

THE NATURAL HISTORY OF THE CRUSTACEA



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INVASION OF THE POLES

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Abstract

Polar Crustacea show high taxonomic and functional diversity and hold crucial roles within regional food webs. Despite the differences in the evolutionary history of the two Polar regions, present data suggest rather similar species richness, with over 2,250 taxa recorded in the Antarctic and over 1,930 noted in the Arctic. A longer duration of isolated evolution resulted in a high percentage of endemic species in the Antarctic, while the relatively young Arctic ecosystem, subjected to advection from adjacent seas, shows a very low level of endemism. Low temperatures and seasonal changes of food availability have a strong impact on polar crustacean life histories, resulting in their slow growth and development, extended life cycles, and reproduction well synchronized with annual peaks of primary production. Many species, Antarctic amphipods in particular, exhibit a clear tendency to attain large size. In both regions, abundant populations of pelagic grazers play a pivotal role in the transport of energy and nutrients to higher trophic levels. The sea-ice habitat unique to polar seas supports a wide range of species, with euphausiids and amphipods being the most important in terms of biomass in the Antarctic and Arctic, respectively. Deep sea fauna remains poorly studied, with new species being collected on a regular basis. Ongoing processes, namely a decline of sea-ice cover, increasing levels of ultraviolet radiation, and invasions of sub-polar species, are likely to reshape crustacean communities in both Polar regions.

INTRODUCTION

The Antarctic Ocean (34.8 million km²) and Arctic Ocean (14 million km²) are significant parts of the world's oceans. Their cold waters (<4°C) resemble the largest marine domain, the deep ocean, but are peculiar in being strongly seasonal with long periods of low primary production and starvation

for consumers. This cycle has been linked to slow growth rates, enhanced resistance to starvation, and reduced ecological competition. The Polar regions are responding the fastest to global warming and therefore stimulate public concern and increasing research efforts in recent decades. Crustacea are the most speciose taxon in the Polar regions and are the subject of large research programs and data management initiatives such as the Census of Antarctic Marine Life (CAML), Arctic Ocean Diversity (ArcOD), ANDEEP, OBIS, SCAR-MarBIN/AntaBIF, etc., which have contributed to the knowledge of diversity, evolution, and biogeography of the Crustacea.

ARCTIC VS. ANTARCTIC: SIMILARITIES AND DIFFERENCES

Whereas the high latitude of the Arctic Ocean permits it to experience polar day and polar night cycles with its associated contrasting productivity regime, the highest latitudes of the Antarctic are continental, and marine areas are distant from extreme latitudes (the southernmost is 78°S) (Table 9.1). Low water temperatures are shared but tend to be stable in the Antarctic, never exceeding –1.8°C in some places, and are more variable even in the high Arctic (80°N) where summer sea surface temperature may reach 3°C. The Arctic comprises an extensive, shallow shelf washed by one of the largest riverine systems on the globe and a deep central basin divided by submarine ridges in four sub-basins. Antarctica has an exceptionally deep shelf and vast areas of deep ocean basins with few major isolating structures (ridges, plateaus) (Post et al. 2014).

The Arctic system is connected with the adjoining oceans via the deep (>2000 m) and wide (450 km) Fram Strait in the Atlantic sector and the shallow (50m) and narrow (85 km) Bering Strait in the Pacific sector. Main transport of heat and salt occurs from the Atlantic Ocean, and it is compensated by the outflow of cold, freshened waters along Greenland coasts (Fig. 9.1). Arctic near-bottom, dense saline waters are exported south and are of key importance to global thermohaline circulation (ACIA 2004).

The Antarctic system, on the other hand, is largely isolated from the warmer subtropical waters from the Pacific, Atlantic, and Indian oceans by the east-flowing Antarctic Circumpolar Current (ACC) and its hydrological fronts. The well-defined Antarctic Polar Front (APF, or Antarctic Convergence) marks the northernmost extent of cold surface Antarctic waters, which at these

Table 9.1. Arctic and Antarctic Specific Features of Importance for Crustacean Life

Factor	Arctic	Antarctic
Evolutionary time of cold climate (ice on the sea)	700 Ka	>30 Ma
Sea ice	Perennial	Annual
Land discharge	Large rivers	Ice sheet
Seabed disturbance by ice scours	Rare and shallow (<100 m)	Common to 250 m
Major pelagic predators	Birds, fish	Birds, sea mammals
Major benthic predators	Sea mammals	Demersal fish
Primary production distribution	Oligotrophic center, rich shallow shelf	Rich extensive frontal zones on the open sea

Source: Modified partly from Dayton et al. 1994.

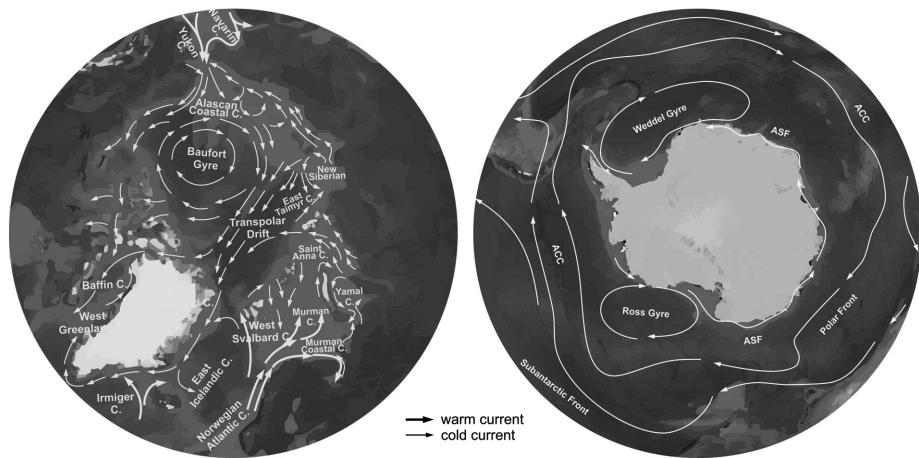


Fig. 9.1.

Major Arctic and Southern Ocean circulation features. ACC, Antarctic Circumpolar Current; ASF, Antarctic Slope Front. Adapted from Post et al. 2014, Rintoul et al. 2001.

latitudes plunges below the warmer subantarctic water masses and indicates the northern boundary of the Southern Ocean (SO) *sensu stricto*. Oceanographers and biogeographers often consider the Southern Ocean to extend to the Subtropical Front (STF) (between 41°S and 48°S; Orsi et al. 1995), and the term in this sense is adopted here (Fig. 9.1). At several locations the Southern Ocean shelf water is a source of deep-sea cold, saline, dense water (Antarctic Bottom Water) that spreads northward to the ocean basins.

These physical features shape the functioning of both systems, mainly primary production, which is highly seasonal, short, and intense in the Arctic with its rich supply of land-derived nutrients but is, conversely, more productive for longer in the Antarctic with a permanent deficit of silica and iron. Sea ice is perennial in the Arctic, with ice floes several meters thick, circulating for several years, and supporting diverse microflora and fauna, whereas in the Antarctic the seasonal/annual pack ice rarely exceeds 2 m in thickness (Arndt and Swadling 2006).

BIODIVERSITY OF POLAR CRUSTACEANS

Soft bottom areas markedly prevail in the Arctic where massive river runoff and coast washout lead to continuous accumulation of fine-grained sediments both on the wide shelf and in the deep basins where they are transported with the sea ice. In the Antarctic terrigenous material input results mostly from creeping down of the continental ice, which transports high amounts of coarse sediments (stones, gravel, and sand) on the narrow and deep shelf. Dropstones densely distributed around the whole Antarctic continent provide a substratum for a variety of sessile and epibenthic species. In the Arctic, dropstones are fairly abundant, but often not exposed, buried in soft sediments, and coarser sediments cover relatively limited areas where wave action or sea currents are strong enough to winnow fine particles (Sirenko 2009, Taylor et al. 2017). As a consequence, hard substratum epifauna, including numerous crustaceans, is rich and diverse in the Antarctic but much poorer in the Arctic, where soft-bottom species constitute a majority of taxa. The pelagic domain is uniform in the Antarctic, due to strong circum-Antarctic currents mixing the upper pelagial around the continent and impeding the penetration of northern species into the Antarctic seas.

On the other hand, the pelagic domain of the Arctic is strongly influenced by advection from the Atlantic and, to a lesser extent, from the Pacific. Thus, pelagic species are more numerous in the Arctic than in the Antarctic. The vast deep-sea Antarctic domain is ice-covered seasonally (allowing tight pelago-benthic coupling), while the Arctic Ocean consists of four deep (3,000–4,000 m) basins (Canada, Makarov, Nansen, and Amundsen) that are largely covered by multi-year ice and receive relatively low input of organic matter from limited primary production. As a consequence, the deep Antarctic fauna is highly diverse and endemic (Brandt et al. 2007b), while that of the Arctic is mostly a subsample of the North Atlantic fauna (Bluhm et al. 2011) (Fig. 9.2).

Peracarida (in particular Amphipoda and Isopoda) dominate the crustacean fauna of the Southern Ocean, while Cirripedia and Decapoda are scarce. Pelagic crustaceans (ostracods, copepods, euphausiids, hyperiid amphipods, natant decapods) number about 550 species, and the benthic and benthic-pelagic ones about 1,750 species (Table 9.2), but many more benthic species, in particular deep-sea isopods and amphipods, await description (De Broyer et al. 2004, Brandt et al. 2007b, Udekem d'Acoz and Verheye 2017). Despite substantial progress during the last two decades, important gaps remain in the faunal survey of Antarctica (Griffiths 2010). On the other hand, as elsewhere, molecular studies are detecting more and more cryptic or pseudocryptic species, challenging our current estimations of SO species richness (Riesgo et al. 2015).

The high species richness of benthic amphipods and isopods in the Antarctic seas has been attributed to their brooding habit, which limits the dispersal of juveniles and enhances reproductive isolation. This leads to reduced gene flow between populations and facilitates speciation. Many Antarctic amphipod species are known to be bottom crawlers, burrowers, nestlers, tube-dwellers, or clingers on or associates of algae or benthic sessile suspension-vores (De Broyer et al. 2003). In addition, the Antarctic shelf offers diverse potential habitats, with macroalgal belts (Huang et al. 2007), biogenic sediments such as sponge spicule mats and bryozoan debris, and abundant and diverse sessile suspension-feeding communities, which provide three-dimensional substrata, shelters, food resources, and opportunities for symbioses (De Broyer et al. 2001, Gutt et al. 2015). Extinction events (in particular that of reptant decapods) during the Tertiary cooling of the Southern Ocean (Clarke and Crame 1989, Brandt 2000, De Broyer et al. 2003) may also have promoted amphipod and isopod diversification.

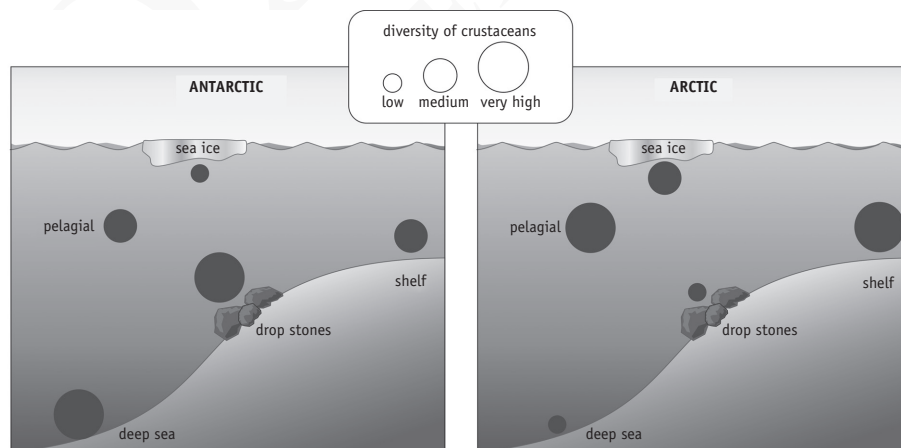


Fig. 9.2. Diversity of Crustacea in different Antarctic and Arctic habitats.

Table 9.2. Biodiversity of Polar Crustaceans

	Habitat	Antarctic				Arctic			
		N. spp.	N. spp. Southern Ocean s.l.	Endemism Rate	Ref.	N. spp.	N. spp. Deep- Water	Endemism Rate	Ref.
Cladocera	P	0				6			[4]
Ostracoda	B	234	357		[1,2]	248	40		[4,5]
Ostracoda	P	47		21%	[2]	9	8		[4]
Copepoda		484			[2]	362			
Copepoda	P	388		14%	[2]	156	97	10%	[4,6]
Calanoidea	P	30	205	14%	[3]	130			[7]
Harpacticoida	B	96	261	78%	[2]	206	56		[4,5]
Ascothoracida	B, S	5			[1]	0	0		
Cirripedia	B	44			[1]	16	7	12.5%	[8]
Leptostraca	B	5			[1]	1	0	0%	[7]
Mysidacea	P, BP, B	44	72		[2]	35	13	17%	[8]
Amphipoda	P, BP, B	630	927			932	140		
Gammaridea + Senticaudata	B, BP	530	801	67%	[2]	920	132		[4,5]
Hyperiidia	P	66	74	12%	[2]	12	8	0%	[4,8]
Isopoda	B, P	441	740	87%	[2]	112	66 (B)		[5,9]
Tanaidacea	B	160		81%	[2]	26	17		[5,9]
Cumacea	B	93	98	80%	[2]	115	24		[2,5]
Euphausiacea	P	8	23	14%	[2]	9	2	0%	[4, 8]
Decapoda	P, B	55			[2]	68	40	7%	[8]
Decapoda (reptant)	B	22			[2]	19	6	0%	[8]
Anomura	B	16			[2]	13	4		[8]
Galatheididae	B	1			[2]	2	1	0%	[8]
Kiwaidae	B	1			[2]				
Lithodidae	B	13			[2]	5	1	0%	[8]
Paguridae	B	0				6	2	0%	[8]
Astacidea	B								
Nephropidae	B	3	4		[2]				
Brachyura	B	2 (+1)		0%	[2]	6	2	0%	[8]
Decapoda (natant)	P, B	23			[2]	49	34	10%	[8]
Malacostraca	P, B, BP	1436				1298			
Crustacea Total		2250				1939			

Habitat: P, pelagic; B, benthic; BP, benthopelagic; S, symbiotic; Deep-Water, >500 m.

Sources: [1] De Broyer and Danis 2011; [2] De Broyer et al. 2014; [3] Park and Ferrari 2009; [4] Sirenko et al. 2016) [5] Bluhm et al. 2011; [6] Kosobokova et al. 2011; [7] Sirenko 2001 (Eurasian Arctic only); [8] Vassilenko and Petryashov 2009 (Eurasian Arctic only); [9] Piepenburg et al. 2011.

The scarcity of Cirripedia, notably sessile species, has been correlated with the lack of suitable littoral habitats (disturbed by ice) and to the Cenozoic glaciations that eradicated the former balaniform species (Newman and Ross 1971).

Antarctic Decapoda are represented by few pelagic and benthic natant and reptant species (Table 9.2), in contrast to the richer Cenozoic fauna of macrurans and brachyurans (Feldmann et al. 1993). Like other invertebrates and fish, this Cenozoic temperate fauna was probably eradicated or forced to migrate by the cooling ocean and periodic extensions of the Antarctic ice cap (Clarke and Crame 1989, 1992). But curiously enough, decapods, in particular reptant species, were apparently unable to re-invade the high Antarctic shelf, although a relatively high diversity of decapod crustaceans is recorded in the subantarctic region (Gorny 1999).

Hypotheses explaining the depauperate decapod fauna in the high Antarctic were based on geological/historical, larval, and/or ecological patterns (De Broyer et al. 2003, Thatje et al. 2005). But physiology appears to be more significant here. Brachyuran and anomuran crabs, excluding caridean shrimps, have a low ability to regulate the concentration of hemolymph magnesium at temperatures $<0^{\circ}\text{C}$, a threshold below which cold-induced cardiac and ventilator performance fails (Frederich et al. 2001). Wittmann et al. (2010) showed that Antarctic caridean decapods and amphipods maintained low hemolymph magnesium levels (6–20% ambient sea-water magnesium concentration), whereas subantarctic brachyuran and anomuran crabs and Antarctic isopods maintained high levels (54–96% ambient sea-water magnesium concentration). They concluded that magnesium regulation may explain the biogeographic pattern of decapods but not that of isopods.

Crustacea are the most species-rich invertebrate group of the pelagic, benthic, and sea-ice realms in the Arctic Ocean (Josefson et al. 2013). Copepods are the most speciose (>150 species) and, with hyperiid amphipods, dominate the metazoan biomass in the pelagic zone. Euphausiids and mysids are abundant but are represented by few species (Buchholz et al. 2010). The Arctic sea-ice community is dominated by four species of amphipods (*Gammarus wilkitzkii*, *Apherusa glacialis*, *Onisimus glacialis*, and *O. nanseni*) and by copepods dwelling inside the ice (harpacticoids, cyclopoids) or grazing on algae under the ice (calanoids). Pelagic (*Themisto* spp.) and benthic (*Gammarus*, *Weyprechtia*, *Gammaracanthus*, *Anonyx*, and *Onisimus*) amphipods may temporarily exploit sea-ice habitat as a feeding ground (Arndt and Swadling 2006).

Malacostraca are the most diverse class of benthic Crustacea, with 805 species recorded on the circum-Arctic shelf (Piepenburg et al. 2011), declining from >500 species in the Barents Sea to >250 in the East Siberian Sea (Sirenko 2001). The western Greenland Sea is also diverse (Brandt 1997). The diverse shallow-water substrata (<50 m), which provide good foraging opportunities and shelter from predators and environmental stressors, often host rich and functionally diverse malacostracan communities dominated by amphipods (Voronkov et al. 2013). The muddy bottom below 50 m supports relatively fewer species and is dominated by burrowing deposit-feeders or carnivores (Legeżyńska et al. 2017). In the Bering and Chukchi Seas, influenced by nutrient-rich Pacific water, strong pelagic–benthic coupling supports dense populations of tube-dwelling, filter-feeding ampeliscid amphipods which aggregate in dense mats over the bottom (up to 21,000 ind. m^{-2} ; Conlan et al. 2013). Littoral communities, characterized by harsh environmental conditions, support the fewest species; mobile amphipods (*Onisimus* spp. and *Gammarus* spp.) and the barnacle *Semibalanus balanoides* associated with the kelp *Fucus* may be abundant where moderate ice scouring occurs (Węśławski et al. 1993).

The deep central Arctic basin has fewer species than the shelf, with only 261 malacostracan species recorded (Bluhm et al. 2011). However, depth-related trends differ between taxa; numbers of tanaidacean and isopod species tend to rise with increasing depth (Brandt 1997, Svavarsson 1997). Meiofaunal diversity is less well known: ostracods and harpacticoids number about 200 species each, but more can be expected (Bluhm et al. 2011, Josefson et al. 2013).

ECOFUNCTIONAL DIVERSITY OF POLAR CRUSTACEANS

Functional Groups and Life History Traits

The sea-ice zone of the Antarctic marine ecosystem is dominated by the Antarctic krill (*Euphausia superba*). Its circumpolar biomass has been estimated most recently at between 67 and 297 Mt, with the mean of 170 Mt (Siegel 2005). This biomass, its circumpolar distribution (Atkinson et al. 2004), and its nutritive value (Nicol et al. 2000) make it the key species of the Antarctic trophic web, providing a staple food resource for many pelagic and benthic (macro)invertebrates (including squid), fish, penguins, seabirds, seals, and whales. The whole SO (*s.l.*) hosts 13 euphausiid species unevenly distributed latitudinally from the coast of the continent to the Subtropical Front zone (Fig. 9.3, Cuzin-Roudy et al. 2014). Most species form swarms, which for *E. superba* can be 250 m thick and extend over several kilometers, with densities of up to 60,000 individuals and 15 kg m⁻³ (Everson 2000).

Postlarval krill is typically concentrated in the epipelagic zone in the summer (Siegel 2005), while in the early winter a significant fraction of the adult population goes to deeper water (150–450 m) (Lawson et al. 1994). Clarke and Tyler (2008) reported ROV observations of adult krill, including gravid females, actively feeding on fresh phytodetritus at the foot of the continental slope (3000 m) and on the abyssal plain (3500 m) in the western Antarctic Peninsula. Krill were observed digging in the sedimented phytodetritus and, just above the bottom, filtering the resuspended material. Abundant and large fast-sinking krill fecal pellets contribute significantly to the pelago-benthic organic flux (Smetacek et al. 2004), which sustains communities of suspension feeders and deposit feeders on the Antarctic shelf (Smith et al. 2006). At subantarctic latitudes (between APF and STF), hyperiid amphipods play a key trophic role in pelagic ecosystems. On the Southern Patagonian Shelf, around the Prince Edward and Marion Islands and around the Kerguelen Islands and South Georgia, *Themisto gaudichaudii* in particular are abundant and play trophic roles similar to that of *Euphausia superba* farther south (Bocher et al. 2001, Padovani et al. 2012, Watts and Tarling 2012). Antarctic benthic crustaceans present a large array of feeding roles, with a dominance of scavengers, micro-predators, and detritophages (Table 9.3).

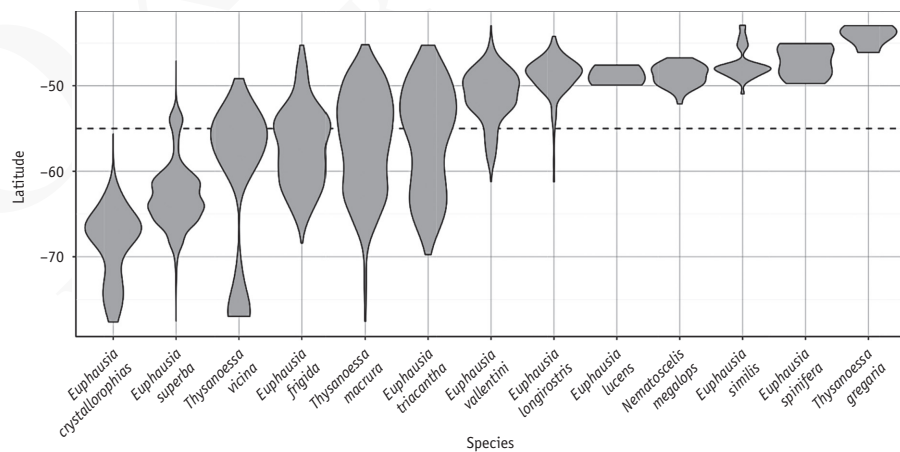


Fig. 9.3.

Latitudinal distributions of the 13 euphausiid species sampled at 14,397 stations in the Southern Ocean (*s.l.*), represented as violins (the wider the violin, the more presence at this latitude). The dashed line indicates the average position of the Antarctic Polar Front zone. From Cuzin-Roudy et al. 2014.

Table 9.3. Main Ecofunctional Groups of Marine Crustaceans in the Southern Ocean and Arctic Shelves with Examples of Key Species

Functional group	Examples from SO (s.s.)	Importance in SO ecosystems	Examples from Arctic	Importance in Arctic ecosystems
Small pelagic herbivores	Calanoid and cyclopoid copepods (<i>Calanus simillimus</i> , <i>Rhincalanus gigas</i> , <i>Oithona similis</i>) <i>Calanoides acutus</i>	Key elements of pelagic food web	Copepods (surface waters: <i>Calanus</i> spp., <i>Oithona similis</i>)	Key element of pelagic food web
Large pelagic herbivores	Six species of euphausiids	Dominant herbivores <i>E. superba</i> : keystone species in the SO (s.s.) ecosystem	Euphausiids (<i>Thysanoessa</i> spp.)	Prey for top predators
Small pelagic carnivores	Hyperiid (<i>Themisto gaudichaudii</i>) Deep-water copepods (<i>Paraeuchaeta antarctica</i> , <i>P. rasa</i>)	Key element in subantarctic waters	Hyperiid (<i>Themisto</i> spp.), copepods (<i>Paraeucheta</i> spp.)	Prey for top predators
Supra-benthic omnivores	Mysids (<i>Antarctomysis maxima</i>)	May contribute significantly to bottom biogenic modification	Mysids (<i>Mysis oculata</i>)	May contribute to bottom biogenic modification
Benthic deposit feeders	Ostracods amphipods (<i>Epimeria</i> spp., <i>Paraceradocus</i> spp.) Shrimps (<i>Notocrangon antarcticus</i>)		Ostracods, amphipods, cumaceans (Leuconidae) shrimps (<i>Sabinea</i>)	
Benthic seston feeders	Amphipods (Ampeliscidae, Melphidippidae). cumaceans	Minor role in suspension-feeding communities	Amphipods (Ampeliscidae) and cumaceans (Diastylidae)	Ampeliscids are of key importance as food for grey whales
Benthic carrion feeders	Lysianassoid amphipods, cirrolanid isopods	May occur in large numbers on food falls	Lysianassoid amphipods	May occur in large number feeding on animal carcasses
Benthic (micro) predators	Amphipods (<i>Epimeria</i> spp., Iphimediidae)	Usually specialized	Decapods (<i>Pandalus borealis</i> , crabs), shrimps (<i>Spirontocaris</i>), amphipods (Oedicerotidae, Phoxocephalidae)	

In the Arctic pelagic realm, copepods (especially Calanidae) and euphausiids are widespread and abundant, holding crucial positions within food webs, directly linking primary production to higher trophic levels. Hyperiid amphipods are epipelagic predators feeding preferentially on *Calanus* spp. Benthic crustaceans have versatile feeding repertoires and are important prey for seabirds, fish, and bottom-feeding sea mammals. Abundant deep-water prawns (*Pandalus borealis*) are fed upon by demersal fish (e.g., cod) and are commercially exploited (Table 9.3).

Adaptations of Polar Crustaceans

Polar Gigantism

Several ecological, physiological, and biogeographic hypotheses have been put forward to explain polar gigantism (Moran and Woods 2012). Antarctic amphipods in particular exhibit a clear tendency to attain large size (Arnaud 1977, De Broyer 1977, Chapelle 2001). Chapelle and Peck (1999, 2004) and Peck and Chapelle (1999) analyzed and compared the size spectra of 2,892 species of benthic amphipods in 15 localities from the tropics to the poles, in fresh and marine waters (but excluding the deep sea). They showed a narrow relationship between the size of gammaridean amphipods and mean absolute oxygen concentration of the surface waters. At higher oxygen concentrations, the increase in size is slight in small animals, more pronounced in the middle of the spectrum, and greatest in the largest animals. This was explained by two physiological factors: the essentially passive nature of respiration in amphipods and the decrease of the surface-volume ratio with increasing size, setting an upper threshold beyond which the respiratory surface becomes insufficient for oxygen to supply the tissues. They concluded that oxygen availability does not act as a selection pressure in favor of large size but rather as a physicochemical ceiling limiting maximum potential size. They also showed that the minimum adult size is probably limited by the minimum possible egg size.

Exploring the links between the physical, chemical, and biological environments of polar seas and the evolution of gigantism, Moran and Woods (2012) distinguished eight major explanatory hypotheses, noting that even if the “oxygen theory” seems the most widely accepted, each deserves additional theoretical and experimental work.

Coping with Variable Food Conditions

Life history strategies at high latitudes are shaped by extreme environmental and resource seasonality. Several strategies to cope with these fluctuations are observed (Clarke and Peck, 1991, Torres et al. 1994, Huenerlage et al. 2015). With primary production restricted to two to four months per year, herbivores are more affected than other consumers (Obermüller et al. 2010). They often build up large lipid reserves during the summer, which sustain them throughout periods of low food supply and permit reproduction. Total lipid content in herbivorous zooplankters may surpass 70% dry weight, allowing survival without food uptake such as 210 days in Antarctic krill and 270 days in the Arctic copepod *Calanus glacialis* (Lee et al. 2006). Lipid-rich zooplankton display different overwintering strategies: herbivorous copepods migrate into deep waters and enter a period of reduced metabolism (diapause), while other species that remain active in surface waters, such as euphausiids, may survive due to reduced metabolism, stagnated growth, sexual regression, catabolism of stored lipids and tissue proteins coupled with occasional feeding (Lee et al. 2006, Huenerlage et al. 2015). In contrast, benthic crustaceans generally do not accumulate lipids and metabolize in the winter as in the summer (Graeve et al. 1997, Legeżyńska et al. 2012). Having access to a variety of year-round food sources, they have developed opportunistic feeding strategies, making them less dependent on fluctuations in primary productivity. A common, though often

only facultative, feeding strategy among Arctic and Antarctic crustaceans is necrophagy, regarded as an important adaptive trait of polar benthos (Arnaud 1977). Mortality of small organisms due to ice scouring, wave action or mixing of different water masses, and large carrion falls (dead fish, mammals) provides food for scavengers year round. A key role in dispersing organic material in both Polar regions is played by lysianassoid amphipods (Britton and Morton 1994). Shallow-water genera, such as *Anonyx*, *Onisimus*, and *Orchomenella* in the Arctic and *Cheirimedon*, *Hippomedon*, *Pseudorchomene*, and *Waldeckia* in the Antarctic have more flexible feeding habits than deep-sea species (e.g., cosmopolitan and bipolar *Eurythenes gryllus*) that rely on infrequent large food falls.

Low temperature and seasonal pulses of food supply strongly influence life histories of polar crustaceans: typically, they demonstrate slow growth and development and extended life cycles (biannual or perennial; Table 9.4) with a single annual breeding period (Peck et al. 2006). Annual cohorts within the same species differ considerably in size, mobility, diet, and microhabitat and therefore may play different roles in the ecosystem (Węśławski et al. 2010).

Since successful recruitment of zooplankton herbivores depends on their ability to synchronize their seasonal migration, reproduction, and growth with local primary production, populations under differing environmental conditions show variable developmental patterns. In regions with long-lasting ice cover where phytoplankton blooms are preceded by ice algae blooms, the Arctic copepod *Calanus glacialis* utilizes ice algae to fuel spawning, while growth and development of the new generation is primarily supported by the later bloom of pelagic microalgae. In ice-free areas, this species uses accumulated lipid reserves to start reproduction early in the season, allowing early life stages to benefit from the phytoplankton bloom (Daase et al. 2013). High-latitude benthic crustaceans are typically characterized by long life spans, small brood sizes, large eggs, and semelparity (one reproduction event in a lifetime) (Sainte-Marie 1991), resulting in their modest reproductive potential. Therefore, reproduction must be well timed to maximum food availability. Success of offspring is ensured by parental care (in peracarids with a marsupium) until the start of the productive season. In most species, release of juveniles coincides with spring phytoplankton/ice algae blooms (Węśławski and Legeżyńska 2002), but in some it may be synchronized with the availability of more specific food sources. The scavenging Arctic amphipod *Onisimus caricus*

Table 9.4. Life Span of some Polar Crustaceans

Taxon	Region, Domain	Life Span	Ref.
<i>Calanus hyperboreus</i> (Copepoda)	Arctic, pelagic	Up to 5 years	[1]
<i>Gammarus wilkitzkii</i> (Amphipoda)	Arctic, sympagic	Up to 5 years	[2]
<i>Sclerocrangon boreas</i> (Decapoda)	Boreo-Arctic, benthic	Over 6 years	[3]
<i>Antarctomysis maxima</i> (Mysida)	Antarctic, suprabenthic	Up to 7 years	[4]
<i>Eurythenes gryllus</i> (Amphipoda)	Bipolar, deep water benthic-pelagic	Over 9 years	[5]
<i>Bovallia gigantea</i> (Amphipoda)	Antarctic, shallow benthic	Up to 4 years	[6]

Sources: [1] Hirche 1997; [2] Poltermann 2000; [3] Sainte-Marie et al. 2006; [4] San Vicente 2010; [5] Ingram and Hessler 1987; [6] Thurston 1972.

releases its juveniles at the same time there is mass mortality of zooplankton during the melting season (Nygård et al. 2009).

Coping with Thermal and Osmotic Stress

Unlike sublittoral and deep-sea polar species that experience little fluctuations of environmental conditions, organisms living in the intertidal zone are faced with temperature extremes and strong fluctuations of salinity resulting from freshwater runoff (Węśławski et al. 1993, Waller 2013). Most inhabitants of this zone migrate from the subtidal to graze on macroalgal detritus, epiphytes, or animal carcasses and bury in sediment or leave the area when conditions become less hospitable. Some species, however, adapt physiologically and stay. For example, some taxa prevent internal ice formation by lowering the freezing point of their body fluids (e.g., the Antarctic amphipod *Proteobbingia gracilis*; Waller et al. 2006). Further, littoral species are usually euryhaline. The Arctic amphipod *Onisimus litoralis*, which is an efficient osmoregulator, can survive at salinities from 5 to 55, enabling its colonization of the littoral zone and the sea-ice underside (Shea and Percy 1990). Species that gradually adjust their hemolymph concentration of sodium and chloride ions to the salinity of seawater (osmoconformers) have narrower tolerance that may limit their occurrence in osmotically stressful habitats (Shea and Percy 1990).

Strong salinity gradients characterize the shallow areas of the Siberian coast that is extensively influenced by riverine waters. Their evolutionary age is very modest, and its colonization probably occurred as a consequence of repeated invasions from the sea. In such habitats, sequences of closely related species of varying salinity tolerance may be found occupying different depth zones along salinity gradients. For example, in the Kara Sea *Onisimus litoralis* and *O. affinis* occur in the littoral and shallow sublittoral tolerating salinity <20, while *O. caricus* and *O. brevicaudatus* require deeper and more saline waters (Vader et al. 2005).

ORIGIN OF POLAR CRUSTACEANS

Antarctic

The origin and evolution of the Antarctic fauna are closely linked to the tectonic, climatic, and glacial history of the region. The rich and diverse Antarctic continental shelf benthos consists of a mixture of taxa with different evolutionary histories and biogeographic affinities and is considered to have originated from three sources (Dell 1972, Clarke and Crame 1989, 1992):

1. From a relict autochthonous fauna of Gondwanan origin, which evolved during the cooling of the polar waters after the opening of the Drake Passage, the onset of the ACC, and thermal isolation of the Antarctic continent. Part of this Gondwanan fauna, such as brachyuran crabs, did not succeed and disappeared, leaving some fossil evidence. The isopod families Serolidae and Antarcturidae (Brandt 1992), the former possibly dating back to the Late Cretaceous (80 Ma), are Gondwanan (Wägele 1994).
2. From the adjacent deep-sea basins, for example, the isopod families Munnopsididae, Haploniscidae, Desmosomatidae, Nannoniscidae, and Ischnomesidae (Brandt et al. 2007a). An abyssal origin was also suggested for Antarctic stenothermic eurybathic tanaidaceans (Sieg 1992).
3. From the southern South American continental shelf by migration along the Scotia Arc. The islands of the Arc may serve as “stepping stones” for species able to cross an expanse of deep water. The configuration of the Scotia Arc has changed and deep water expanses found today

between the Arc islands didn't always exist in the past (Thomson 2004). Serolid isopods (Held 2000) and some notothenoid fishes (Bargelloni et al. 2000) colonized the Antarctic shelf from South America before the opening of the Drake Passage, which occurred about 33 Ma. According to Sieg (1986), some Antarctic shelf Tanaidacea migrated from the Magellan region, and Watling and Thurston (1989) suggested a similar origin for some iphimeriid amphipods. This migration may still be ongoing on the Scotia Ridge, as suggested, for example, for Isopoda *Asellota* (Winkler 1994).

Whatever their origin(s), it is widely recognized that some benthic lineages have successfully radiated in the cold but constant environmental conditions of the Antarctic shelf (Clarke and Crame 1989). Examples are the isopod families Serolidae (Held 2000) and Antarcturidae (Brandt 2000) and the amphipod families Iphimeriidae (Lörz and Held 2004) and Epimeriidae (Verheye et al. 2016).

The high diversity in Antarctic waters is also attributed to the "Antarctic Climatic Biodiversity Pump," which refers to several scenarios favoring persistence and speciation of Antarctic biota. During the Pliocene-Pleistocene glacial periods, the continental ice over the shelf extended and contracted on Milankovitch frequencies of about 100,000 years (Clarke and Crame 1989, 1992). The advance of grounded ice sheets across the continental shelf may have eradicated sessile or poorly mobile benthos over large parts of their ranges (e.g., Thatje et al. 2005, Allcock and Strugnell 2012). More motile animals may have been displaced to refugia: to the slope and deep sea, to ice-free areas on the shelf, to the Scotia Arc, northern Antarctic Peninsula and peri-Antarctic islands, or to oceanic ridges. Arguments against complete eradication of the shelf fauna during glacial maxima refer to the persistence of taxa present before the onset of glaciations (Clarke and Crame 1989, 1992), survival of benthic species under floating ice shelves (e.g., Riddle et al. 2007), and the occurrence of ice-free areas on the shelf. Grounded ice did not advance to the shelf edge during the Last Glacial Maximum, e.g., off Adélie Land, Prydz Bay, and George V Land (Anderson et al. 2002), and ice advances did not cover all the shelf at the same time. The isolation of fragmented populations during glacial periods may have resulted in some level of genetic differentiation. During interglacial periods, coalescence of fragmented populations during recolonization of the shelf from transient mosaic refuges may have led to allopatric speciation, explaining the apparently common occurrence of complexes of sibling or cryptic species (Allcock and Strugnell 2012, Rogers 2012).

Arctic

The Arctic Ocean was a cool embayment of the Pacific Ocean until ~80 Ma when this deep connection closed. Exchange with the Atlantic started ~40 Ma, with deep (>1000 m) and wide (>500 km) connection existing since the Eocene (27 Ma). Shallow-water (<100 m) and narrow (50 km) contact with the Pacific opened again in the Pliocene (3.5 Ma). The Arctic Ocean was initially cool-temperate (10°C) and gradually started to get colder, reaching negative temperatures and permanent pack ice cover in mid-Pleistocene (0.7 Ma). Cold-water, brackish species associated with sea ice and Siberian river mouths evolved less than 100,000 years ago. The Wisconsin/Würm shield developed 18,000 years ago, causing widespread extinctions. Deglaciation started 14,000 years ago, and the Pacific contributed to an inflow of shelf species, while the Atlantic contributed both deep water and littoral fauna (Dunton 1992). As a result of geological history and existing dispersal barriers, the majority of crustaceans occurring nowadays in the Arctic are boreo-Arctic forms of Atlantic origin, while species of Pacific origin and true Arctic taxa account for around 10% each (Josefson et al. 2013).

BIOGEOGRAPHY OF POLAR CRUSTACEANS

Antarctic

The general distribution pattern of pelagic crustaceans is mostly driven by the highly structured water masses and current system of the Southern Ocean, dominated by the ACC. Most epi- and mesopelagic species are circumpolar, but some, such as the Antarctic krill (e.g., Atkinson et al. 2004), show distinct longitudinal patterns in biomass, or in occurrence, such as some other euphausiids (Cuzin-Roudy et al. 2014). Oceanographic fronts are the main boundaries in the latitudinal ranges of pelagic species. Epi- and mesopelagic ostracods, copepods, amphipods, and euphausiids are distributed in somewhat consistent biogeographic bands around Antarctica; Antarctic species range from the seasonal sea-ice zone to the Antarctic Polar Front Zone (APFZ), or toward the subantarctic Front Zone (SAFZ), the Subtropical Front Zone (STFZ), or beyond (Kouwenberg et al. 2014).

Deep-sea zooplankton species are not restricted by hydrographic fronts and may be widely dispersed by deep-water currents (Park and Ferrari 2009). Meso- and bathypelagic species in particular appear widely distributed north of the Subtropical Front, even as far as Arctic regions. For instance, 66% of the 127 Antarctic deep-water calanoid copepods have been reported north of the Subtropical Front (Park and Ferrari 2009), 9 being considered bipolar. However, using a comprehensive molecular approach, Laakmann et al. (2012) found that the mesopelagic *Aetideopsis minor* represented two (Antarctic and Arctic) clades whereas no intraspecific genetic differences were found between populations of the bathypelagic *A. rostrata*.

The giant lysianassoid amphipod *Eurythenes gryllus* was long considered a cosmopolitan and eurybathic deep-sea species, but Havermans et al. (2013), using morphology and molecular methods, identified 12 species-level clades (d'Udekem d'Acoz and Havermans 2015, Havermans 2016). Bipolar pattern has been detected in some other pelagic and benthic taxonomic groups on morphological grounds (see Allcock and Griffiths 2014). More complete sampling, in particular for deep-sea species in tropical regions, and an approach combining molecular, morphological, and ecological data are needed to recognize the true distributions, detect potential cryptic species, and resolve this recurrent bipolar issue.

Antarctic pelagic species show a low rate of endemism (12% in copepods; 14% in euphausiids) in clear contrast to benthic species (Table 9.2). The biogeography of Antarctic benthic Crustacea is largely driven by the ACC and the front systems, as for pelagic crustaceans, but the timing of past continental connectivity, the geomorphology-associated physical and environmental factors, depth, sea temperature, and ice cover appear also to be key parameters (Koubbi et al. 2014).

Until recently, circumpolar distribution was a paradigm for most Antarctic benthic species (Hedgpeth 1969, 1970, Dell 1972, Arntz et al. 1997, Clarke and Johnston 2003). However, during the last decade, molecular phylogenetic and phylogeographic analyses revealed that this paradigm may be the exception rather than the rule: more and more so-called "circum-Antarctic" benthic species appeared to be complexes of cryptic species with restricted spatial and bathymetric distributions (Allcock and Strugnell 2012, Riesgo et al. 2015). Examples can be found in ostracods (Brandao et al. 2010), isopods (e.g., Leese and Held 2008), and amphipods (e.g., Havermans et al. 2010, Havermans 2012, Verheye et al. 2016).

On the other hand, a circumpolar distribution has been confirmed for some benthic species, e.g., the shrimps with planktotrophic larvae *Notocrangon antarcticus* and *Nematocarcinus lanceopes* (Raupach et al. 2010), and in some lysianassoid and epimeriid amphipods (Havermans 2012, 2014, Verheye et al. 2016). Circumpolar dispersal by rafting on the bull kelp *Durvillaea* has been observed in some subantarctic shallow-water crustaceans (Nikula et al. 2010).

The APF has long been recognized as the main biogeographic barrier for shelf and (upper) slope benthic species, clearly delimiting an Antarctic fauna pattern (De Broyer et al. 2014). However, in most crustacean groups, a significant fraction of the Antarctic species also occurs within the subantarctic region, supporting the concept of Southern Ocean *sensu lato*. This is the case for 20% (106 species) of benthic amphipods (De Broyer and Jażdżewska 2014), 25% of tanaidaceans (Błażewicz-Paszkowycz 2014), and 30% of pycnogonids (Soler-Membrives et al. 2014).

The Antarctic biogeographic region has usually been split in two—east and west—subregions (Ekman 1953, Hedgpeth 1969, De Broyer and Koubbi 2014). Relying on wider and improved recent data, Griffiths et al. (2009) suggested that the Antarctic region constitutes instead a “single functional unit,” as initially proposed by Dell (1972), for Bivalvia, Bryozoa, Pycnogonida, Porifera, Ascidiacea, and Echinoidea. In contrast, this “single Antarctic province” does not hold true for Amphipoda (De Broyer and Jażdżewska 2014) with a high proportion of endemic species (24%) in the Antarctic Peninsula and Scotia Sea sub-region, interpreted as a discrete “West Antarctic” fauna distinguished from the continental Antarctic fauna. A clear distinction between the “Antarctic Peninsula and Scotia Sea Province” and the “Continental High Antarctic Province” (Clarke et al. 2007) was also observed in Hydrozoa (Peña Cantero 2004), Gastropoda (Linse et al. 2006), Actiniaria (Rodríguez et al. 2007), and less distinctly in Tanaidacea (Błażewicz-Paszkowycz 2014).

The isolating conditions of the SO, dating back to the Oligocene 33 Ma (Barker and Thomas 2004), have resulted in high species endemism of the shelf fauna (Dell 1972, De Broyer et al. 2014) (see Table 9.2). At the species level, Antarctic benthic crustaceans have no or few doubtful faunal links with the peripheral continental shelves of South Africa, Australia, or New Zealand but show strong affinities with southern South America due to long-lasting past and possibly ongoing connectivity (Arntz et al. 1999, 2005). Besides seafloor water temperature and geomorphological features, depth is a key parameter defining distribution patterns of benthic species. A clear distinction can be made between the shelf (approximately 0–1000 m) and the deep-sea faunas, but actual depth ranges of most species are unknown because of limited deep-sea sampling. Taking the well-documented amphipods as examples, some clear bathymetric clusters distinguish the shelf fauna (0–800 m), the upper slope (800–2,200 m), lower slope–upper abyssal (2,200–3,700 m), and abyssal fauna (3,700–4,500 m), keeping in mind that most records (89%) came from depths of less than 1,000 m (De Broyer and Jażdżewska 2014). On the other hand, many Antarctic benthic species show greater eurybathy than species in other oceans (Brey et al. 1996). This has been interpreted as an evolutionary adaptation or pre-adaptation to the oscillation of shelf ice during Cenozoic glacial-interglacial cycles. A fair number of Antarctic crustaceans show a wide bathymetric range of more than 1000 m (Table 9.5), assumed to be facilitated by the deep shelf habitats, the generation of cold, highly oxygenated Antarctic Bottom Water from shelf waters, and the mostly isothermal conditions of the water column. This view is challenged by the discovery of cryptic species along depth gradients, e.g., the isopods *Glyptonotus antarcticus* (Held and Wägele 2005) and *Betamorphia fusiformis* (Raupach et al. 2007), the ostracod complex *Macroscapha tensa* (Brandao et al. 2010), and the amphipod *Eurythenes gryllus* (Havermans et al. 2013).

Arctic

The contemporary Arctic fauna is characterized by low endemism (Table 9.2) and domination of species originating from the North Atlantic. Circumpolar taxa are numerous, especially within the sea ice and pelagic domain (e.g., *Apherusa glacialis*, *Gammarus wilkitzkii*, *Calanus glacialis*—key species of the Arctic food web) (Josefson et al. 2013). The biogeography of pelagic communities is impacted by the advection of Atlantic and Pacific waters bringing subarctic species of copepods and euphausiids into the Arctic basin (Buchholz et al. 2010, Kosobokova et al. 2011). Many abundant benthic taxa are widely distributed: *Ampelisca eschrichtii*, *Anonyx nugax*, *Arrhis phyllonyx*, *Byblis*

Table 9.5. Examples of Extreme Eurybathy in Polar Crustaceans

Species	Min.-max. Depth (m)	Depth Range (m)	Habitat
Antarctic			
<i>Byblisoides juxtacornis</i> (Amphipoda)	160–2315	2155	B
<i>Liljeborgia homospora</i> (Amphipoda)	1180–4392	3212	B
<i>Orchomenella</i> (<i>Orchomenopsis</i>) <i>cavimanus</i> (Amphipoda)	6–3683	3677	B
<i>Pseudorchomene coatsi</i> (Amphipoda)	0–2889	2889	B
<i>Abyssorchomene scotianensis</i> (Amphipoda)	385–3408	3023	BP
<i>Parschisturella carinata</i> (Amphipoda)	14–2081	2067	B
<i>Necochea pardella</i> (Amphipoda)	170–3725	3555	B
<i>Alexandrella schellenbergi</i> (Amphipoda)	340–2889	2549	B
<i>Dodecasella elegans</i> (Amphipoda)	68–2894	2826	B
Arctic			
<i>Halirages quadridentatus</i> (Amphipoda)	32–2681	2649	B
<i>Andaniexis abyssis</i> (Amphipoda)	174–2681	2507	B
<i>Arrhis phyllonyx</i> (Amphipoda)	30–2681	2651	B
<i>Tarasovium cornutum</i> (Cirripedia)	348–3941	3593	B
<i>Munna acanthifera</i> (Isopoda)	32–2681	2649	B
<i>Eusergestes arcticus</i> (Decapoda)	250–5030	4780	P
<i>Hymenodora glacialis</i> (Decapoda)	300–3900	3600	P
<i>Caecognathia stygia</i> (Isopoda)	180–2681	2501	B
<i>Eurycope producta</i> (Isopoda)	180–2681	2501	B
<i>Parakanthophoreus longiremis</i> (Tanaidacea)	50–2681	2631	B

gaimardi, *Diastylis* spp., and *Leucon nasica* (Piepenburg et al. 2011). The shelf seas adjoining the major gateways to the Arctic—the Barents and Kara Seas in the Atlantic section and the Chukchi Sea in the Pacific section—host the most diverse benthic communities. The share of Pacific and Atlantic species diminishes with increasing distance from the Bering Strait and Fram Strait, respectively (Josefson et al. 2013). Biogeographical zonation in the Russian Arctic is strongly influenced by freshwater discharge from the large Siberian Rivers. Cold brackish habitats of shallow estuaries established ~10,000 years ago after the final retreat of the ice sheet and harbor some Arctic relict species including the isopod *Saduria sibirica* (Josefson et al. 2013). The isolated populations of stenothermic cold-water species may also find refugia in the innermost basins of the glaciated fjords (Węśławski et al. 2011).

Polar Deep Seas

Despite recent progress, the Antarctic deep-sea fauna remains much less known than continental shelf faunas. The ANDEEP program (Brandt and Hilbig 2004, Brandt and Ebbe 2007) explored the deep-sea

basins in the Weddell and Scotia seas and discovered significant numbers of unknown benthic crustacean species, in particular isopods and amphipods (De Broyer et al. 2004, Brandt et al. 2007b, 2012). In Munnidopsidae (Isopoda), 80% of collected species were unknown (Malyutina and Brandt 2007). While most taxa became less diverse with depth, the species richness of Isopoda is lowest on the shelf and upper slope (<400 species, mostly endemic) and greatest at bathyal and abyssal depths where ~600 mostly undescribed morphospecies have been recorded (Brandt et al. 2007b, 2009). In addition, this abyssal fauna was highly endemic, possibly simply reflecting undersampling but suggesting connectivity with the adjacent deep-sea basins in the Atlantic. This confirms that, in contrast to the shelf fauna, the Antarctic deep-sea benthos is not isolated from other deep-sea basins but connected via the cold isothermal environment and circulation of the Antarctic Bottom Water.

In the deep central Arctic Basin more than 300 benthic crustacean species occur (Table 9.2) with three tanaidacean species: *Parakanthophoreus gracilis*, *Pseudosphyrapus anomalus*, and *Pseudotanais affinis* being the most widely distributed. The deep Arctic fauna shows low endemism, high shares of subarctic species, and significant taxonomic overlap with the shelf fauna. Over 60% of macrobenthic species found below 500 m depth occur also on the shelf (Bluhm et al. 2011). The predominance of eurybathic species observed in the Atlantic section results from the glaciation history of this area, which favored survival of species able to escape to the great depths during the shelf glaciation and re-invade shallow waters when ice sheet retreated (Josefson et al. 2013). Brandt (1997) found only 10 exclusively deep-sea genera of Peracarida, while 60 genera had a wide bathymetric range in the deep Greenland Sea.

SEA ICE—A UNIQUE HABITAT

Sea-ice cover is a characteristic feature of both Polar regions but differs between the Arctic and the Antarctic. More than half of the sea ice in the Arctic is perennial ice (five to seven years), ranging from 2 to 4 m thick. In contrast, the majority of Antarctic ice is first-year ice less than 1 m thick that melts in the summer (Arndt and Swadling 2006). Both the extent and thickness of the Arctic perennial multi-year ice has been significantly decreasing over the past 30 years. At the same time, sea ice extent in the Southern Ocean has shown strong regional differences but overall is increasing (Parkinson 2014).

Sea ice provides a complex semisolid platform, which allows the development of diverse sympagic (ice-associated) communities unique to polar seas. The underside and interior network of channels and pores filled with brine constitute an “up-side down” benthic habitat colonized by numerous protozoan and metazoan grazers of pelagic and benthic origin that use ice as a breeding, nursery, and feeding ground and refuge area. Crustaceans represented by about 50 species in each area are prominent members of sympagic assemblages at both poles (Figure 9.4). In the Arctic, the fauna is dominated by four amphipod species inhabiting the ice–water interface: *Gammarus wilkitzkii*, *Apherusa glacialis*, *Onisimus nanseni*, and *O. glacialis* with abundances up to 500 individuals m^{-2} (Arndt and Pavlova 2005). In the upper layer of the water column beneath the ice, sibling species of predatory hyperiid amphipods, *Themisto libellula* and *T. abyssorum*, occur in swarms of up to 430 and 270 individuals m^{-2} , respectively. The ice interior in the Arctic is inhabited by small harpacticoid genera, *Harpacticus*, *Halectinosoma* and *Tisbe*, and cyclopoid copepods (*Cyclopina* spp.). Several species of calanoid copepods (including key Arctic species: *Calanus glacialis* and *C. hyperboreus*) perform diel vertical migrations to the ice subsurface where they graze on ice algae but do not enter the brine-channel system. Additionally, young stages of ice and pelagic copepods (eggs and nauplii) may accumulate in sea and ice in numbers of more than 100,000 m^{-2} . Other crustacean taxa (mysids, decapods, and euphausiids) do not contribute considerably to the sympagic communities in the Arctic (Arndt and Swadling 2006).

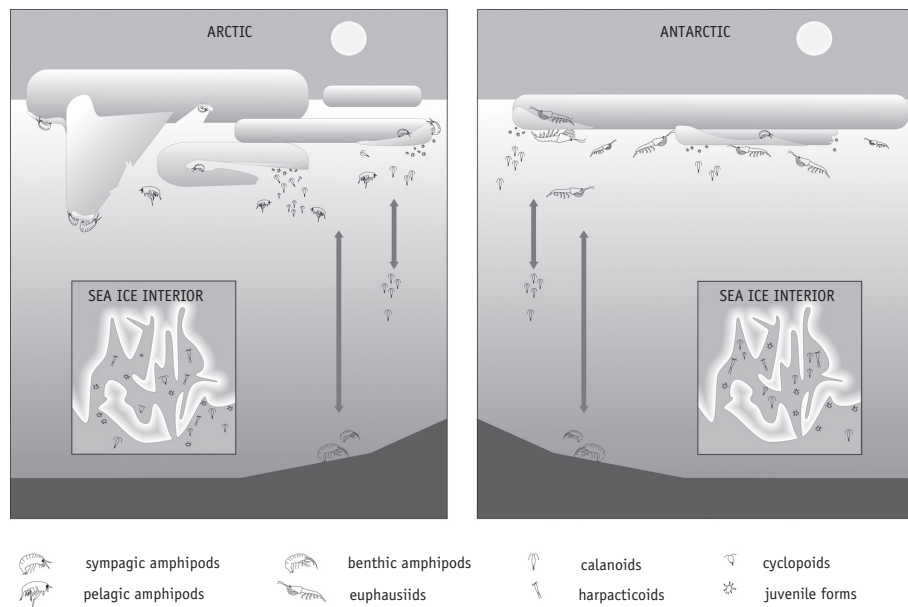


Fig. 9.4.

Sea-ice-associated crustaceans in the Arctic (left) and Antarctic (right). See color version of this figure in centerfold.

In contrast to the Arctic, euphausiids are important members of the Antarctic ice fauna. Pack ice has direct and indirect effect on krill distribution, life cycle, and population dynamics. *Euphausia crystallorophias*, the neritic “ice krill,” is found under the ice only over the continental shelf. The circumpolar distribution of Antarctic krill, *E. superba*, on the other hand, is limited to the area bound by the maximum sea ice extent, with the exception of populations around South Georgia (Siegel 2005, Atkinson et al. 2008; Figure 9.5). During winter, larval krill settles under Antarctic annual sea ice, preferably in complex under-ice habitats of eroded ice floes. Larval *E. superba* feeds on ice-associated biota, in particular microbial communities, a food source that is one to three orders of magnitude more abundant in winter than the food sources in the water column immediately below (Quetin and Ross 2009). The reproductive cycle, in particular ovarian development in spring and larval survival during the first winter, may be impacted by the timing and extent of sea ice in winter and/or spring, which mediates the food availability (Loeb et al. 1997, Quetin and Ross 2001). Stabilization of the water column by melting pack ice in late winter or early spring favorably affects planktonic diatom growth, the preferred food of krill, which in turn may enhance egg production during summer.

An important difference between the sympagic assemblages of the two Polar regions is the much higher abundance and biomass of copepods inhabiting the brine channels in the Antarctic. The three most frequently observed copepod species, calanoids *Stephos longipes* and *Paralabidocera antarctica*, and harpacticoid *Drescheriella glacialis* are circumantarctic, but with differing abundances. Cyclopoid copepods, which dominate the water column, remain loosely associated with the ice. Few amphipod species recorded from the Antarctic ice are thought to be strongly ice-associated, with *Eusirus* spp. being the most numerous (Krapp et al. 2008). Some benthic gammarids, however, (e.g., *Paramoera walkeri*, *Debroyerella fougneri*, *Gondogeneia antarctica*, *Pseudorchomene cf. plebs*), may periodically extensively use the ice–water interface as a feeding ground reaching densities close to 13,000 individuals m^{-2} (Swadling 2014).

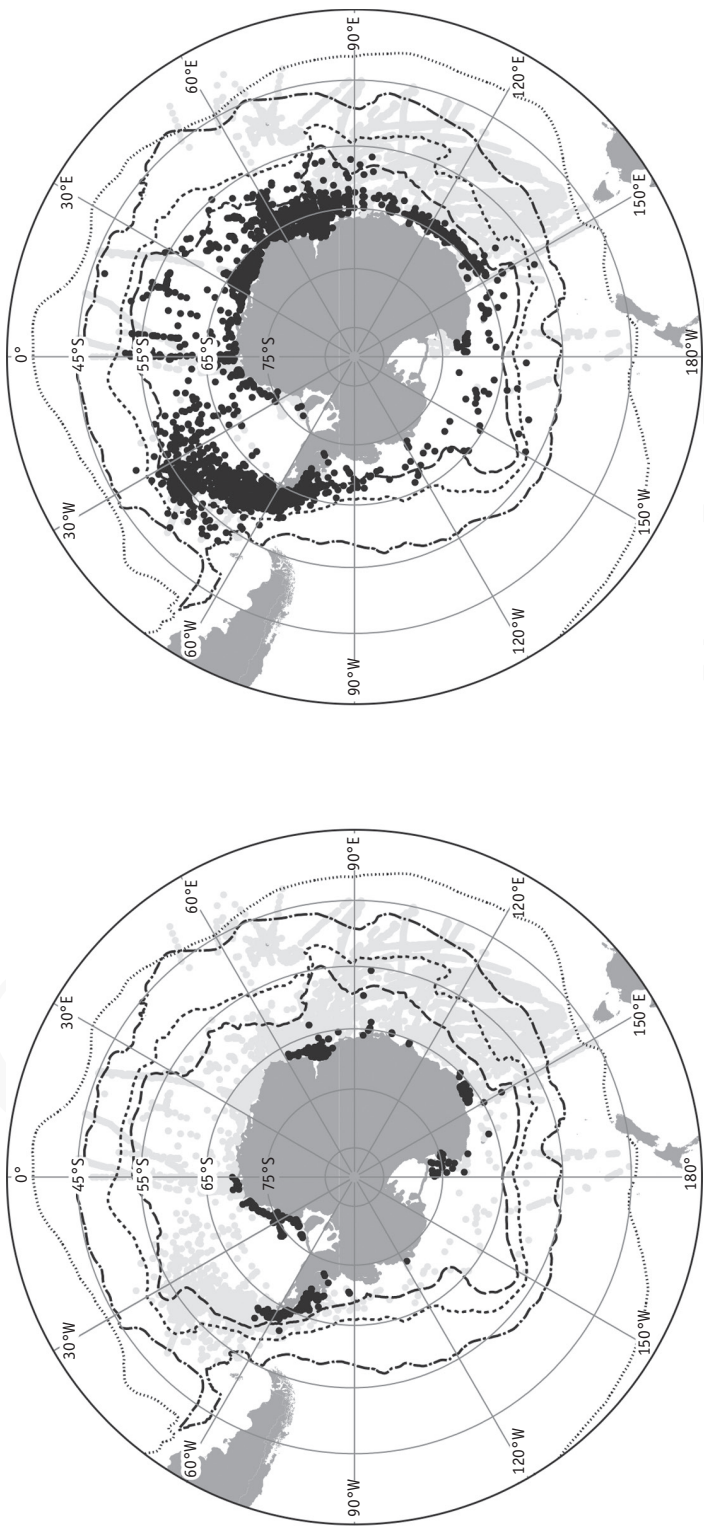


Fig. 9.5. Comparative geographic distribution of *Euphausia crystallorophias* (left) and *Euphausia superba* (right). Dotted circumpolar lines: Polar Front (second from the south); Subtropical Front (northernmost line) From Cuzin-Roudy et al. 2014.

ON-GOING CHANGES

Loss of Sea Ice

Polar regions have experienced greater warming in recent decades than other oceans (ACIA 2004). Summer melting and ice export through the Fram Strait into the Greenland Sea strongly diminish ice cover in the Arctic each year, and it is predicted that the Arctic Ocean will be ice-free during the summer within 30 years (Berge et al. 2012). Rapid decrease of the extent and thickness of perennial ice is alarming, because due to its complicated underwater topography and good feeding conditions, it is a preferred habitat for amphipods, considered to be obligate residents of this habitat (Lønne and Gulliksen 1991). It has been estimated that the annual biomass loss of sympagic amphipods due to ice export through the Fram Strait could be up to 38×10^5 t WW (Arndt and Lønne 2002). Some released specimens, however, survive when advected to shallow coastal waters. Arndt and Pavlova (2005) identified continental shelves and coastal areas as temporary habitats for sympagic organisms during ice-free periods and as stepping stones for recolonization. *Gammarus wilkitzkii* may occur both in pelagial (Werner et al. 1999) and intertidal zones among macroalgae (Węśławski 1994). Berge et al. (2012) proposed that during ice melt *Apherusa glacialis*, the most numerous of ice-associated amphipods, may perform deep downward migrations, is transported by circum-Arctic currents, and ascends in areas more likely covered by ice.

Increasing Ultraviolet Radiation

Increased ultraviolet radiation (UVR) due to severe ozone loss has been recognized as an important ecological stressor for polar ecosystems (Dahms et al. 2011). Polar organisms are thought to be particularly vulnerable because they have adapted to substantially lower UV irradiance than that imposed by ozone depletion and sea ice thinning (Rautio et al. 2009, Dahms et al. 2011). Ozone depletion is less pronounced in the Arctic than in the Antarctic, where an ozone hole is observed every year (Manney et al. 2011). Biologically relevant doses of UV may penetrate the water and affect plankton and benthic taxa occurring down to 20–30 m depth (Agusti 2008). Exposure to UV radiation, especially UV-B radiation, is deleterious at molecular and cellular levels by damaging lipids, proteins, and DNA either by direct photochemical reaction or by indirect oxidative damage from reactive oxygen species (Llabres et al. 2013).

Pelagic crustaceans, particular early life stages present within the first few meters depth, are especially prone to physiological disorder and death from UVR. Browman et al. (2000) reported deformation, reduced hatching, and survival of first-stage nauplii of the subarctic copepod *Calanus finmarchicus*. Jarman et al. (1999) noted that Antarctic krill DNA may be particularly susceptible to damage from UV-B and that a 60-fold decline in abundance in the Southern Ocean observed between 1970 and 2003 attributed to reduction of sea-ice cover might have been partially caused by increased exposure to UV-B (Llabres et al. 2013). Organisms have evolved a range of behavioral, physiological, and biochemical adaptations that prevent or repair UVR-induced DNA damage. In crustaceans, UVR may be effectively blocked by the exoskeleton (Obermüller and Abele 2004, Van den Broecke et al. 2012). Some species avoid UVR by using unexposed habitats or by downward migrations during the day (Newman et al. 2003, Wold and Norrbin 2004, Dahms et al. 2011). Photoprotection (accumulation of light-filtering compounds) and antioxidant protection (quenching agents and antioxidant enzymes) are widespread (Obermüller et al. 2007, Rautio et al. 2009). Since most of the sun-screening compounds are acquired through an algal-rich diet, herbivorous species (e.g., *Gammarus homari*, Obermüller et al. 2005; and Antarctic krill *Euphausia superba*, Newman et al. 2000) seem to be better protected than carnivorous ones (such as the lysianassoid amphipod *Anonyx nugax*, Obermüller et al. 2005). The last line of defense, when all

above-mentioned protective measures are not sufficient, are DNA repair mechanisms that ensure the genomic integrity (Malloy et al. 1997).

Long-term effects of increasing UVR in polar systems are difficult to assess. Since different species differ in their sensitivity towards UVR shifts in species diversity and community composition may be a consequence. However, it has been suggested that possible consequences of indirect UVR effects via changes in trophic interactions and combined effects of UVR with other environmental stressors can have a more pronounced impact on polar ecosystems (Dahms et al. 2011).

Invasive Species

Ongoing warming is likely to increase the risk of non-indigenous species invasion to the Polar regions since it gradually reduces environmental barriers preventing the colonization by lower-latitude species and enables a rapid increase in human activity and marine traffic. Ballast water and hull biofouling are the two main anthropogenic vectors for marine species introduction, although plastic debris may also contribute to the spread of invasive species within Polar regions (Barnes 2002, Ware et al. 2016, Hughes and Ashton 2017). Invasive species are considered the important threat for native marine biodiversity in both Polar regions, especially in the Antarctic inhabited by highly endemic fauna (Barnes 2002).

Antarctic

A unique case of alien invasive species has been documented so far in Antarctic seas: two adults of the boreo-Arctic crab *Hyas araneus* were recorded off the Antarctic Peninsula (Tavares and De Melo 2004) with no subsequent records (Clarke et al. 2005). However, in the Southern Ocean warming context (Turner et al. 2009, 2013), subantarctic species expanding their range southward, emerging slope species, or organisms introduced by humans may be expected, with potentially harmful consequences for the native biota (Barnes et al. 2006, Aronson et al. 2007). Decapod crustaceans, lithodids in particular, relatively well represented at subantarctic latitudes in contrast to their rare Antarctic occurrences, have been considered potential invasive candidates (Thatje et al. 2005, Aronson et al. 2007, 2015, Smith et al. 2012, Griffiths et al. 2013, 2014). Among the 11 lithodid species so far recorded in Antarctic and subantarctic seas, none occurs on the cold Antarctic continental shelf. Their distribution was shown to be constrained by temperature, with no records from waters colder than 0°C (Hall and Thatje 2011). In contrast to brachyuran crabs, lithodid crabs of the Southern Ocean and adjacent waters present life-history adaptations (eurybathy, cold tolerance, lecithotrophic larvae) predisposing them to be “invaders” of the Antarctic continental shelf in cases where the shelf waters warm up (Aronson et al. 2015).

Arctic

As the Arctic fauna is relatively young, it has close relatives in the areas of its origin, the sub-arctic Atlantic and Pacific. Those species have a potential to expand their ranges with increasing sea temperature and stronger northward advection of North Atlantic waters along the west Spitsbergen or Pacific waters through the Bering Strait. The boreal hyperiid *Themisto compressa* has expanded northward by ~1000 km to Spitsbergen and is now able to reproduce and coexist in the Arctic with two sibling species, *T. abyssorum* and *T. libellula* (Kraft et al. 2013). Similarly, rapid northward movement of the North Atlantic copepods has been reported, with true Arctic species, such as *Calanus glacialis*, being replaced by temperate *Calanus finmarchicus* (Beaugrand

et al. 2009). In addition to natural enhanced dispersal, greater shipping activity (e.g., opening of trans-Arctic shipping routes) and an extended shipping season are likely to increase the ship-mediated invasion risk in the region. Ware et al. (2016) detected 23 non-indigenous zooplankton species in the ballast waters from just eight ships visiting Svalbard in 2011. While current environmental conditions prevent their survival in this area, invasion threat will increase over the coming decades. Invasive benthic species have been discovered in the region at a rather slow pace. The littoral, boreal amphipod *Gammarus oceanicus* has been spreading along Svalbard for at least 20 years, sharing habitat with a local cold-water species, *G. setosus* (Węśławski et al. 2011). The decapod fauna of Isfjorden, Svalbard, has not changed during the last 150 years (Berge et al. 2009). On the other hand, over the last decades, two alien species of large crabs have established their populations in the Arctic. The king crab *Paralithodes camtschaticus* from the northern Pacific was introduced to the Murmansk area in the 1960s, spread in the southern Barents Sea, and then started to move south along the Norwegian coast and northeast of the Kola Peninsula (Falk-Petersen et al. 2011). The snow crab *Chionoecetes opilio*, native to the north-west Atlantic, the north Pacific, and the Japan Sea, was recorded for the first time in the Barents Sea in 1996, presumably introduced through ballast water (Alsvåg et al. 2009). At present, it is expanding in the Barents Sea, and it was detected for the first time in Svalbard (Raudfjorden) in summer 2017 (University Centre in Svalbard data, www.unis.no). Both species are likely to have a significant impact both ecologically (predation and competition with local fauna) and economically (commercial fishery).

FUTURE DIRECTIONS

There are several possible avenues for future studies in polar Crustacea. On the one hand, additional sampling is needed to complete species inventories, particularly in hitherto poorly investigated deep seas, but also across wide geographic gradients since the quality and quantity of available information still varies broadly among both regions and taxa. It might be expected that an increased use of molecular methods would bring about identification of many unknown cryptic species. More research is necessary to better understand the role of crustaceans in the polar food web and ecosystem functioning, especially in the context of climate change. Here the question arises: What will be the ecological, physiological and genetic response of polar crustacean populations to the sea ice shrinking and water temperature increase? Sympagic species currently hold a crucial position in the food webs, hence resolving how they may react to changes in ice cover and duration is of fundamental importance to quantify the magnitude of future changes of polar ecosystems. Studies are also needed to assess possible consequences of the non-native species invasion from the boreal regions. Attention should be paid to the possibility of them becoming established residents and their ability to compete and replace native polar taxa, which may lead to the alterations in the food web.

CONCLUSIONS

Crustaceans are widespread and functionally important members of pelagic, benthic, and sea-ice communities of both Polar regions. The number of hitherto recorded species is slightly higher in the Antarctic (over 2,250) than in the Arctic (over 1,930). Species inventory, however, is still far from complete, and discoveries of new species, especially in poorly studied deep seas, may be expected. In comparison with the lower-latitude species, polar crustaceans typically exhibit slower growth and development, have extended life cycles, and attain larger final size. Despite many similarities, the two Polar regions are distinctly different ecosystems due to their different age, geographical and

oceanographical settings, and degree of isolation. An old age and long history of isolation resulted in a high rate of endemism within the Antarctic benthic fauna, while the relatively young advective Arctic ecosystem contains few endemics and is dominated by widely distributed Arctic-boreal species. Abundant populations of pelagic microalgal grazers (large euphausiids in the Antarctic and much smaller copepods in the Arctic) play a crucial role in the polar ecosystems supporting upper trophic levels: fish, birds, and sea mammals. Sea-ice communities are similarly diversified but different at both poles. The most notable features of the Southern Ocean sympagic fauna are high abundance and biomass of calanoid copepods and euphausiids and the lack of any species that appear fully dependent on the ice. In the Arctic, tiny harpacticoids and cyclopoids are most numerous in the ice interior, while the ice underside is dominated by four species of amphipods that are thought to be obligate ice dwellers. Within the benthic domain, fewer species are observed in the littoral zone, while heterogeneous sublittoral habitats often host rich and diversified crustacean communities. In the Antarctic, amphipods and isopods are particularly numerous and speciose, while decapods and cirripeds are scarce. In the Arctic, Amphipoda considerably outnumber other taxa in terms of species richness, followed by Cumacea and Isopoda. Changes inducted by ongoing warming, such as decline of sea-ice cover, increase of UV radiation, and advection of invasive species, may negatively affect biodiversity of polar crustaceans, but detailed studies are needed to assess the actual threat.

See also supplementary Figure 9.s1 (Antarctic species) and Figure 9.s2 (Arctic species), in the centerfold of the volume.

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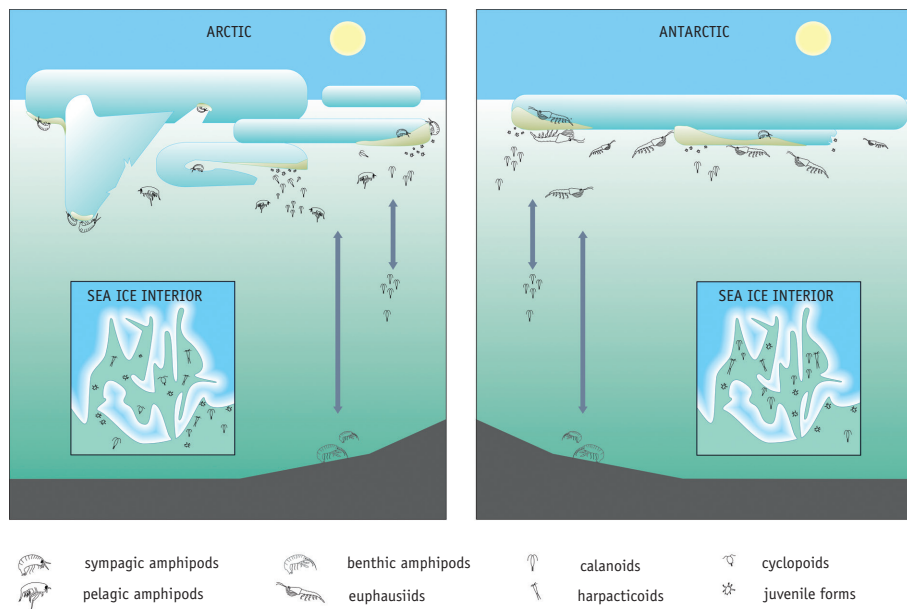


Fig. 9.4. Sea-ice-associated crustaceans in the Arctic (left) and Antarctic (right).

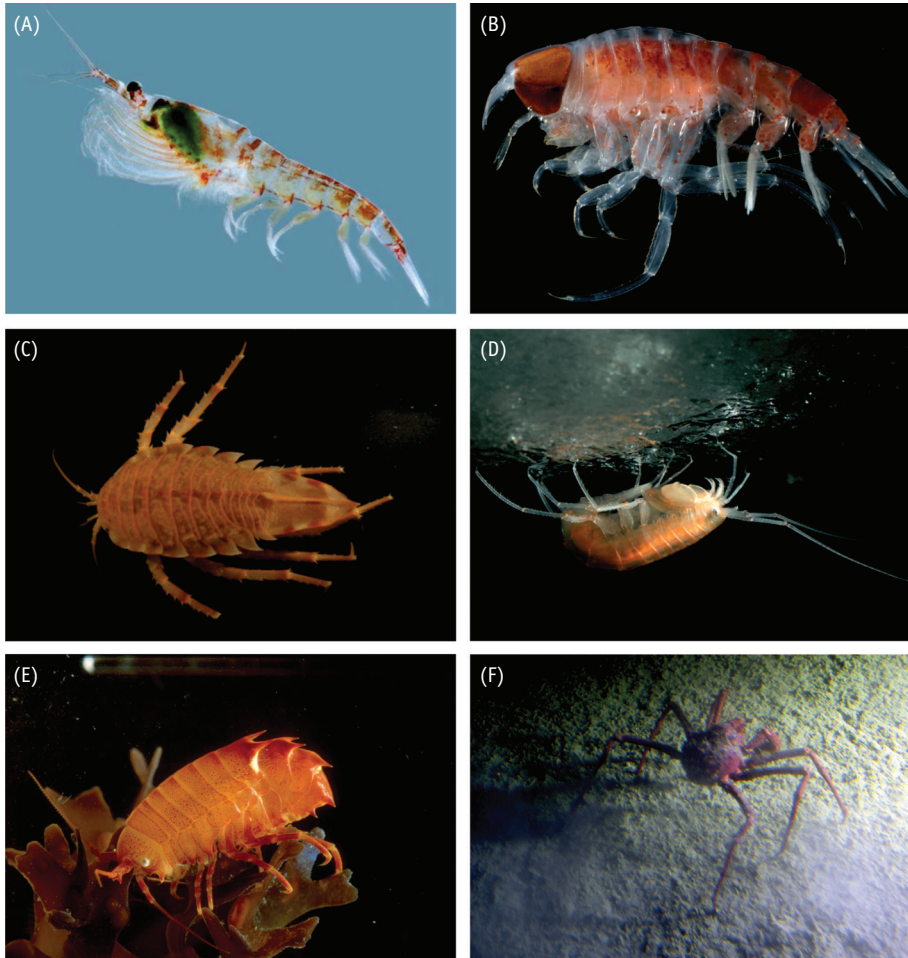


Fig. 9.s1.

Antarctic crustaceans: (A) Antarctic krill (*Euphausia superba*); photo courtesy of Volker Siegel; (B) pelagic hyperiid amphipod *Cyllopus lucasii*; photo courtesy of Martin Rauschert; (C) benthic giant isopod *Glyptonotus antarcticus*, 120 mm; photo courtesy of Cédric d'Udekem d'Acoz; (D) cryoplectic amphipod *Eusirus microps*; photo courtesy of Ingo Arndt & Rupert Krapp; (E) benthic amphipod *Gnathiphimedia fuschi*; photo Claude de Broyer; (F) a potential invader of the Antarctic shelf, the king crab *Neolithodes yaldwini*, detected at 980 m in Palmer Deep (West Antarctic Peninsula) by the NHK submarine expedition 2017; photo Claude De Broyer, courtesy of NHK.

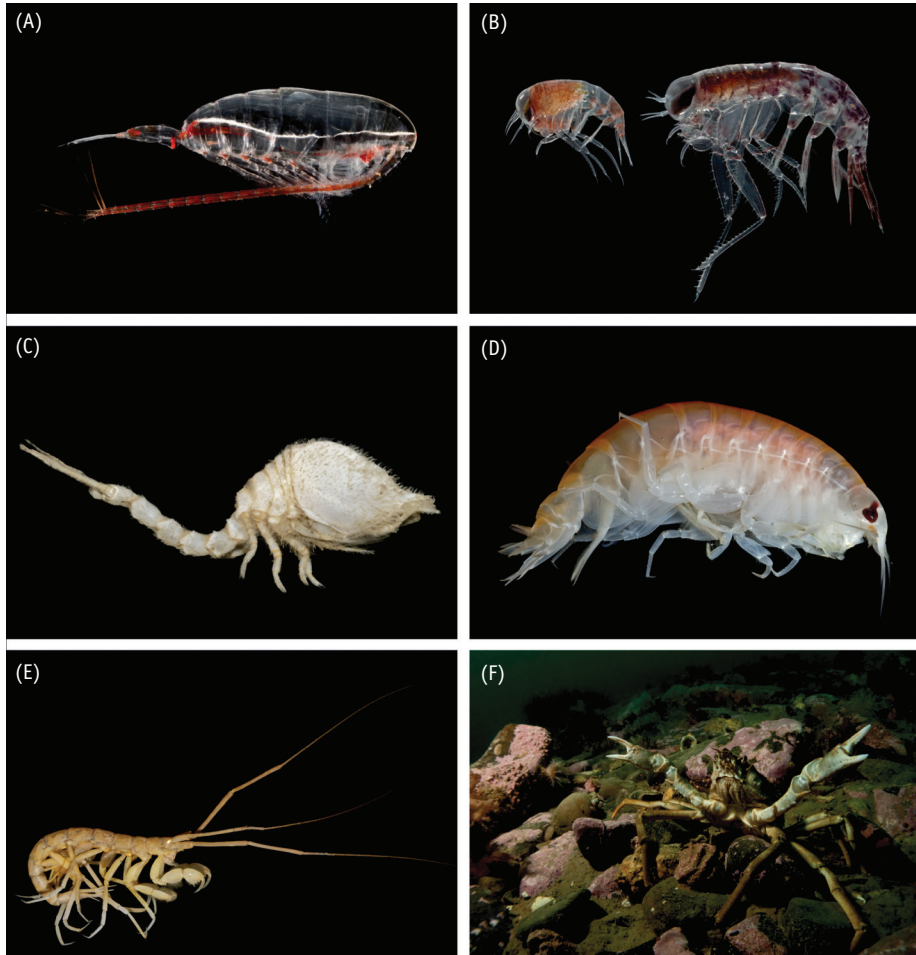


Fig. 9.s2.

Arctic crustaceans: (A) copepod *Calanus hyperboreus*; photo courtesy of Maria Włodarska-Kowalczyk, IO PAN; (B) hyperiid amphipods *Themisto abyssorum* (left) and *Themisto libellula* (right); photo courtesy of Maria Włodarska-Kowalczyk, IO PAN; (C) the largest world's cumacean, *Diastylis goodsiri*; photo courtesy of Kajetan Deja, IO PAN; (D) necrophagic amphipod *Anonyx nugax*; photo courtesy of Kajetan Deja, IO PAN; (E) benthic amphipod *Neohela monstrosa*; photo courtesy of Kajetan Deja, IO PAN; (F) crab *Hyas araneus*; photo courtesy of Piotr Balazy, IO PAN.
