>
Detecting and locating carrion source	Chemosensory organs (callynophores) Mechanoreception organs
Arriving (quickly) to carrion	Good swimming ability
Ingesting (quickly)	Cutting mandible
Storing food	Enlarged foregut or midgut

Typical behavioural sequence of Morphological and physiological scavengers adaptations

Feeding opportunities

Unpredictable

Resistance to starvation

Reduced metabolism

Mandible morphology appears of primary importance in amphipod evolution in general and in the scavenger feeding types in particular (Dahl 1979, De Broyer 1985b, Barnard and Karaman 1991, Watling 1993). The evolutionary trend toward necrophagy is marked by several transformations of the mandible from the relatively basic type found in the opportunistic scavengers *Orchomenopsis* (e.g. *O. obtusa*; see Olerod, 1975) or *Abyssorchomene* to the types found in the deep sea species that are obligate scavengers *Eurythenes*, *Hirondellea* and *Paralicella* (Dahl 1979, Thurston 1979, De Broyer 1983). The following morphological transformations are considered adaptations to necrophagy:

- widening and sharpening of the incisor cutting edge;
- modification of the molar process from a relatively basic subcolumnar type with oval triturative surface (*Orchomenopsis*; see Olerod 1975, Fig. 62 & 63) to the ridge-shaped type with elongate and reduced triturative surface (*Abyssorchomene*; see Dahl 1979, Fig. 9), and ultimately to the non triturative semitubular or “flap-like” setiferous molar found in *Hirondellea* or *Eurythenes* respectively (see Dahl 1979, Fig. 5 & 6);
- transformation of the flat mandibular body found in *Orchomenopsis* to the strongly bowl-shaped type found in *Eurythenes* or in *Alicella* (see De Broyer and Thurston 1987). Together with the development of the raker spine row and the setal row prolonging the molar, and the widening of the incisor, this adaptation allows relatively large fragments or shreds of food to be passed directly into the oesophagus (Thurston 1979, De Broyer and Thurston 1987). In common with the present deep sea material, all the abyssal scavenger species recorded by Thurston (1990) with the exception of *Valettieta gracilis*

have a mandibular molar considerably modified from the basic gammaridean pattern.

Another important adaptation to necrophagy is the development of the storage capacity of either the foregut, *e.g.* in *Abyssorchomene* or the midgut in *Eurythenes*, *Hirondellea* or *Paralicella* (Dahl 1979, De Broyer 1983). The “storing stomodeum” extending along the whole length of the pereion has been found in most lysianassid and uristid species we collected from shelf and deep-sea traps: *Abyssorchomene*, *Hippomedon*, *Parschisturella*, *Pseudorchomene*, *Tryphosella*, *Uristes* and *Waldeckia*. In *Orchomenella* (*Orchomenopsis*) it extends to the fourth pereionite.

Because several steps can be detected along the evolutionary pathway to the necrophagous mode of life in amphipods, it seems obvious from the morphological comparison of the different scavenger groups (in particular: eurytheneids, hirondelleids, alicellids, scopelocheiridae) that these adaptations arose independently several times during the evolution within the Lysianassoidea.

Previous studies have shown that baited traps attracted facultative, opportunistic scavengers as well as (presumed) obligate scavengers (*e.g.* Arnaud 1970, Britton & Morton 1994, Dauby et al. 2001a). The distinction between the two categories on the basis of morphological traits is by no means straightforward in amphipods. Mandible and gut morphology can help indicate scavenger status, but only within certain limitations. Eurytheneids, alicellids, some Lysianassidae such as *Waldeckia obesa* are considered to be exclusive scavengers. Within the genus *Hirondellea*, for instance, which has a typical advanced scavenger-type mandible, deep-sea species probably are exclusive scavengers (Hessler et al. 1978). However, the shelf species *H. antarctica* is collected regularly in traps but is supposed to be mainly a micropredator on hydrozoans and sea anemones (Dauby et al. 2001a). *Abyssorchomene plebs* is frequently taken and sometimes is extremely abundant in bottom traps (*e.g.* Rakusa-Suszczewski 1982, De Broyer and

Klages 1990). This species, as well as the less common *A. rossi*, are typical benthopelagic species that are also able to prey on copepods, salps and coelenterates in the water column (Dauby et al. 2001a). These *Abyssorchomene* species can feed on phytoplankton and microzooplankton organisms (Hopkins 1985, 1987) presumably aggregated prior to ingestion (see Riebesell et al. 1991) as these species have no filtering appendages.

Stomach content studies of animals from trap collections, as well as fatty acid and stable isotope analyses (Graeve et al. 2001, Nyssen et al. 2002), have revealed that the opportunistic scavengers may be primarily predators (e.g. *Eusirus antarcticus*, *E. bouvieri*, *Hirondellea antarctica*, *Tryphosella murrayi*) or mainly deposit feeders (e.g. *Uristes gigas*).

5.3.4. BATHYMETRIC DISTRIBUTION

The bathymetric distribution of amphipods collected in traps in the eastern Weddell Sea is given in Fig. 5.5 (next page). The chart is not representative of the complete bathymetric distribution of these species as it does not include depth records from other gears.

In terms of bathymetric distribution, the trap results (Fig. 5.5, next page) may indicate a faunal break for scavenger amphipods at a depth of about 800 to 1000 m in the eastern Weddell Sea that may be related to the shelf break depth. The same faunal limit is suggested by the scavenger isopod distribution (Fig. 5.6).

Fig. 5.6. Bathymetric distribution of cirrolanid isopods collected with the autonomous trap system in the eastern Weddell Sea.

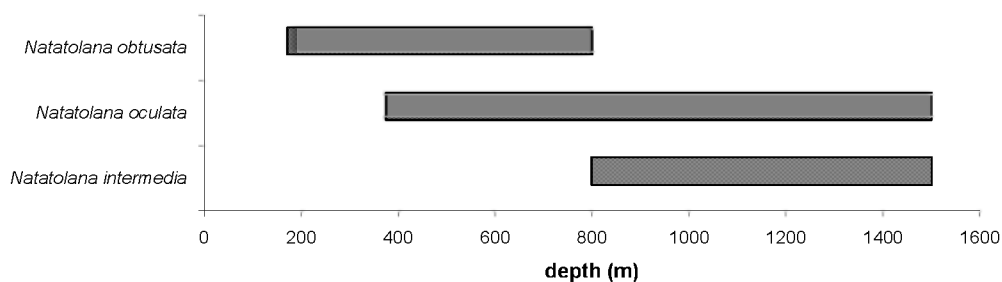
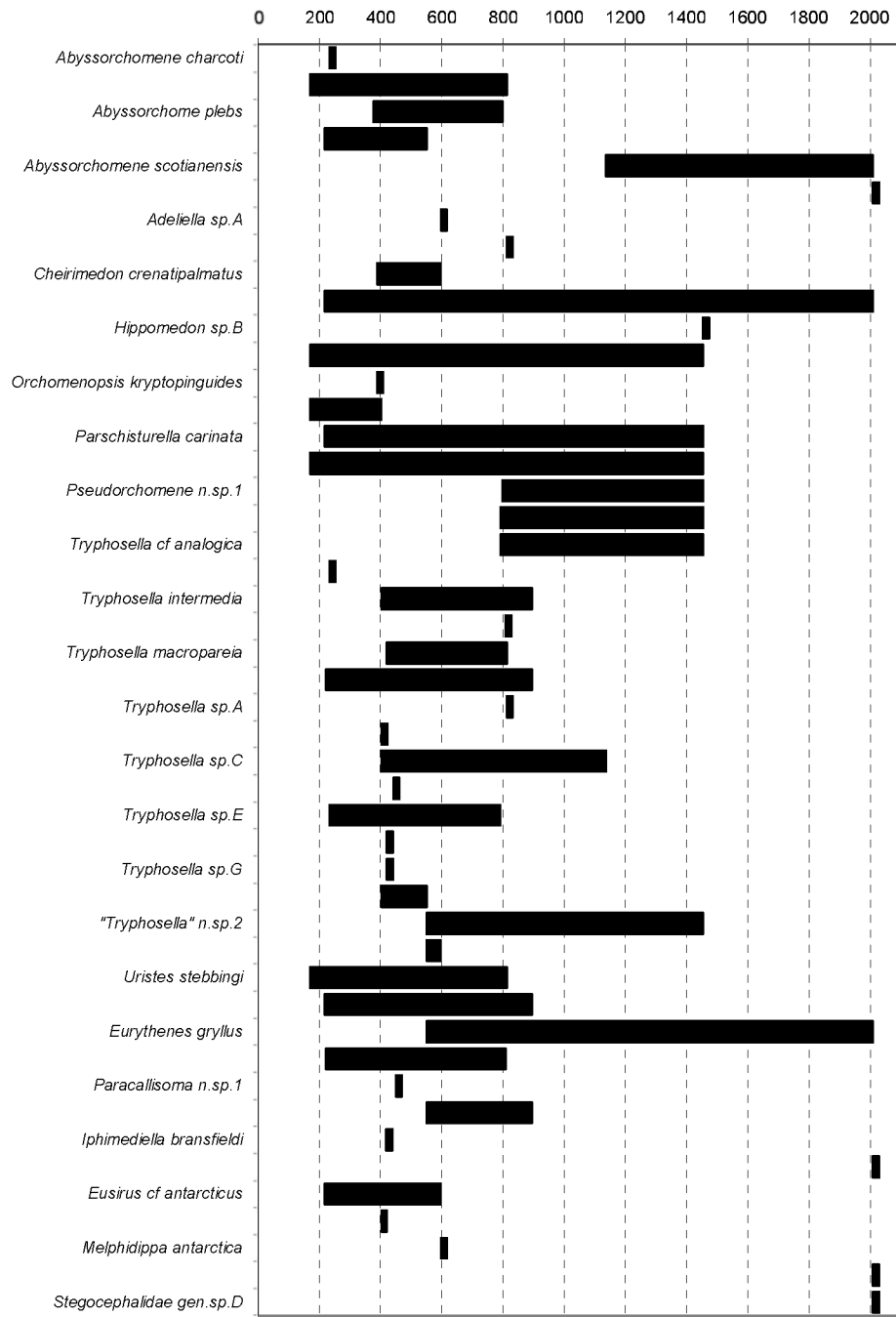


Fig. 5.5. Bathymetric distribution of amphipods collected with the autonomous trap system in the eastern Weddell Sea.



5.3.5. FEEDING EXPERIMENTS

Table 5.6 gives the mean (and range) of the average feeding rates (in % dry weight.day⁻¹) measured during several experiments for the 4 studied species of Lysianassoidea. The egestion rate and digestion efficiency (both in % of ingested food) are given for *Waldeckia obesa*. Available data for other Lysianassoidea are also reported.

Table 5.6. Estimated and reported feeding rates of scavenging lysianassoid amphipods. F: given food, N: number of experiments, FR: feeding rate (%body dry weight.day-1), MS: meal size (% body weight), ER: egestion rate (% food.day-1), DE: digestion efficiency (% food)

species	F	N	FR	MS	ER	DE	reference
<i>Abyssorchomene nodimanus</i>	squid	5	4.1 (2.5 – 5.1)				<i>this study</i>
<i>Parschisturella carinata</i>	squid	5	1.9 (1.3 – 2.7)				" "
<i>Tryphosella murayi</i>	fish	8	2.1 (0.4 – 4.5)				" "
	squid	14	1.4 (0.9 – 4.5)				" "
<i>Waldeckia obesa</i>	fish	3	3.1 (2.6 – 10.4)		33	67	" "
	squid	10	2.2 (1.0 – 7.7)				" "
<i>Eurythenes gryllus</i>	fish			30 – 60			Hargrave, 1985
	fish			up to 150			Meador, 1981
<i>Anonyx sarsi</i>	squid			10 – 37			Sainte-Marie, 1987
<i>Anonyx</i> sp.	squid			10 – 18			Sainte-Marie et al., 1989
<i>Orchomenella pinguis</i>	squid			11 – 33			Sainte-Marie et al., 1989
<i>Onisimus litoralis</i>	squid			9 – 11			Sainte-Marie et al., 1989
<i>Alicella gigantea</i>	fish			12			De Broyer and Thurston, 1987

It appears that feeding rates (averaged for each single experiment) encompass relatively large variations, ranging from 0.4 to 10.4 % \cdot day⁻¹. These variations could be explained partly by the differences in the duration of the experiments (from 7 to 29 days, see Fig. 8), and by the fact that the number of experiments differed from species to species. The mean rate (averaged over all the different experiments), however, was not very different among the four species. The type of food given (squid vs fish) influences this rate but the difference is not statistically significant. However, it has been shown (Moore 1994) that *Orchomenopsis zschau* digested soft tissues far more rapidly than epidermal material.

Fig. 5.7. Day-to-day variations of the mean feeding rate (in % dry weight \cdot day⁻¹) of the scavenging lysianassid *Abyssochomene nodimanus* (group of 50 individuals) during an aquarium experiment. Day 1 is the day following the starvation period.

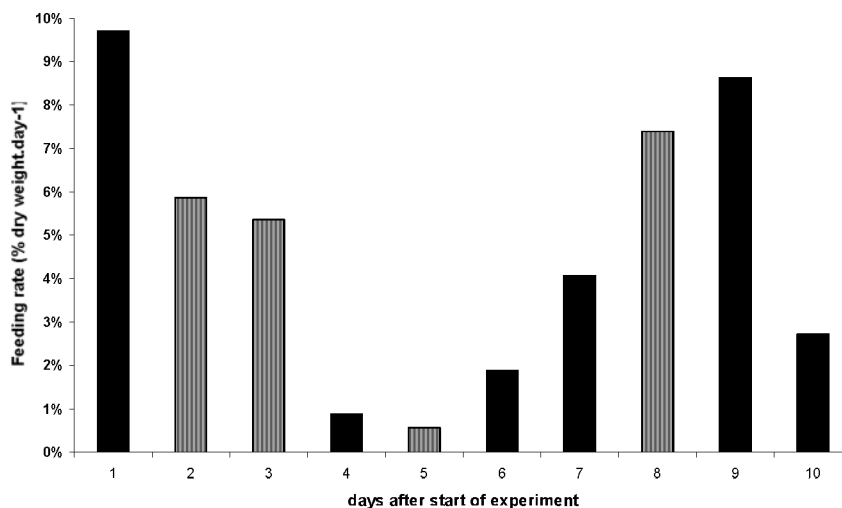
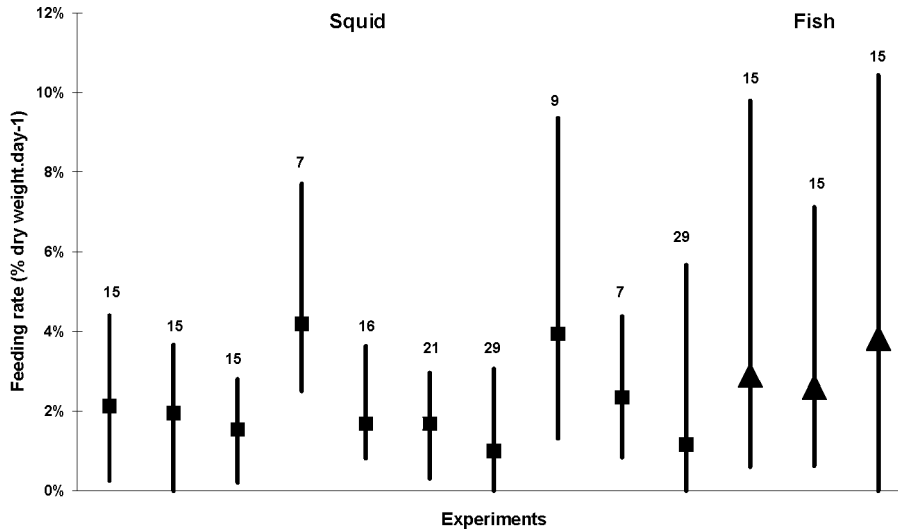


Fig. 5.8. Between experiment variations of the feeding rate (in % dry weight.day⁻¹) of a scavenging lysianassid (*Waldeckia obesa*). Lines show the range of the day-to-day variations; symbols show the mean values (square: fed with squid; triangles: fed with fish). Numbers above the lines give the durations (in days) of experiments.



It is difficult to compare our estimates with literature data, as the latter are expressed in a different way, usually referring to meal size (*vs* body mass) often inferred from *in situ* camera observations (*e.g.* Hargrave 1985). This kind of estimate is made by offering scavengers a large quantity of bait and evaluating the ingested mass over short periods of time. It does not take into account eventual periods of lower feeding activity, such as we observed in aquaria (see below), and is thus a measure of instantaneous ingestion capacity rather than an estimate of feeding rate over longer periods. This may explain the differences between the two sets of values.

The feeding rate of a group of individuals from a given species varied strongly from day to day (Fig. 5.7). Following starvation, lysianassids feed initially at a high rate (up to 15%.day⁻¹ for some species) but afterwards, this

rate decreases gradually over a period of 4 to 8 days, depending on species. A subsequent increase rate is observed, followed again by a decrease. This kind of rhythm, alternating between periods of intense feeding activity and periods of quasi fasting, may be related to the time needed for digesting part of the ingested food or at least for clearance of the foregut. This behaviour could also suggest that tested scavenging amphipods are "topping up" whenever food is available, which would be consistent with a low level of dependency on necrophagy and a plug-flow feeding/digestion strategy (see Penry and Jumars 1987). At the opposite, the gluttonous feeding reported for *e.g.* *Eurythenes* or *Anonyx* in the literature (Table 5.6) is consistent with a high level of dependency on necrophagy and a batch feeding/digestion strategy. It must be pointed out, however, that on the basis of digestive tract observations (Dauby et al. 2001a) species such as *Abyssorchomene nodimanus*, *Parschisturella carinata* or *Waldeckia obesa* have been reported to be obligate –or at least preferential– necrophages.

On the other hand, feeding rates can vary by a factor of 4 to 5 among different experiments on the same species (Fig. 5.8). A huge food intake of bait may occur in the trap (see Table 5.6, meal size), that might be responsible for satiation of some collected animals and for a low feeding rate in aquarium experiments, even after a week-long starvation period. Animals maintained in aquaria can survive unfed for months (Chapelle et al. 1994).

The mean feeding rates, based on our experiments, vary between 1 and 5 % dry weight.day⁻¹, regardless of species. Very few data on digestion and assimilation rates of scavenging lysianassoid amphipods exist in the literature. Sainte-Marie (1992), assuming complete assimilation of the food bolus, calculated that for *E. gryllus* between 8.3 and 17.8 days would be required for complete digestion and assimilation of one meal. Hargrave et al. (1995) estimated from exponential curves fitted to decreases in gut contents of the same species, that digestion would be 95% complete within 15-46 h in the Canada Basin, and within 99-255 h in the Nares and Sohm Abyssal Plain.

Comparing the organic matter in bait and in well-digested gut contents, they estimated a digestion efficiency of 85%, which is not very different from the value we obtained for *W. obesa*, i.e. 67%, using another method. Rapid digestion, associated with liquefaction of food, would enable amphipods to regain mobility as soon as possible after feeding, which is advantageous for these opportunistic feeders in food-poor environments (McKillup and McKillup 1994, Hargrave et al. 1995).

Considering the numerous and diverse benthic fauna recorded on the Antarctic shelf (see Gutt *et al.* 2000) it appears that relatively few species, mostly lysianassoid amphipods, are attracted to baited traps. Similar observations were made in the high Arctic (Legezynska et al. 2000). Some species may occur in huge numbers (*e.g.* Slattery and Oliver 1986, who claimed 264,000 *Abyssorchomene plebs* in a single trap) indicative either of high local densities that are difficult to precisely evaluate, or of low chemosensory thresholds and high mobility allowing some species to congregate from large areas of bottom. The apparently significant role of the scavenger guild in the rapid dispersal of organic matter over the Antarctic shelf and deep-sea bottoms remains to be quantified more precisely.

Acknowledgements

This research was supported by the Scientific Research Programme on the Antarctic (Phases IV and V) of the Belgian Federal Science Policy (contracts n° A4/DD/B02 and EV/36/24A). Samples were collected during the European '*Polarstern*' Study (EPOS), sponsored by the European Science Foundation and the Alfred-Wegener-Institut für Polar- und Meeresforschung (AWI, Bremerhaven, Germany), during both EASIZ I & II campaigns (Ecology of the Antarctic Sea-Ice Zone), sponsored by AWI, and during the three consecutive cruises ANDEEP I, ANDEEP II (Antarctic Benthic Deep-

Sea Biodiversity) and LAMPOS (Latin America *Polarstern* Study). We are indebted to the Officers and Crews of RV *Polarstern* for their skillful support of the sampling effort.

We would like to thank Profs. Wolf Arntz and Dieter Fütterer (AWI) and Prof. Angelika Brandt (Univ. Hamburg) for the invitation to participate to these cruises. Thanks are also due to Drs Dieter Gerdes, Michael Klages, Thomas Brey, Julian Gutt (AWI), Brigitte Hilbig (Univ. Hamburg), as well as all colleagues who helped in collecting, sorting and analysing the samples. Our colleagues from IRScNB, Drs. Yves Scailteur and Gauthier Chapelle are acknowledged for their efforts in performing feeding experiments. The ATS system could not be built without the *savoir-faire* of Camille Jamar. Thierry Kuyken and Angelino Meerhaeghe greatly helped in finalising figures and tables. We are grateful to Profs. Geoff Moore (Millport, UK), Mike Thurston (Southampton, UK), Wim Vader (Tromsø, Norway) and an anonymous referee who carefully and critically read and improved the manuscript.

This is ANDEEP contribution No. 20, and MARE publication No. 45.

References

- Arnaud PM (1970) Feeding and ecological significance of necrophagy among the benthic species of Antarctic coastal waters. In: Holdgate M.W. (Ed.) Antarctic Ecology, 1. Academic Press, London, pp 259-267
- Arntz W, Gutt J (Eds) (1997) The Expedition ANTARKTIS XIII/3 (EASIZ I) of "Polarstern" to the Eastern Weddell Sea in 1996. Ber Polarforsch 249: 1-148
- Arntz, W., Gutt, J. (Eds), 1999. The expedition ANTARKTIS XV/3 (EASIZ II) of RV "Polarstern" in 1998. Ber Polarforsch 301: 1-229
- Barnard JL, Karaman GS (1991) The families and genera of marine gammaridean Amphipoda (except marine gammaroids). Rec Austr Mus 13: 1-866
- Bellan-Santini D (1998). Ecology. In: Ruffo S (Ed), The Amphipoda of the Mediterranean, Part 4. Mém Inst Océanogr, Monaco 13: 869-893
- Berge J, Vader W (2001) Revision of the amphipod (Crustacea) family Stegocephalidae. Zool J Lin Soc 133: 531-592
- Berge J, Vader W (2003) Stegocephalidae (Crustacea: Amphipoda) from Australia and New Zealand, with description of eight new species. Rec Austr Mus 55: 85-112
- Biernbaum CK, Wenner EL (1993) Trapping of necrophagous crustaceans on the upper continental slope off South Carolina, U.S.A. J Crust Biol 13: 601-608
- Bowman TE (1974) The "sea flea" *Dolobrotus mardenis* n.gen., n.sp., a deep-water American lobster bait scavenger (Amphipoda, Eusiridae). Proc Biol Soc Wash 87: 129-138
- Bowman TE, Manning RB (1972) Two arctic bathyal crustaceans: the shrimp *Bythocaris cryonesus* new species, and the amphipod *Eurythenes gryllus*, with in situ photographs from ice island T-3. Crustaceana 23: 187-201
- Brandt A, De Broyer C, Gooday AJ, Hilbig B, Thomson MRA (2003) Introduction to ANtartic benthic DEEP-sea biodiversity (ANDEEP): colonization history and recent community patterns. Ber Polarforsch 470: 45-49
- Bregazzi PK (1972) Life cycle and seasonal movements of *Cheirimedon femoratus* (Pfeffer) and *Tryphosella kergueleni* (Miers)(Crustacea: Amphipoda). Brit Antarctic Surv Bull 30:1-34
- Britton JC, Morton B (1994) Marine carrion and scavengers. Oceanog Mar Biol: An Rev 32: 369-434

- Bruchhausen PM, Raymond JA, Jacobs SS, DeVries AL, Thorndike EM, Dewitt HH (1979) Fish, crustaceans, and the sea floor under the Ross Ice Shelf. *Science* 203: 449-450
- Bucklin A, Wilson Jr RD, Smith Jr KL (1987) Genetic differentiation of seamount and basin populations of the deep-sea amphipod *Eurythenes gryllus*. *Deep-Sea Res* 34: 1795-1810
- Chapelle G, Peck LS, Clarke A (1994) Effects of feeding and starvation on the metabolic rate of the necrophagous Antarctic amphipod *Waldeckia obesa* (Chevreux, 1905). *J exp mar Biol Ecol* 183: 63-76
- Chevreux E (1935) Amphipodes provenant des campagnes scientifiques du Prince Albert I^{er} de Monaco. Résultats des Campagnes scientifiques accomplies sur son Yacht par Albert I^{er} Prince Souverain de Monaco 90: 1-214
- Clarke A, Johnston NM (2003) Antarctic marine benthic biodiversity. *Oceanogr mar Biol: annu Rev* 41, 47-114
- Coleman CO (1989a) On the nutrition of two Antarctic Acanthonotozomatidae (Crustacea: Amphipoda). *Polar Biol* 9: 287-294
- Coleman CO (1989b) *Gnathiphimedia mandibularis* K.H. Barnard 1930, an Antarctic amphipod (Acanthonotozomatidae, Crustacea) feeding on Bryozoa. *Antarct Sci* 1: 343-344
- Dahl E (1979) Deep-sea carrion feeding amphipods: evolutionary patterns in niche adaptation. *Oikos* 33: 167-175
- Dauby P, Scailteur Y, De Broyer C (2001a) Trophic diversity within eastern Weddell Sea amphipod community. *Hydrobiologia* 443 : 69-86
- Dauby P, Scailteur Y, Chapelle G, De Broyer C. (2001b) Potential impact of the main benthic amphipods on eastern Weddell Sea shelf ecosystem (Antarctica). *Polar Biol* 24 : 657-662
- De Broyer C (1983) Recherches sur la systématique et l'évolution des crustacés amphipodes gammarides antarctiques et subantarctiques. PhD Thesis, Catholic Univ., Louvain, Belgium
- De Broyer C (1985a) Amphipodes lysianassoïdes nécrophages des Îles Kerguelen (Crustacea): 1. *Orchomenella guillei* n.sp.. *Bull Mus ntl Hist nat (Sér 4)* 7 : 205-217
- De Broyer C (1985b) Description de *Falklandia* gen. n. de l'Océan Austral et définition des Lysianassoïdea uristidiens (Crustacea, Amphipoda). *Zool Scr* 14: 303-312
- De Broyer C, Jazdzewski K (1993) Contribution to the marine biodiversity inventory. A checklist of the Amphipoda (Crustacea) of

the Southern Ocean. Doc Trav Inst r Sci nat Belg 73 : 1-154

De Broyer C, Klages M (1990) Studies on amphipod biology. In: Arntz, W., Ernst, W., Hempel, I. (Eds.), The Expedition ANTARKTIS VII/4 (EPOS Leg 3) and VII/5 of RV "Polarstern" in 1989. Ber Polarforsch 68: 113-115

De Broyer C, Thurston MH (1987) New Atlantic material and redescription of the type specimen of the giant abyssal amphipod *Alicella gigantea* Chevreux (Crustacea). Zool Scr 16: 335-350

De Broyer C, Rauschert M, Chapelle G (1997). Trophodynamics, biodiversity and gigantism of the amphipod crustacean taxocoenoses. In: Arntz W, Gutt J (Eds.), The Expedition ANTARKTIS XIII/3 (EASIZ I) of "Polarstern" to the Eastern Weddell Sea in 1996. Ber Polarforsch 249: 76-79

De Broyer, C., Rauschert, M., Scailteur, Y., 1999. Structural and ecofunctional biodiversity of the benthic amphipod taxocoenoses. In: Arntz, W., Gutt J (Eds.), The expedition ANTARKTIS XV/3 (EASIZ II) of RV "Polarstern" in 1998. Ber Polarforsch 301: 163-174

De Broyer C, Dauby P, Nyssen F, Martin P (2003) Biodiversity, molecular phylogeny and trophodynamics of amphipod crustaceans in the Antarctic deep-sea. Ber Polarforsch 470: 81-86

Desbryères D, Geistdoerfer P, Ingram CL, Khripounoff A, Lagardère JP (1985) Répartition des populations de l'épibenthos carnivore. In: Laubier L, Monniot C (Eds), Peuplements profonds du Golfe de Gascogne, Campagnes BIOGAS. IFREMER, Brest, pp. 233-251

Gage JD, Tyler PA (1991) Deep-sea biology: a natural history of organisms at the deep-sea floor. Cambridge University Press, Cambridge, 504 pp.

Graeve M, Dauby P, Scailteur Y (2001) Combined lipid, fatty acid and digestive tract content analyses: a penetrating approach to estimate feeding modes of Antarctic amphipods. Polar Biol 24 : 853-862

Guennegan Y, Martin V (1985) Techniques de prélèvements. In: Laubier L, Monniot C (Eds.), Peuplements Profonds du Golfe de Gascogne. IFREMER, Brest, pp. 571-602

Gutt J, Sirenko BI, Arntz WE, Smirnov IS, De Broyer C (2000) Biodiversity of the Weddell Sea: macrozoobenthic species (demersal fish included) sampled during the expedition ANT XIII/3 (EASIZ I) with RV "Polarstern". Ber Polarforsch 372: 1-103

Hargrave BT (1985) Feeding rates of abyssal scavenging amphipods (*Eurythenes gryllus*) determined *in situ* by time-lapse photography. Deep-Sea Res 32: 443-450

- Hargrave BT, Germain P, Philippot JC, Hemon G, Smith JN (1992) Stable elements and ^{210}Po in the deep-sea amphipod *Eurythenes gryllus*. Deep-Sea Res 39: 37-44
- Hargrave BT, Phillips GA, Prouse NJ, Cranford PJ (1995) Rapid digestion and assimilation of bait by the deep-sea amphipod *Eurythenes gryllus*. Deep-Sea Res (I) 42: 1905-1921
- Hessler RR, Ingram CL, Yayanos AA, Burnett BR (1978) Scavenging amphipods from the floor of the Philippine Trench. Deep-Sea Res 25: 1029-1047
- Hopkins TL (1985) Food web of an Antarctic midwater ecosystem. Marine Biol 89: 197-212
- Hopkins TL (1987) Midwater food web in McMurdo Sound, Ross Sea, Antarctica. Marine Biol 96: 93-106
- Hurley DE (1965) A common but hitherto undescribed species of *Orchomenella* (Crustacea Amphipoda: family Lysianassidae). Trans r Soc NZ, Zool 6: 1: 107-113
- Isaacs JD, Schwartzlose RA (1975) Active animals on the deep-sea floor. Sc Am 233: 84-91
- Jones EG, Tselepidis A, Bagley PM, Collins MA, Priede IG (2003) Bathymetric distribution of some benthic and benthopelagic species attracted to baited cameras and traps in the deep eastern Mediterranean. Mar Ecol Prog Ser 251: 75-86
- Klages M, Muyakshin S, Soltwedel T, Arntz WE (2002) Mechanoreception, a possible mechanism for food fall detection in deep-sea scavengers. Deep-Sea Res (I) 49: 143-155
- Legezynska J, Weslawski JM, Presler P (2000) Benthic scavengers collected by baited traps in the high Arctic. Polar Biol 23: 539-544
- Lipps JH, Ronan TE Jr, Delaca TE (1979) Life below the Ross Ice Shelf, Antarc Sci 203 (4379): 447-449
- Lowry JK (1986) The callynophore, a eucaridan/peracaridan sensory organ prevalent among the Amphipoda (Crustacea). Zool Scripta 15: 333-349
- Lowry JK, Stoddart HE (1989) Stephonyx, a new, widespread genus of lysianassoid Amphipoda. Zool Scripta, 18: 519-525
- Lowry JK, Stoddart HE (1994) Crustacea Amphipoda: Lysianassoids from the tropical western South Pacific Ocean. In: Crosnier, A. (Ed.). Résultats des Campagnes MUSORSTOM 12. Mém Mus ntl Hist nat, Paris. 161: 127-233
- McKillup SC, McKillup RV (1994) The decision to feed by a scavenger in relation to the risks of predation and starvation. Oecologia 97: 41-48

- Meador JP (1981) Chemoreception and food-finding abilities of a lysianassid amphipod. Ph.D. Thesis, San Diego State Univ., US
- Moore PG (1994) Observations on the behaviour of the scavenging lysianassoid *Orchomene zschau* (Crustacea: Amphipoda) from South Georgia (South Atlantic). *Mar Ecol Prog Ser* 113: 29-38
- Nagata K (1986) Amphipod crustaceans found near Syowa Station, Antarctica. *Mem ntl Inst Polar Res, Spec Iss* 40, 249-258
- Nyssen F, Brey T, Lepoint G, Bouquegneau JM, De Broyer C, Dauby P (2002) A stable isotope approach to the eastern Weddell Sea trophic web: focus on benthic amphipods. *Polar Biol* 25: 280-287
- Olerod R (1975) The mouthparts in some North Atlantic species of the genus *Orchomene* Boeck (Crustacea, Amphipoda). *Zool Scripta* 4: 205-216
- Paul AZ (1973) Trapping and recovery of living deep-sea amphipods from the Arctic Ocean floor. *Deep-Sea Res* 20: 289-290
- Penry DL, Jumars PA (1987) Modeling animal guts as chemical reactors. *Am Nat* 129: 69-96
- Presler P (1986) Necrophagous invertebrates of the Admiralty Bay of King George Island (South Shetland Islands, Antarctica). *Pol Res* 7: 25-61
- Rakusa-Suszczewski S (1982) The biology and metabolism of *Orchomene plebs* (Hurley, 1965) (Amphipoda: Gammaridea) from McMurdo Sound, Ross Sea, Antarctic. *Polar Biol* 1: 47-54
- Rauschert M (1985) *Eurythenes gryllus* (Lichtenstein) (Crustacea, Amphipoda) in der marinen Fauna von King George (Südshetlandinseln, Antarktis). *Milu* 6: 319-324
- Richard J (1934) Liste générale des stations des campagnes scientifique du Prince Albert de Monaco avec notes et observations. Résultats des Campagnes scientifiques accomplies sur son Yacht par Albert I^{er} Prince Souverain de Monaco 89: 1-348
- Riebesell U, Schloss I, Smetacek V (1991) Aggregation of algae released from melting sea ice: implications for seeding and sedimentation. *Polar Biol* 11: 239-248
- Sainte-Marie B (1987) Meal size and feeding rate of the shallow-water lysianassid *Anonyx sarsi* (Crustacea: Amphipoda). *Mar Ecol Prog Ser* 40: 209-219
- Sainte-Marie B (1992) Foraging of scavenging deep-sea lysianassoid amphipods. In Rowe GT, Pariente V (Eds), *Deep-Sea Food Chains and Global Carbon Cycle*. Kluwer Academic, Netherlands: 105-124
- Sainte-Marie B, Hargrave BT (1987) Estimation of scavenger

abundance and distance of attraction to bait. *Mar Biol* 94: 431-444

Sainte-Marie B, Percy JA, Shea JR (1989) A comparison of meal size and feeding rate of the lysianassid amphipods *Anonyx nugax*, *Onisimus* (= *Pseudalibrotus*) *litoralis* and *Orchomenella pinguis*. *Mar Biol* 102: 361-368

Slattery PN, Oliver JS (1986) Scavenging and other feeding habits of lysianassid amphipods (*Orchomene* spp.) from McMurdo Sound, Antarctica. *Polar Biol* 6: 171-177

Stockton WL (1982) Scavenging amphipods from under the Ross Ice Shelf, Antarctica. *Deep-Sea Res* 29: 819-835

Takeuchi I, Watanabe K, Tanimura A, Fukuchi M (2001) Assemblages of necrophagous animals off Enderby Land, East Antarctica. *Polar Biol* 24: 650-656

Thurston MH (1979) Scavenging abyssal amphipods from the North-

East Atlantic Ocean. *Mar Biol* 51: 55-68

Thurston MH (1990) Abyssal necrophagous amphipods (Crustacea: Amphipoda) in the northeast and tropical Atlantic Ocean. *Prog Oceanog* 24: 257-274

Vader W (1972) Notes on Norwegian marine Amphipoda. 5. New records of *Leptamphopus sarsii* (Calliopiidae). *Sarsia* 50: 25-28

Vinogradov G (1997) Scavenger amphipods (Amphipoda Gammaridea, Crustacea) of the continental slope of the Norwegian Sea. In: *Benthos of the northern seas of Eurasia*. VNIRO, Moscow. (In Russian).

Walker AO (1907) Crustacea. III. Amphipoda. National Antarctic Expedition 1901-1904. *Nat Hist* 3: 1-38

Watling LE (1993) Functional morphology of the amphipod mandible. *J Nat Hist* 27: 837-849