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BIOGEOGRAPHIC ATLAS OF THE SOUTHERN OCEAN

► CHAPTER 6.4. SOUTHERN OCEAN PTEROPODS.

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THE BIOGEOGRAPHIC ATLAS OF THE SOUTHERN OCEAN

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6.4. Southern Ocean Pteropods

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1. Introduction

Pteropods are small free-swimming planktonic gastropods. Their informal name derives from the modified molluscan foot ('-poda') to form paired swimming wings ('ptero-') in both the Thecosomata ('covered' or shelled pteropods) and the Gymnosomata ('naked' or shell-less pteropods). Both orders are found in the surface ocean to the deep sea, have a global distribution, although population densities are often highest in polar and sub-polar regions, and exhibit distinct biogeographic patterns in the Southern Ocean. It should be appreciated that the two orders are taxonomically distinct from each other within the gastropods (there are major differences in their morphologies, trophic levels, mode of predation and contribution to carbon export). Consequently, they should be cautiously lumped together under the general term 'pteropod', and ideally described as either Thecosomata (shelled) or Gymnosomata (naked) in order for there to be a clear distinction between the group under discussion.

The shelled pteropods have a thin external shell composed of a form of calcium carbonate known as aragonite. They are the largest planktonic producer of aragonite in the world's oceans (Orr *et al.* 2005) and contribute significantly to the carbon cycle of the ocean (Lalli & Gilmer 1989, Noji *et al.* 1997, Singh & Conan 2008) and the Southern Ocean south of the Polar Front in particular (Accornero *et al.* 2003, Honjo 2004), where densities can be as high as 100–1000s individuals/m³ (Hopkins 1987, Pakhomov *et al.* 1997, Seibel & Dierssen 2003, Hunt *et al.* 2007).

The naked pteropods have a thin external shell only during their early life stage (Lalli & Gilmer 1989). They are specialised carnivorous feeders, do not tend to form swarms and not usually significant contributors to the zooplankton biomass of a region, except in some polar areas (van der Spoel & Dadon 1999).

All thecosomatous pteropods are protandric hermaphrodites (i.e. change from male to female throughout their lives). However, details of the life histories of pteropods, and Southern Ocean pteropods in particular, remain a significant knowledge gap. It is assumed that most shelled species entire life cycles are of the order of a year with eggs released in gelatinous masses followed by veliger larval hatching, metamorphoses and development into juveniles. *Limacina helicina* varieties are thought to follow this cycle (van der Spoel & Dadon, 1999) whereas ovoviparity (the maintenance of eggs within the mothers body to hatch 'live' offspring) has been seen in some pteropods, especially those adapted to the deep-sea habitat such as *Thielea helicoides* (van der Spoel & Dadon 1999). Gymnosomes have a similar reproductive anatomy to thecosome pteropods but may function as simultaneous hermaphrodites at maturity, male reproductive organs not degenerating in females as they do in thecosomes (Lalli & Gilmer 1989).

The number of generations per year appears to differ between Antarctic and sub-Antarctic populations. Antarctic pteropods are thought to produce just one generation per year. Seasonal density observations by Hunt *et al.* (2008) support this suggestion for *Limacina rangii* although Bednaršek *et al.* (2012) have recently proposed that a small number of *Limacina rangii* may live for more than 2 years in Southern Ocean waters. Note that *Limacina rangii* is often referred to in the literature as *Limacina helicina antarctica* but we follow the nomenclature of the World Register of Marine Species here. Sub-Antarctic pteropods have been proposed to have different generation modes and growth rates. Dadon & de Cidre's (1992) work on the life history of *Limacina retroversa australis* remains the only detailed study of a Southern Ocean pteropod's life history to date. They found this taxon survived for a maximum of one year, producing two generations: the first in spring and the second in late summer. The first generation has a high growth rate and matures early to reproduce in late summer while the second grows during autumn but not at all over winter, reproducing in the spring. This annual cycle matches the general primary production cycle of the sub-Antarctic zone.

Pteropods are thought to undergo diel migrations, residing in surface waters at night and descending to deeper waters during the day (typical distances travelled are species specific but of the order of 10–100 m) (Hunt *et al.* 2008, Lalli & Gilmer 1989, van der Spoel & Dadon 1999). They play important roles as both grazers and prey in the Southern Ocean community. Shelled pteropods feed on suspended phytoplankton using free-floating mucous webs (Lalli & Gilmer 1989) and can have a significant grazing impact, particularly in high latitude regions. In the Southern Ocean, they favour diatoms, dinoflagellates, tintinnids, copepods, silicoflagellates, polychaetes and foraminifers and can consume as much as 19% of the daily primary production when they are aggregated (Hopkins 1987, Hunt *et al.* 2008). Thecosomata are the exclusive prey of the Gymnosomata (Lalli & Gilmer 1989) as well as food for higher trophic level predators such as krill, salps, fish, birds and whales (Foster 1987, Karnovsky *et al.* 2008, Hunt *et al.* 2008). The carnivorous Gymnosomata have specialised hunting and feeding structures used for capturing Thecosomata and are themselves food for medusa, ctenophores, fish, sea birds and whales (Lalli & Gilmer 1989).

Given the rate of environmental change the Southern Ocean is experiencing, we are faced with the question of whether or not pteropods will thrive, cope, adapt or decline. Pteropods are often referred to as 'sentinel' organisms as we expect them to be among the first organisms to be impacted by changing water chemistry, temperature, oxygen and nutrient deficiencies in our southern polar regions in the future. If pteropods undergo significant decreases in abundance, or even face a complete loss of species (Comeau *et al.* 2012), this could have significant implications for Southern Ocean biodiversity and the ecological services it is able to provide (Orr *et al.* 2005, Cooley *et al.* 2009).

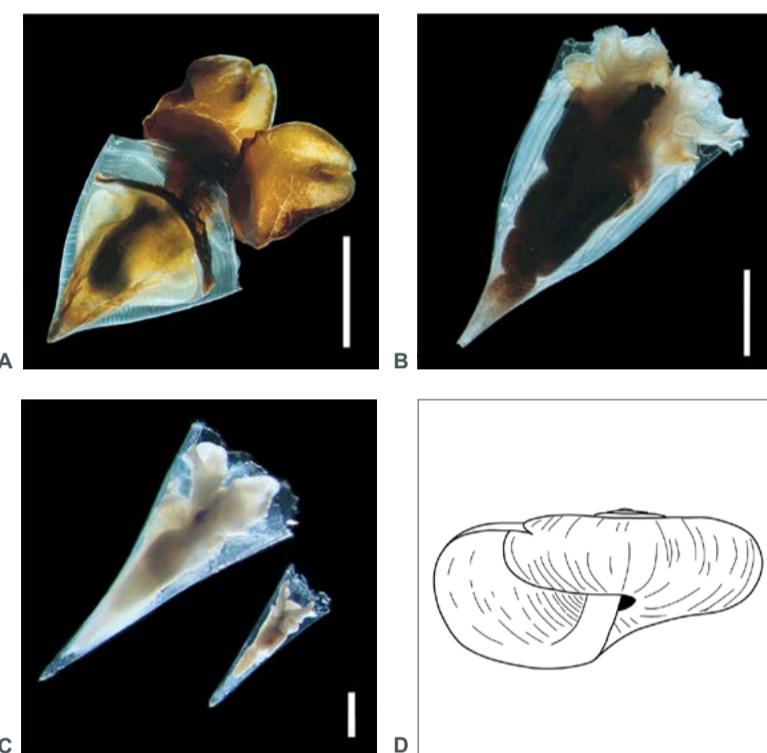


Photo 1 The major varieties of Antarctic shelled pteropods found in Southern Ocean waters. (a) *Clio recurva balantium* Rang, 1834 [this specimen was collected during the CEAMARC Voyage – we suggest *Clio piatkowskii* is not taxonomically separable from *Clio recurva balantium*]. (b) *Clio pyramidata* f. *excisa* van der Spoel, 1963. (c) *Clio pyramidata* f. *sulcata* (Pfeffer, 1879). (d) *Limacina rangii* f. *antarctica* Woodward, 1854 [this form has a very depressed spire and prominent striation]. Scale bars: (a) 10 mm, (b) 5 mm, (c) and (d) 1 mm. Images ©: R. Hopcroft University of Alaska Fairbanks & CoML, except (d) after van der Spoel & Dadon (1999), © Backhuys Publishers, Leiden, The Netherlands, (1999).

2. Methods

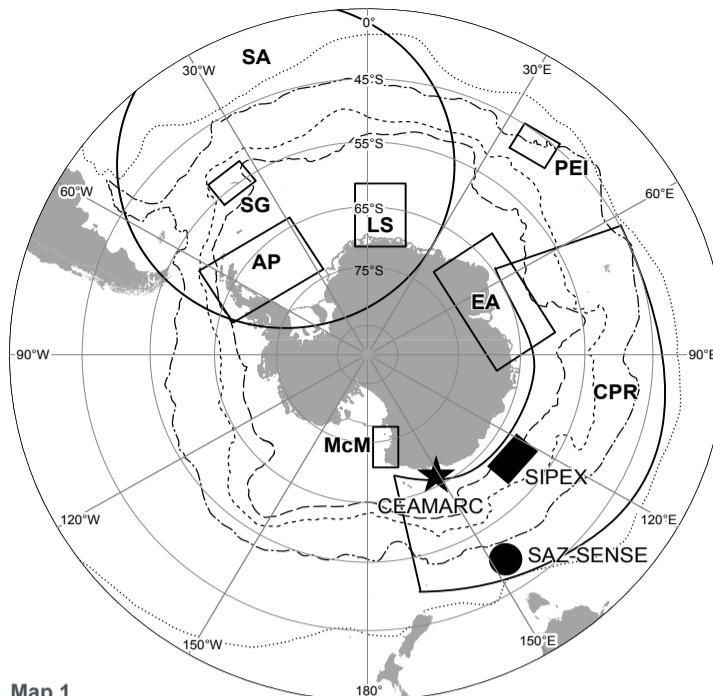
Observations, biodiversity and biogeographic distributions of pteropods included in our Southern Ocean synthesis have been collated from general (Lalli & Gilmer 1989, van der Spoel *et al.* 1997) and regional (van der Spoel & Dadon 1999, Hunt *et al.* 2008, Howard *et al.* 2011, Roberts *et al.* 2011, Cantwell 2012, Hopcroft unpublished data) sources which incorporate distribution surveys of vertical or obliquely hauled plankton nets of various types (including bongo, trawl, IKT and Norpac) and mesh sizes (150 µm – 4.5 mm) — typically in the upper 500 m of the water column, continuous plankton recorder observations — typically in surface waters, sediment trap collections — to as deep as 2000 m, and literature collations. Source areas are summarised in Map 1 and taxa specific distributions from these areas represented in Maps 2–21. Our taxonomic classifications follow the World Register of Marine Species nomenclature.

3. Biodiversity & Biogeographic Distributions

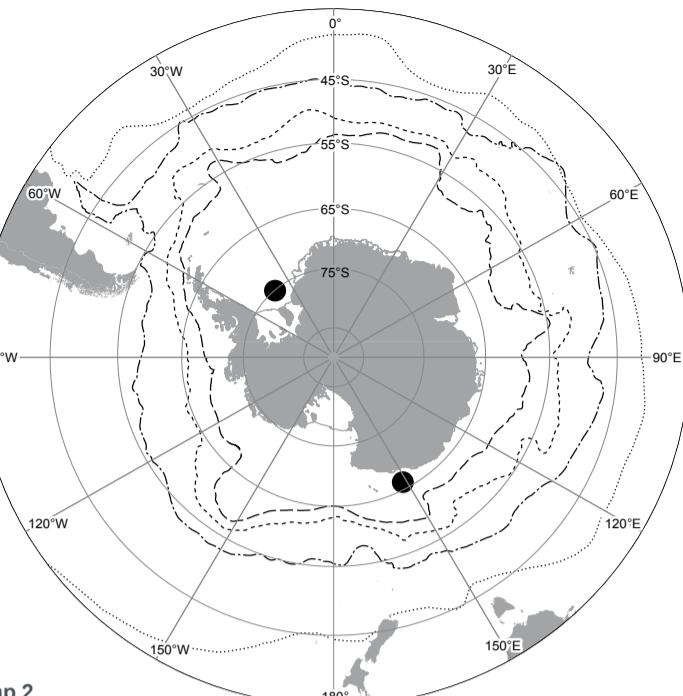
The distribution of Southern Ocean pteropods shows marked temporal and spatial variation greatly influenced by climate, physical properties of water masses, currents and seasonal primary production (Knox 1994, Seibel & Dierssen 2003, van der Spoel & Dadon 1999, Hunt *et al.* 2008).

3.1. Thecosomata

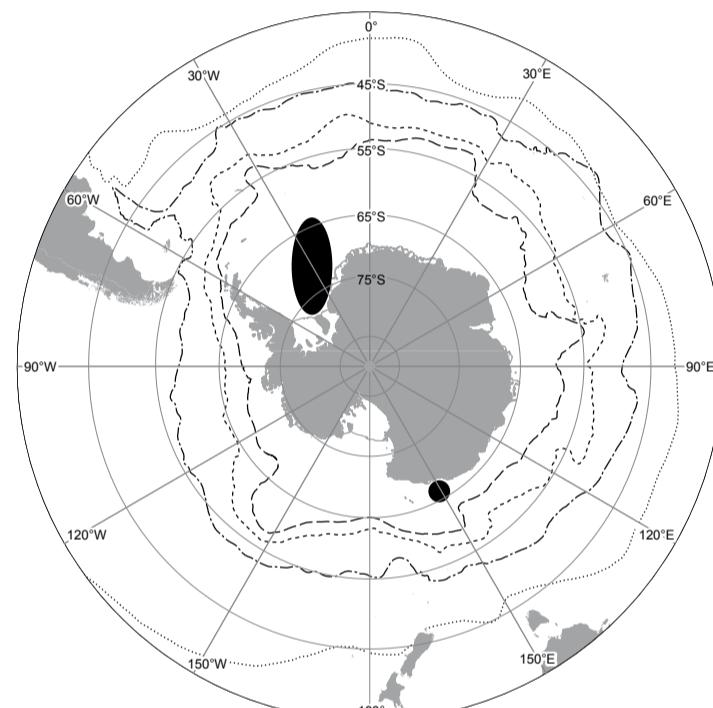
The Thecosomata are distinguished by shell morphology, which includes coiled, cone, pyramidal and globulose forms (Lalli & Gilmer 1989). Of the approximately 40,000 marine gastropod species, only about 140 are wholly planktonic (Lalli & Gilmer 1989) and 86 of these pteropods (van der Spoel *et al.* 1997). Whilst there are over 70 species of shelled pteropod known from the South Atlantic sector of the Southern Ocean alone (van der Spoel & Dadon 1999) the typical diversity in the Southern Ocean proper is much lower (Table 1, Photos 1–3).



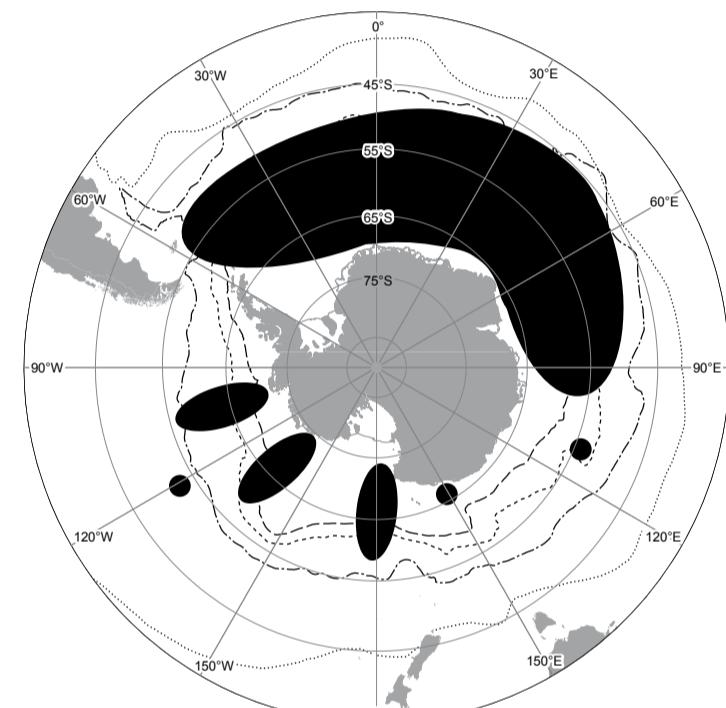
Map 1
Areas considered



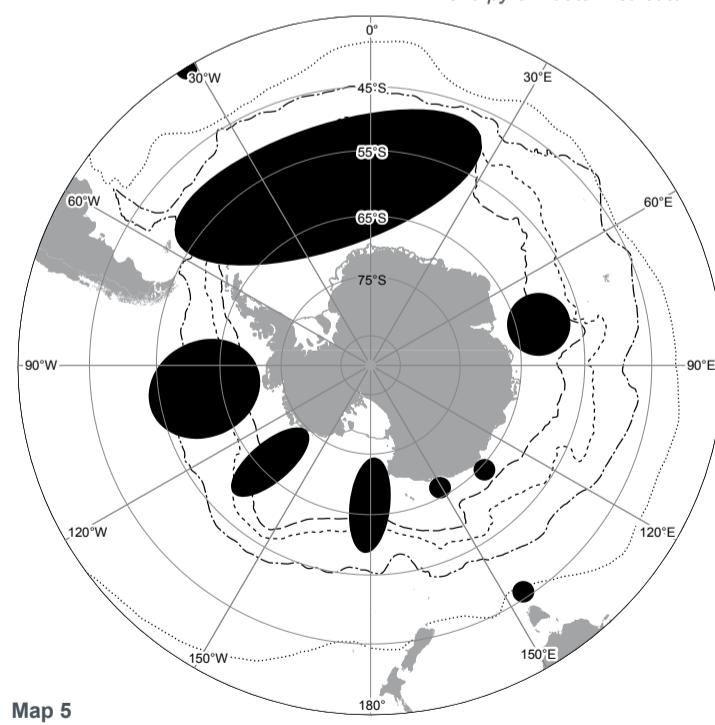
Map 2
Clio piatkowskii



Map 3
Clio pyramidata f. excisa



Map 4
Clio pyramidata f. sulcata

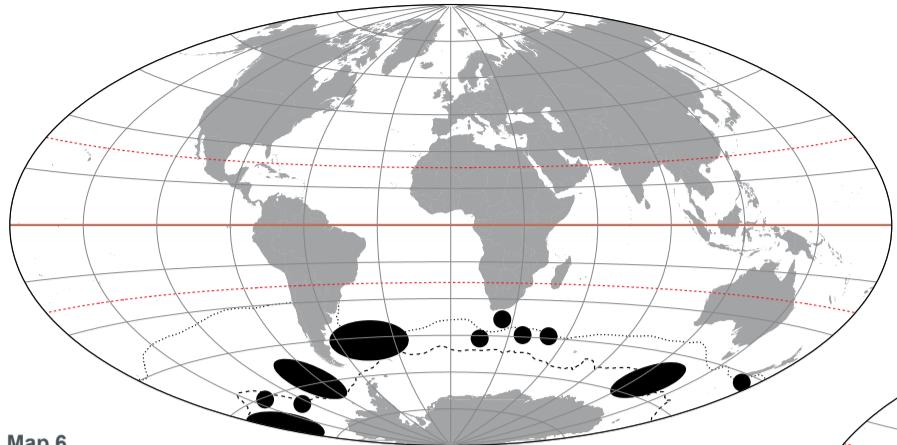


Map 5
Limacina rangii f. antarctica

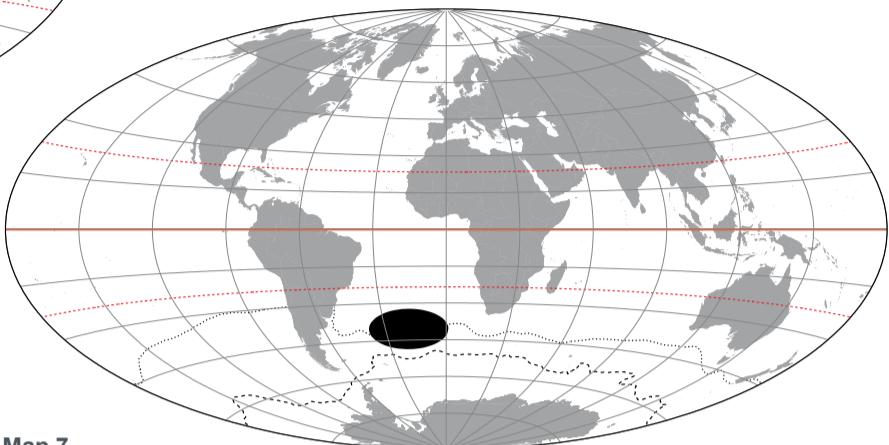
Pteropods Map 1 Map of the Southern Ocean (adapted from van der Spoel & Dadon 1999, Hunt *et al.* 2008, Howard *et al.* 2011, Cantwell 2012, Hopcroft unpublished data) highlighting areas included in this synthesis. The areas of study denoted by open boxes are: AP – Antarctic Peninsula, SG – South Georgia, LS – Lazarev Sea, PEI – Prince Edward Islands, EA – Eastern Antarctica, McM – McMurdo Sound/Ross Sea and CPR – continuous plankton recorder surveys. The open circle denotes the taxonomic treatise undertaken for the South Atlantic – SA – by van der Spoel & Dadon (1999). The solid areas denote survey cruises undertaken in 2007/08: (circle) Sub-Antarctic Zone Sensitivity to Environmental Change (SAZ-SENSE) Voyage (Jan–Feb 2007), (star) Collaborative East Antarctic Marine Census (CEAMARC) Voyage (Dec 2007–Jan 2008) and (box) Sea Ice Physics and Ecosystem eXperiment (SIPEX) Voyage (Sep–Oct 2007). **Pteropods Maps 2–5** Distribution of Antarctic shelled pteropods. Map 2. *Clio piatkowskii* van der Spoel, Schalk & Bleeker, 1992. Map 3. *Clio pyramidata f. excisa*, van der Spoel, 1963. Map 4. *Clio pyramidata f. sulcata* (Pfeffer, 1879). Map 5. *Limacina rangii f. antarctica* Woodward, 1854.



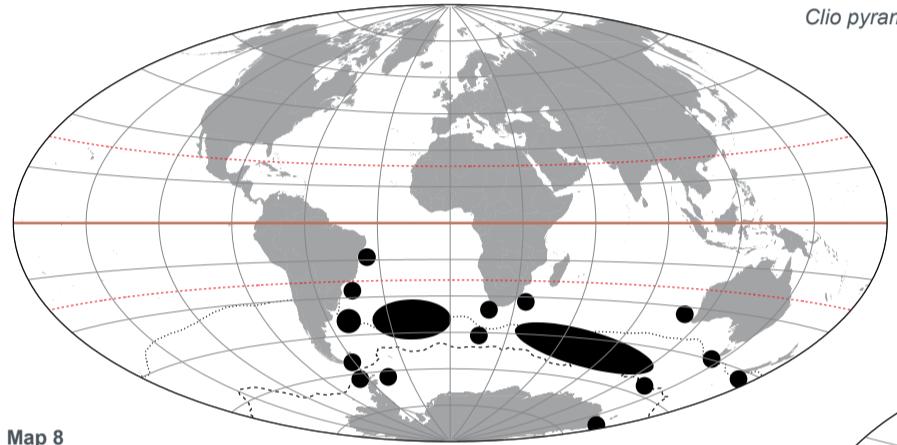
► Mollusca : Pteropods



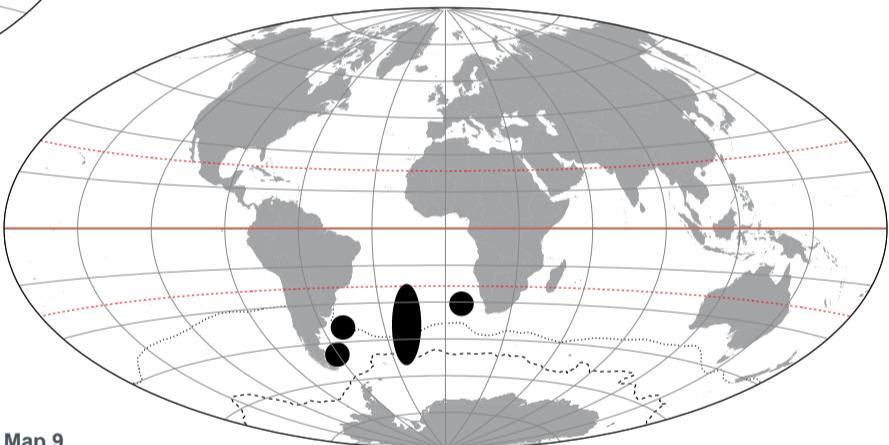
Map 6
Clio pyramidata f. antarctica



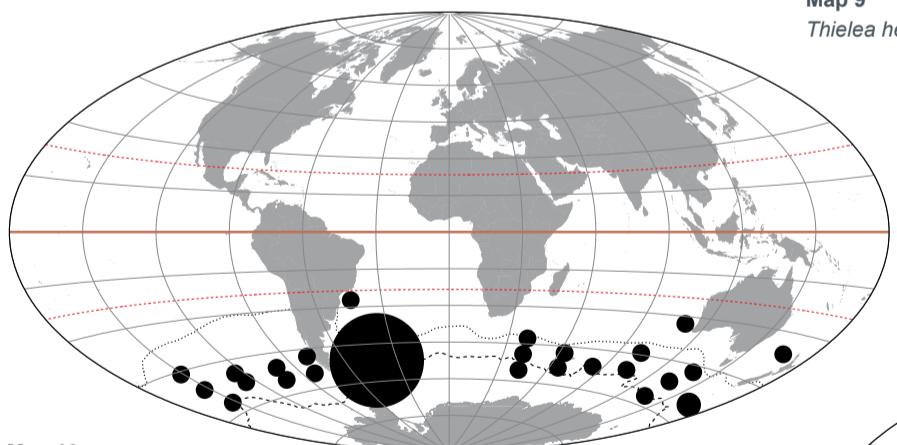
Map 7
Clio pyramidata f. martensi



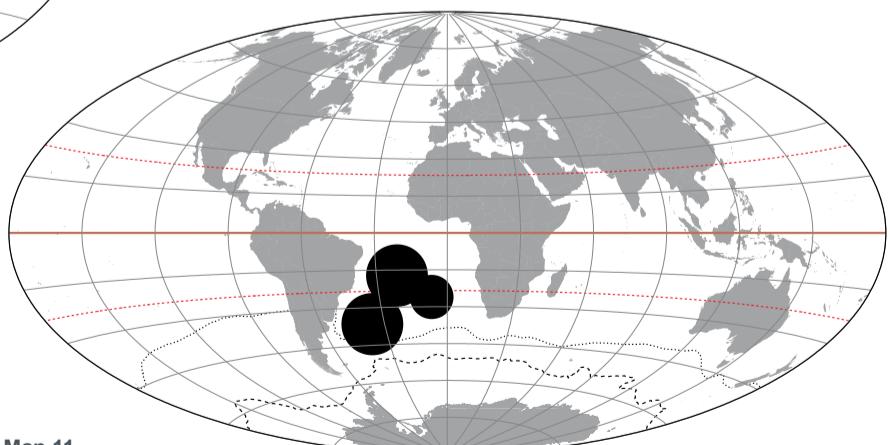
Map 8
Limacina rangii f. rangii



Map 9
Thielea helicoides



Map 10
Limacina retroversa australis



Map 11
Peracle reticulata

Pteropods Maps 6–11 Distribution of sub-Antarctic shelled pteropods. Map 6. *Clio pyramidata f. antarctica* Dall, 1908. Map 7. *Clio pyramidata f. martensi* (Pfeffer, 1880). Map 8. *Limacina rangii f. rangii* (d'Orbigny, 1834). Map 9. *Thielea helicoides* (Jeffreys, 1877). Map 10. *Limacina retroversa australis* (Eydoux & Souleyet, 1840). Map 11. *Peracle reticulata* (d'Orbigny, 1834).

Table 1 Varieties of shelled Southern Ocean pteropods. STF = Sub-Tropical Front (~43°S), PF = Polar Front (~55°S), ACC = Antarctic Circumpolar Current (~60°S). Distribution, biogeographic and depth affinity derived from van der Spoel *et al.* (1997) and van der Spoel & Dadon (1999) with supporting observations by Hunt *et al.* (2008), Howard *et al.* (2011), Roberts *et al.* (2011) and Hopcroft (unpublished data). Taxonomic nomenclature as per World Register of Marine Species database (2013).

Species	Authority	Typical Distribution	Biogeographic Affinity	Depth Range
<i>Cavolinia tridentata</i>	(Forsskål in Niebuhr, 1775)	Circumglobal	Cosmopolitan	Cosmopolitan
<i>Clio cuspidata</i>	(Bosc, 1802)	Circumglobal	Cosmopolitan	Epi-Mesopelagic
<i>Clio piatkowskii</i>	van der Spoel, Schalk & Bleeker, 1992	Weddell Sea	Antarctic	Bathypelagic
<i>Clio pyramidata</i>	Linnaeus, 1767			
<i>f. antarctica</i>	Dall, 1908	north of PF	Sub-Antarctic	Epipelagic
<i>f. excisa</i>	van der Spoel, 1963	south of PF	Antarctic	Epi-Mesopelagic
<i>f. martensi</i>	(Pfeffer, 1880)	north of PF	Sub-Antarctic	Epipelagic
<i>f. sulcata</i>	(Pfeffer, 1879)			
<i>Clio recurva balantium</i>	Rang, 1834	Circumglobal	Cosmopolitan	Meso-Bathypelagic
<i>Diacria trispinosa</i>	(de Blainville, 1821)	Circumglobal	Cosmopolitan	Epi-Mesopelagic
<i>Heliconoides inflatus</i>	(d'Orbigny, 1834)	Circumglobal	Cosmopolitan	Epipelagic
<i>Limacina rangii</i>	(d'Orbigny, 1834)			
<i>f. antarctica</i>	Woodward, 1854	south of ACC	Antarctic	Epipelagic
<i>f. rangii</i>	(d'Orbigny, 1834)	STF to PF	Sub-Antarctic	Epipelagic
<i>Thielea helicoides</i>	Jeffreys, 1877	north of PF	Sub-Antarctic	Bathypelagic
<i>Limacina retroversa australis</i>	(Eydoux & Souleyet, 1840)	STF to PF	Sub-Antarctic	Epipelagic
<i>Peracle reticulata</i>	(d'Orbigny, 1834)	Cosmopolitan	Sub-Antarctic	Mesopelagic
<i>Peracle valdiviae</i>	(Meisenheimer, 1905)	Circumglobal	Cosmopolitan	Meso-Bathypelagic

Antarctic shelled fauna include *Clio piatkowskii*, *Clio pyramidata* f. *excisa*, *Clio pyramidata* f. *sulcata* and *Limacina rangii* f. *antarctica* (Photo 1). *Clio piatkowskii* has been considered to be restricted to the deep Weddell Sea (van der Spoel *et al.* 1992, 1997, 1999) (Map 2) although Hunt *et al.* (2008) recorded it in small numbers in mesoplanktonic South Atlantic Polar Front waters and the Lazarev Sea. Dozens were also collected during the CEAMARC expedition in the East Antarctic (Hopcroft, unpublished data), thus lack of more numerous observations may simply reflect a lack of bathy-mesoplanktonic depth sampling rather than an actual absence of this taxa (which is able to migrate over 1000 m daily). We note here that we follow van der Spoel *et al.* (1997) and van der Spoel & Dadon (1999) who considered *Clio balantium* to be synonymous with *Clio recurva* and that most of the specimens we have observed are typical of *C. balantium* descriptions. We also have concerns about the taxonomic differences between *C. recurva*, *C. balantium* and *C. piatkowskii* and suggest they may be different ages of a single Southern Ocean *Clio* species, particularly as *C. piatkowskii* is a third of the size of *C. balantium*, typical *C. recurva* is half the size of *C. balantium* shells and the *C. balantium* type are as long as 3 cm. It is likely these represent a spectrum of juvenile to adult *Clio* species in the deep Southern Ocean. Clearly molecular research is needed to determine if we have separate species or forms in southern waters.

Forms of *Clio pyramidata*, particularly f. *sulcata*, are common in Antarctic waters (Maps 3–4). *Clio pyramidata* f. *sulcata* is typically found in the surface waters of the cold Southern Ocean between the Antarctic coast and the range of *Clio pyramidata* f. *antarctica* where it can occur in mass blooms (van der Spoel *et al.* 1997). Hunt *et al.* (2008) reported *Clio pyramidata* f. *sulcata* to be consistently present in their East Antarctic sector samples although not always in high abundances. This taxa is known to undergo pronounced diel migration (Hunt *et al.* (2008) found its range to be between 200 m and 1000 m during summer) and its lack of numbers in surface net and CPR samples may belie their true distribution in the Southern Ocean.

Limacina rangii is one of the most common pteropods in the Southern Polar Ocean. Its cold water form — f. *antarctica* — is typical of waters to the south of the Polar Front (Map 5). van der Spoel *et al.* (1997) report *Limacina rangii* f. *antarctica* to be stenothermic (showing a clear preference for cold waters) while the sub-Antarctic *Limacina rangii* f. *rangii* is eurythermic (shows a preference for higher temperatures). Hopkins (1987) noted that densities of *Limacina rangii* can be as high as 300 individuals/m³ in the Ross Sea, and other studies have report this pteropod to be a dominant component of the Ross Sea plankton and the dominant pteropod observed in waters south of the Polar Front (Hunt *et al.* 2008 and references therein). We note here that these researchers are likely referring to f. *antarctica* but have not attempted to determine between the two forms (as is unfortunately common in the pteropod literature due to the difficulty in identifying between forms in continuous plankton recorder collected samples) however, f. *antarctica* and f. *rangii* exhibit distinct morphologies and biogeographic patterns and should be separated where possible.

Sub-Antarctic shelled fauna include *Clio pyramidata* f. *antarctica*, *Clio pyramidata* f. *martensi*, *Limacina rangii* f. *rangii*, *Thielea helicoides*, *Limacina retroversa australis* and *Peracle reticulata* (Photo 2, Maps 6–11). Of the two sub-Antarctic forms of *Clio pyramidata*, f. *antarctica* is typical of intermediate Southern Ocean waters. Similarly, the sub-Antarctic form of *Limacina rangii* — f. *rangii* — is particularly prevalent in warmer waters north of the Polar Front (Bé & Gilmer 1977, van der Spoel & Dadon 1999) (Map 8). This taxa accounted for at least a third of all shells collected to sub-Antarctic zone sediment traps (Roberts *et al.* 2011). *Thielea helicoides* (Map 9) is typical of

deep-sea microplankton, although it never occurs in large numbers (van der Spoel *et al.* 1997). Again, its absence in East Antarctic collections may reflect the surface sample bias in collated research collections to date rather than an actual absence of the taxa in the region.

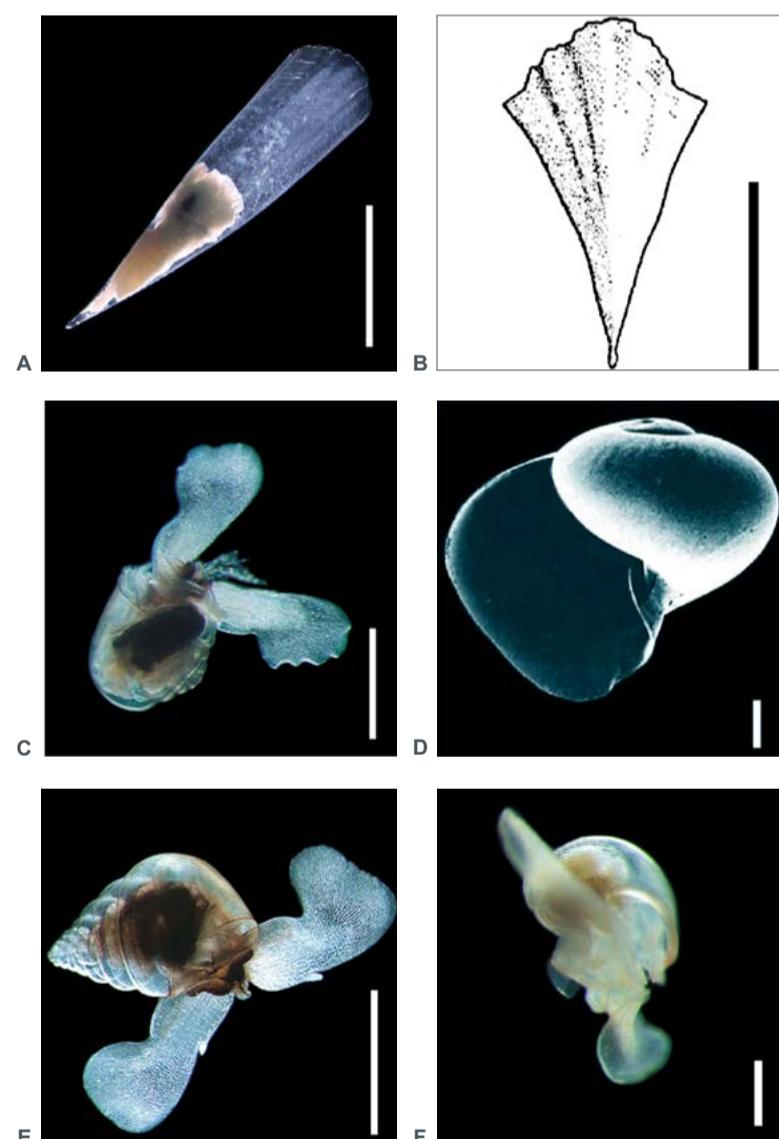


Photo 2 The major varieties of sub-Antarctic shelled pteropods found in Southern Ocean waters. (a) *Clio pyramidata* f. *antarctica* Dall, 1908. (b) *Clio pyramidata* f. *martensi* (Pfeffer, 1880). (c) *Limacina rangii* f. *rangii* (d'Orbigny, 1834) [this form has a less depressed spire than f. *antarctica* and no, or faint, striation]. (d) *Thielea helicoides* (Jeffreys, 1877). (e) *Limacina retroversa* f. *retroversa* (Flemming, 1823) [*Limacina retroversa australis* (Eydoux & Souleyet, 1840) is slightly smaller with a more highly coiled spire than *Limacina retroversa retroversa*]. (f) *Peracle reticulata* (d'Orbigny, 1834). Scale bars: (a) 5 mm, (b) 10 mm, (c–e) 1 mm and (f) 0.5 mm. Images ©: (a), (c), (e) and (f) R. Hopcroft University of Alaska Fairbanks & CoML; (b) and (d) after van der Spoel *et al.* (1999), © Backhuys Publishers, Leiden, The Netherlands, (1999).



Table 2 Species and subspecies of naked Southern Ocean pteropods. STF = Sub-Tropical Front (~43°S). Distribution, biogeographic and depth affinity derived from van der Spoel *et al.* (1997) and van der Spoel & Dadon (1999) with supporting observations by Hunt *et al.* (2008) and Hopcroft (unpublished data). Taxonomic nomenclature as per World Register of Marine Species database (2013).

Species	Authority	Typical Distribution	Biogeographic Affinity	Depth Range
<i>Clione limacina antarctica</i>	E.A. Smith, 1902	STF-Antarctic coast	Ant/Sub-Antarctic	Epipelagic
<i>Pneumodermopsis brachialis</i>	Minichev, 1976	Sub-Antarctic waters	Sub-Antarctic	Epipelagic
<i>Platybrachium antarcticum</i>	Minichev, 1976	Antarctic waters	Antarctic	Epipelagic
<i>Spongibranchaea australis</i>	d'Orbigny, 1834	STF-Antarctic coast	Sub/Antarctic	Epi-Mesopelagic

Limacina retroversa australis (Map 10) has been described as one of the most common pteropods in sub-Antarctic waters (van der Spoel & Dadon 1999, Hunt *et al.* 2008). van der Spoel *et al.* (1997) report it most frequently between 50°S–60°S and this taxa was observed as the dominant pteropod in the vicinity of the Prince Edward Islands, reaching up to 800 individuals/m³. South of the PF this species occurs at low densities or is completely absent (Hunt *et al.* 2008). *Peracle reticulata* (Map 11) has been reported to be a sub-Antarctic pteropod (van der Spoel & Dadon 1999) but hasn't been reported in significant numbers in Southern Ocean studies. Again, this may be related to its mesopelagic habitat preference rather than an actual absence in Southern Ocean waters.

Although not typical, occasionally cosmopolitan shelled pteropods have been reported, collected or observed in Southern Ocean waters (Photo 3, Maps 12–17), likely introduced within eddies from northern waters. *Cavolinia tridentata* (Map 12), *Clio cuspidata* (Map 13), *Clio recurva balantium* (Map 14), *Diacria trispinosa* (Map 15), *Heliconoides inflatus* (Map 16) and *Peracle valdiviae* (Map 17) have all been collected in sub-Antarctic zone nets (Howard *et al.* 2011) and deep sea traps (Roberts *et al.* 2011) as well as being observed during Census of Marine Life voyages (e.g. CEAMARC 2007/08: Hopcroft unpublished data).

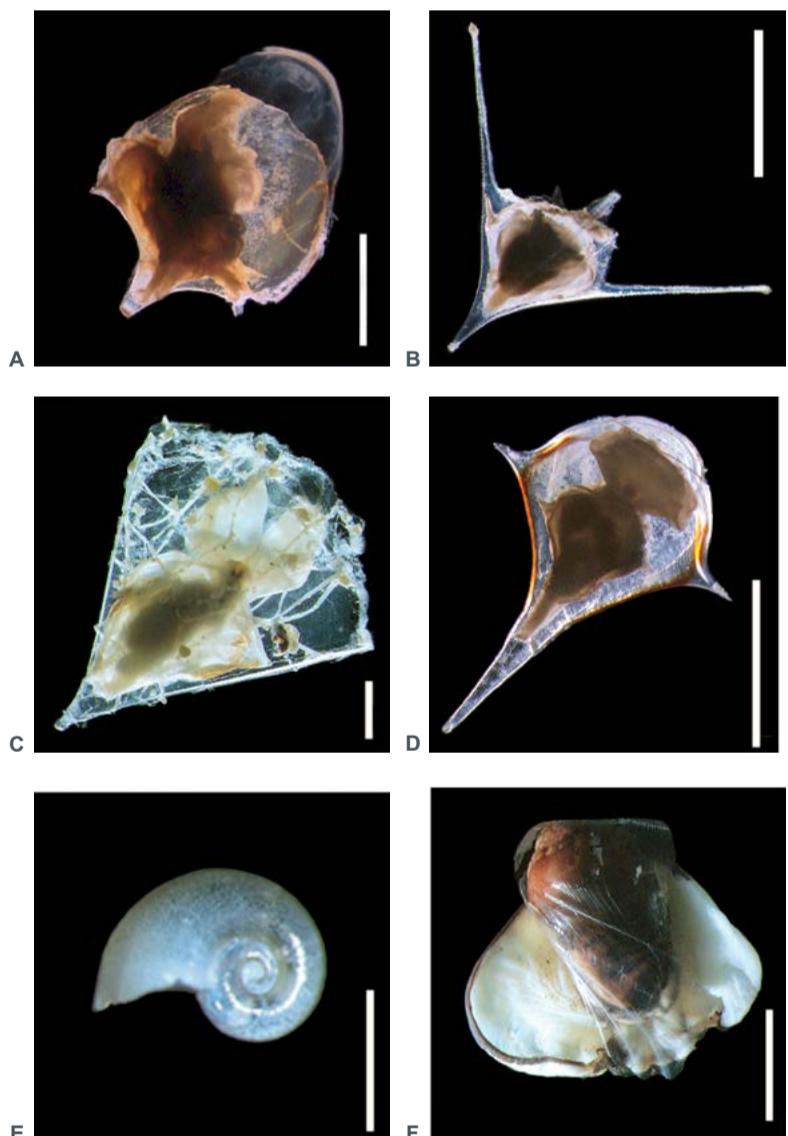


Photo 3 The major varieties of cosmopolitan shelled pteropods found in Southern Ocean waters. (a) *Cavolinia tridentata* (Forsskål in Niebuhr, 1775). (b) *Clio cuspidata* (Bosc, 1802). (c) *Clio recurva* (Children, 1823). (d) *Diacria trispinosa* (de Blainville, 1821). (e) *Heliconoides inflatus* (d'Orbigny, 1834). (f) *Peracle valdiviae* (Meisenheimer, 1905). Scale bars: (a–d) and (f) 5 mm, (e) 0.5 mm. Images ©: (a–d) and (f) R. Hopcroft University of Alaska Fairbanks & CoML; (e) D. Roberts Antarctic Climate & Ecosystems CRC.

3.2. Gymnosomata

The Gymnosomata are distinguished by their shell-less adult forms. Whilst there are 45–50 species of naked pteropod (Lalli & Gilmer 1989), including 20 from the South Atlantic sector of the Southern Ocean alone (van der Spoel & Dadon 1999), the typical diversity in the Southern Ocean is much lower (Table 2, Photo 4, Maps 18–21).

Antarctic naked fauna include *Clione limacina antarctica* (Photo 4a) and *Platybrachium antarcticum* (Photo 4b). *Clione limacina antarctica* is specific to the Southern Ocean, occurring in both Antarctic and sub-Antarctic waters but found predominantly south of the Polar Front (Hunt *et al.* 2008)(Map 18). This colourful taxa is a specialist predator on shelled pteropods, preferentially *Limacina rangii* in Antarctic waters and *Limacina retroversa australis* is sub-Antarctic waters (Lalli & Gilmer 1989) and its distribution and diel migration pattern accordingly tracks densities of *Limacina* pteropods in Southern Ocean waters (Hunt *et al.* 2008). Relatively little is known about *Platybrachium antarcticum* although it is thought to have an Antarctic Ocean only distribution (Map 19) and we note that Hopcroft (unpublished data) recorded three sightings of this species during the CEAMARC cruise.

Sub-Antarctic naked fauna include *Pneumodermopsis brachialis* (Photo 4c) and *Spongibranchaea australis* (Photo 4d). Relatively little is known about *Pneumodermopsis brachialis* in the Southern Ocean and what we do know is restricted to van der Spoel & Dadon's (1999) observations in the South-Atlantic Southern Ocean (Map 20). Conversely, *Spongibranchaea australis* is known to be both Antarctic and sub-Antarctic but particularly common in waters north of the Polar Front (Map 21). In East Antarctic waters, it tends to stay within the upper 150 m during both the day and night (Hunt *et al.* 2008). Observations indicate that *Spongibranchaea australis* is a specialist predator on *Clio pyramidata* (Lalli & Gilmer 1989, Hunt *et al.* 2008).

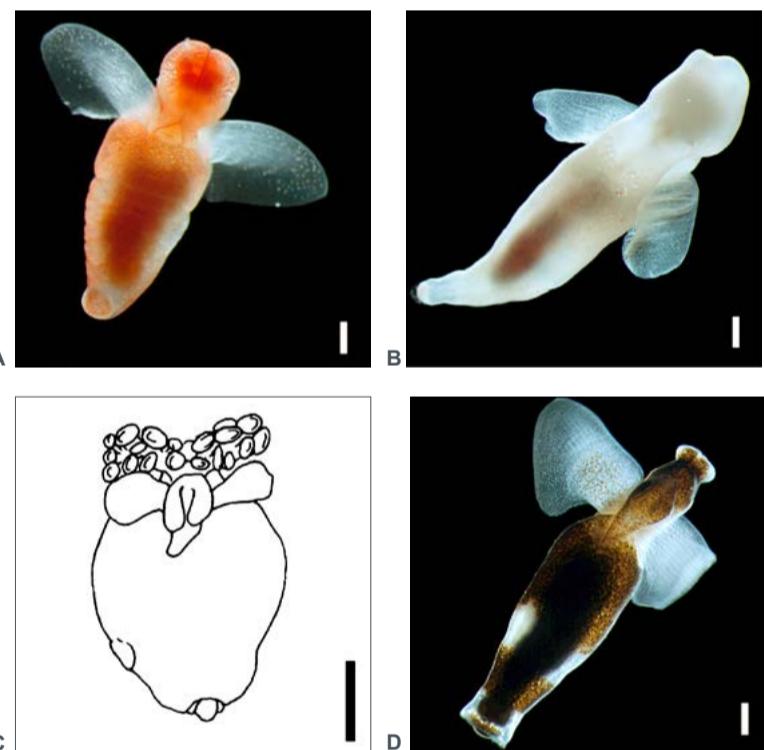
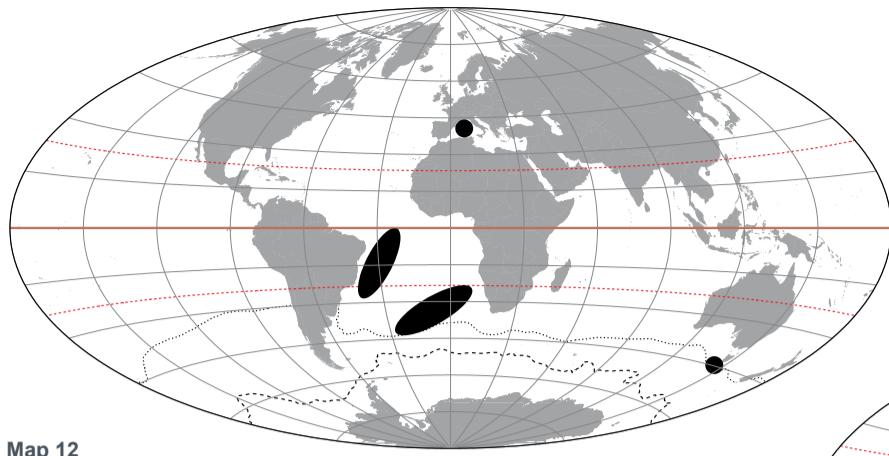


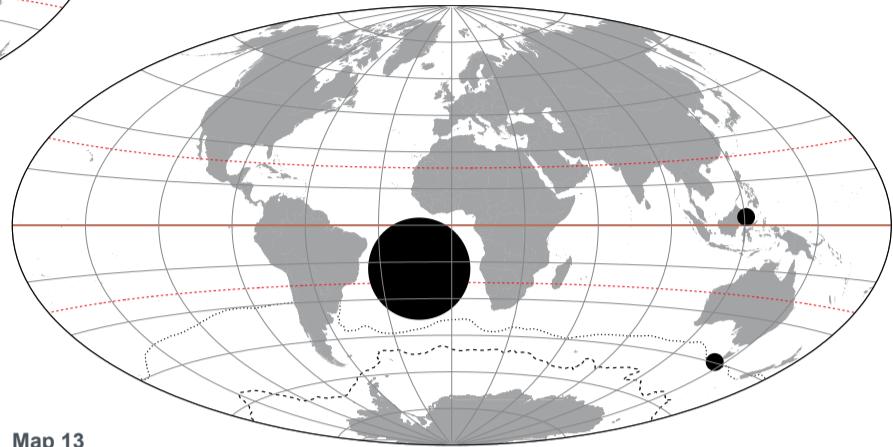
Photo 4 The major varieties of naked pteropods found in Southern Ocean waters. (a) *Clione limacina antarctica* E.A. Smith, 1902. (b) *Platybrachium antarcticum* Minichev, 1976. (c) *Pneumodermopsis brachialis* Minichev, 1976. (d) *Spongibranchaea australis* d'Orbigny, 1834. Scale bars: 1 mm. Images ©: (a), (b) and (d) R. Hopcroft University of Alaska Fairbanks & CoML; (c) after van der Spoel & Dadon (1999), © Backhuys Publishers, Leiden, The Netherlands, (1999).

4. Biogeographic processes and future research priorities

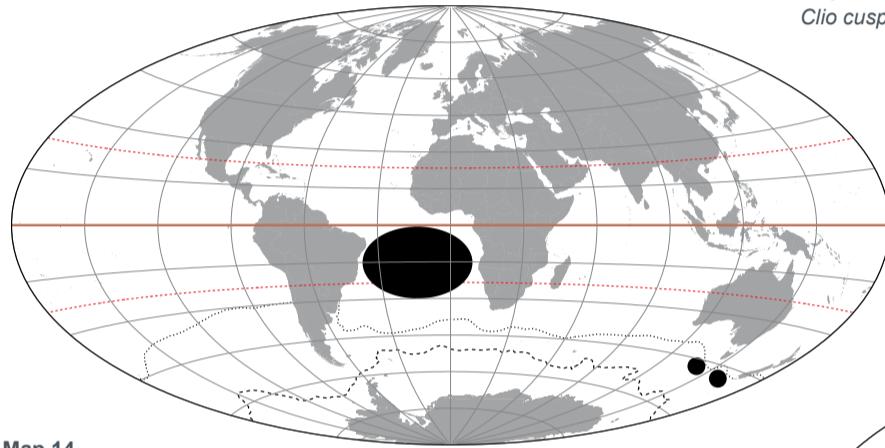
Pteropods (both shelled and naked varieties) are known to exist in epi- to bathypelagic waters in the Southern Ocean, although high abundances are only found in the epipelagic realm (van der Spoel & Dadon 1999). Accordingly, climatic influences on meso- (e.g. *Peracle reticulata*) to bathy- (e.g. *Thielea helicoides*) pelagic species are undetectable. However, species common in the epipelagic ocean layer are influenced by climate and climate change in addition to currents, water masses, prey and predators. For example: forms of *Clio pyramidata* are directly related to climatic belts including cold southern polar waters (*f. sulcata*), sub-polar waters (*f. antarctica*) and warmer waters in more temperate ecosystems (*f. lanceolata*) and *Limacina* species have a strong seasonal cycle and interannual variability in Southern Ocean waters. Regional and interannual variation in primary production has been proposed as the major determinant of spatial and temporal variability in thecosome pteropod population densities in the Southern Ocean (Comiso *et al.* 1993, Seibel & Dierssen 2003) and, for gymnosomes, the distribution and diel migration pattern of their prey (predominantly *Limacina* and *Clio* pteropods in Southern Ocean waters) dictates their distribution (Hunt *et al.* 2008).



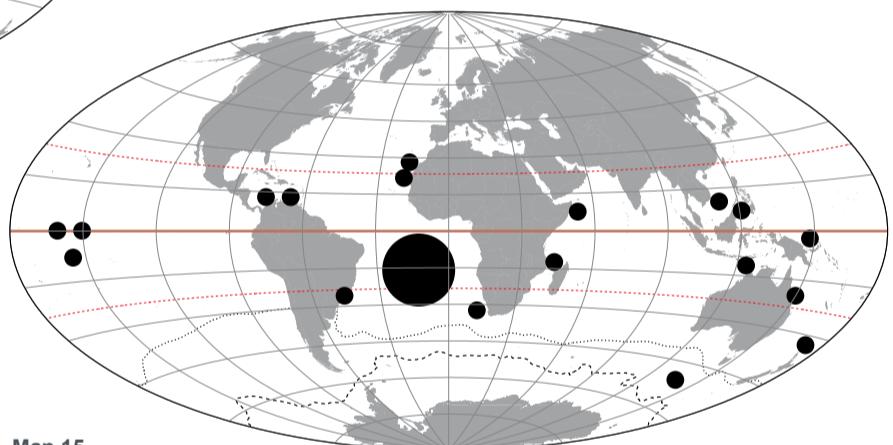
Map 12
Cavolinia tridentata



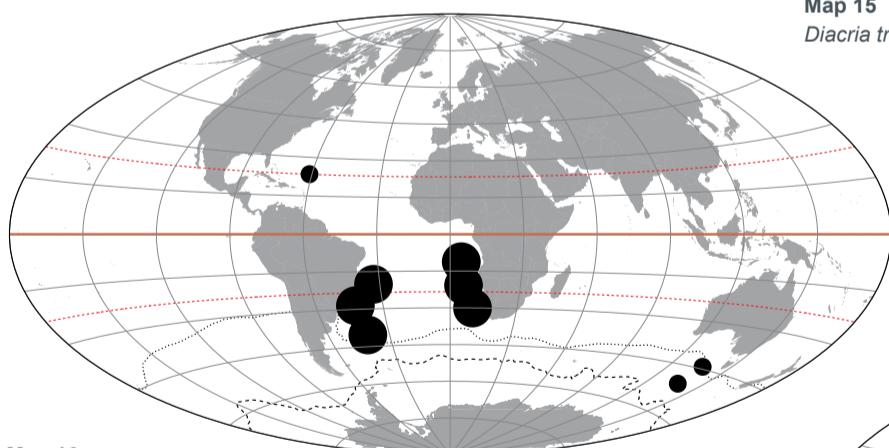
Map 13
Clio cuspidata



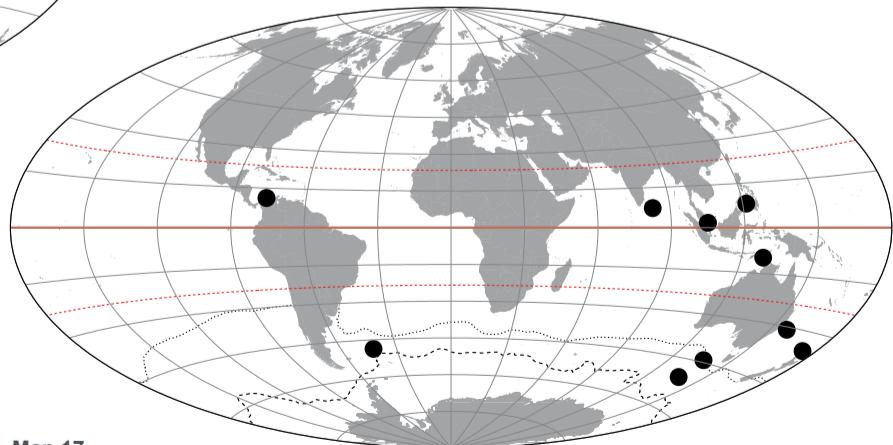
Map 14
Clio recurva balantium



Map 15
Diacria trispinosa

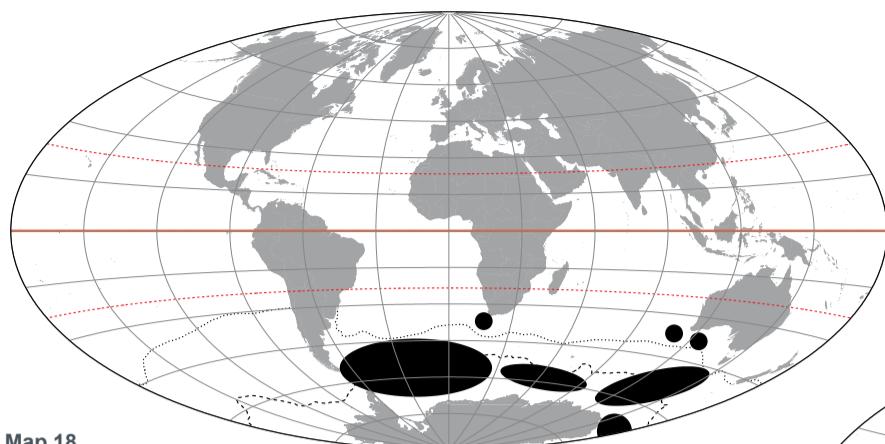


Map 16
Heliconoides inflatus

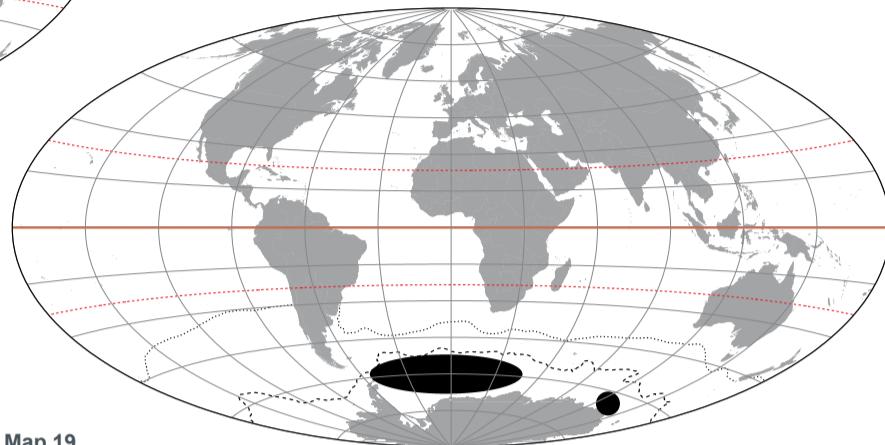


Map 17
Peracle valdiviae

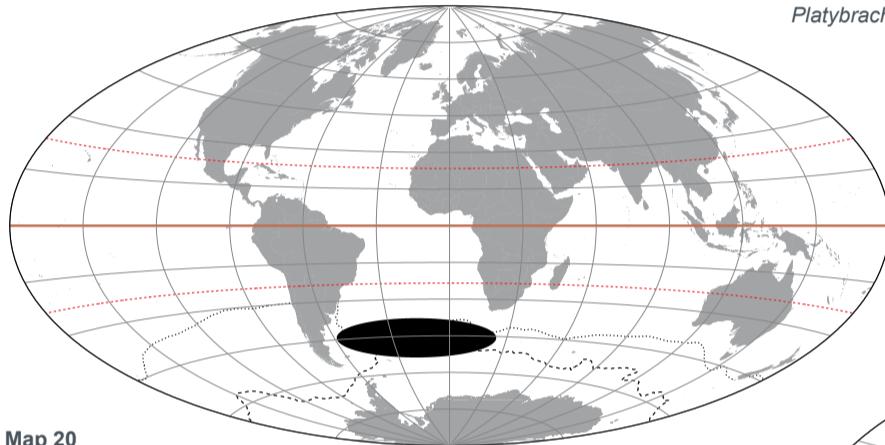
Pteropods Maps 12–17 Distribution of cosmopolitan shelled pteropods. Map 12. *Cavolinia tridentata* (Forsskål in Niebuhr, 1775). Map 13. *Clio cuspidata* (Bosc, 1802). Map 14. *Clio recurva balantium* Rang, 1834. Map 15. *Diacria trispinosa* (de Blainville, 1821). Map 16. *Heliconoides inflatus* (d'Orbigny, 1834). Map 17. *Peracle valdiviae* (Meisenheimer, 1905).



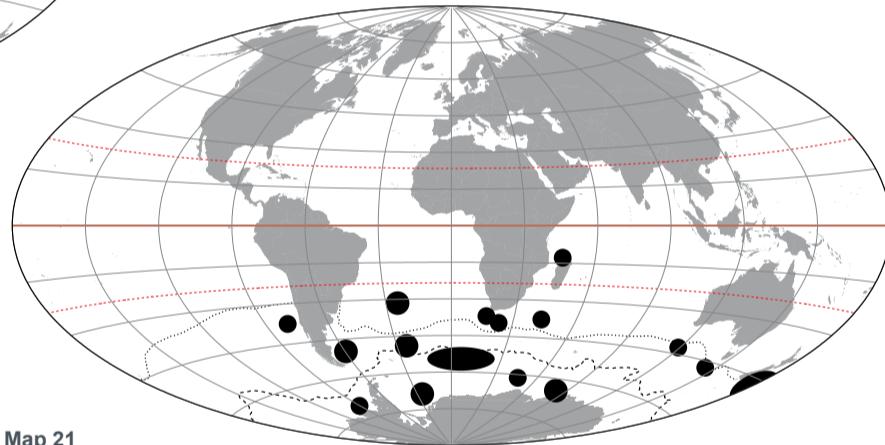
Map 18
Clione limacina antarctica



Map 19
Platybrachium antarcticum



Map 20
Pneumodermopsis brachialis



Map 21
Spongiobranchaea australis

Pteropods Maps 18–21 Distribution of Antarctic naked pteropods. Map 18. *Clione limacina antarctica* E.A. Smith, 1902. Map 19. *Platybrachium antarcticum* Minichev, 1976. Map 20. *Pneumodermopsis brachialis* Minichev, 1976. Map 21. *Spongiobranchaea australis* d'Orbigny, 1834.

Unfortunately, we currently know very little about Southern Ocean pteropod population structures, production rates, metabolic rates, trophic relationships or the biogeographic processes that dictate distributions on the range of time scales required to make informed predictions about the fate of these important zooplankton in the future Southern Ocean ecosystem. For example, very little is known about the place of the gymnosomata in the Southern Ocean ecosystem. They are little reported from the gut contents of Antarctic organisms, likely due to their novel allomone compounds which have been shown to deter a number of fishes from feeding on them (e.g. Bryan *et al.* 1995, Phleger *et al.* 1999).

The final major gap in Southern Ocean pteropod research is regional shell production and calcification rates despite the shelled order providing significant ecosystem services to humanity: the production and export of calcium carbonate pteropod shells is an important regulating mechanism for the transport of both organic (Francois *et al.* 2002) and inorganic (Honjo 2004) carbon to the deep ocean. In fact, pteropod shells contribute at least 12% to the global carbonate flux (Berner & Honjo 1981) and may contribute as much as 50% in Polar Front waters (Honjo *et al.* 2000, Honjo 2004).

The general paucity of information on Southern Ocean pteropods is of particular concern, particularly in light of predictions for populations of marine calcifiers (shell makers) in polar regions in a future high CO₂ ocean. It is predicted that if CO₂ emissions continue unabated, Southern Ocean surface waters will become undersaturated with respect to aragonite (the material pteropods use for their shells) by 2100 (Orr *et al.* 2005) likely resulting in

a decline in Southern Ocean pteropod densities and ultimately a northward shift in their distribution (Fabry *et al.* 2009). Impacts of this ongoing change in ocean chemistry, known as ocean acidification, may have significant ecological consequences for the Southern Ocean. There is an urgent need for targeted research on pteropods, and particularly the thecosomes, in order to quantify the likely ecosystem impacts of ocean acidification (in concert with other climatic stressors such as warming and freshening in the Southern Ocean).

Acknowledgements

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THE BIOGEOGRAPHIC ATLAS OF THE SOUTHERN OCEAN

Scope

Biogeographic information is of fundamental importance for discovering marine biodiversity hotspots, detecting and understanding impacts of environmental changes, predicting future distributions, monitoring biodiversity, or supporting conservation and sustainable management strategies.

The recent extensive exploration and assessment of biodiversity by the Census of Antarctic Marine Life (CAML), and the intense compilation and validation efforts of Southern Ocean biogeographic data by the SCAR Marine Biodiversity Information Network (SCAR-MarBIN / OBIS) provided a unique opportunity to assess and synthesise the current knowledge on Southern Ocean biogeography.

The scope of the Biogeographic Atlas of the Southern Ocean is to present a concise synopsis of the present state of knowledge of the distributional patterns of the major benthic and pelagic taxa and of the key communities, in the light of biotic and abiotic factors operating within an evolutionary framework. Each chapter has been written by the most pertinent experts in their field, relying on vastly improved occurrence datasets from recent decades, as well as on new insights provided by molecular and phylogeographic approaches, and new methods of analysis, visualisation, modelling and prediction of biogeographic distributions.

A dynamic online version of the Biogeographic Atlas will be hosted on www.biodiversity.aq.

The Census of Antarctic Marine Life (CAML)

CAML (www.caml.aq) was a 5-year project that aimed at assessing the nature, distribution and abundance of all living organisms of the Southern Ocean. In this time of environmental change, CAML provided a comprehensive baseline information on the Antarctic marine biodiversity as a sound benchmark against which future change can reliably be assessed. CAML was initiated in 2005 as the regional Antarctic project of the worldwide programme Census of Marine Life (2000-2010) and was the most important biology project of the International Polar Year 2007-2009.

The SCAR Marine Biodiversity Information Network (SCAR-MarBIN)

In close connection with CAML, SCAR-MarBIN (www.scarmarbin.be, integrated into www.biodiversity.aq) compiled and managed the historic, current and new information (i.a. generated by CAML) on Antarctic marine biodiversity by establishing and supporting a distributed system of interoperable databases, forming the Antarctic regional node of the Ocean Biogeographic Information System (OBIS, www.iobis.org), under the aegis of SCAR (Scientific Committee on Antarctic Research, www.scar.org). SCAR-MarBIN established a comprehensive register of Antarctic marine species and, with biodiversity.aq provided free access to more than 2.9 million Antarctic georeferenced biodiversity data, which allowed more than 60 million downloads.

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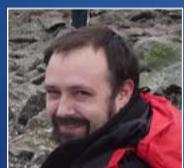
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