ANTARCTIC BENTHIC FAUNA IN THE GLOBAL CLIMATE CHANGE

ANNA KIDAWA, TOMASZ JANECKI

Polish Academy of Sciences, Department of Antarctic Biology in Warsaw Ustrzycka 10/12, 02-141 Warszawa, Poland akidawa@arctowski.pl, tomek@wigry.org.pl

ABSTRACT: In the last 50 years a significant climatic shift has been observed along the Antarctic Peninsula (air and seawater temperature rise, glacial retreat, localized instances of lowered shallow waters salinities). Many Antarctic marine benthic invertebrates are adapted to specific environmental conditions (e.g. low stable temperatures, high salinity and oxygen content). Changes caused by global climate changes and subsequent glacial melting can be expected to have significant impacts on species physiology and distribution. The rise of sea water temperature coupled with such additional stress factors as melt water run-off, increased ice disturbance, disruption of food webs or invasion of alien species can be a serious problem for their long-term survival.

KEY WORDS: Antarctic, climate change, marine ecosystem, benthos.

ANTARCTIC MARINE ENVIRONMENT

The Southern Ocean is isolated from other marine environments by the Antarctic Circumpolar Current and Polar Front, which can be observed as a significant change in surface water temperature and salinity, and be detectable to depths exceeding 1000 m. They form a strong barrier to free north-south exchange of water, isolating Antarctic shelf fauna from other continental shelf faunas of the world (Clarke *et al.* 2005, Kim and Thurber 2007).

Waters of the Southern Ocean outside the intertidal zone are characterized by low (from -1.8°C to +1.5°C) and highly stable temperatures, with the total annual variation rarely exceeding 3°C in the region of Antarctic Peninsula, and

1.5°C at high Antarctic (Peck 2005). The other stable environmental factors are high seawater salinity and high oxygen content (Peck 2005). Other characters of the Antarctic environment vary markedly with the change of seasons. Photoperiod fluctuates between no direct sunlight during austral winter to 24 hrs sunlight during the summer. About 10–15 million km² of sea ice forms in winter and melts in summer. In the result, the Southern Ocean is characterized by intense seasonality of phytoplankton productivity. In many places primary production is restricted to 2–3 months a year, reducing food availability for benthic organisms (Peck 2005, Barnes and Clarke 1995).

Antarctic bottom environments are also characterized by physical disturbance by ice phenomena (icebergs, anchor ice, growlers), which scour sea floor and destroy fauna living there (Gutt 2001). This disturbance varies with depth, bottom topography, currents and proximity to ice fronts and glaciers, with Antarctic tubular icebergs bulldozing sea floor to the depth of ca 600m (Gutt and Starmans 2001). It was estimated that every square meter of the Antarctic shelf will be impacted by an iceberg once in every 340 years (Gutt 2001).

ANTARCTIC BENTHIC FAUNA

The Antarctic region is the most faunistically distinct part of the world ocean (O'Loughlin *et al.* 2011). The Southern Ocean, surrounding the Antarctic continent, comprise 9.6% of the world ocean and is home to thousands of invertebrate species living on its bottom (Clarke 2003). The exact number of Antarctic benthic species is unknown due to inaccessibility of some areas (e.g. Amundsen Sea, Bellingshausen Sea) and difficulties connected with deep-sea sampling, which comprises ca 80% of the Southern Ocean (Clarke 2008). The number of benthic macroinvertebrate species described from the Southern Ocean currently exceeds 4100 (Clarke 2008), but the total macrofaunal richness may well exceed 17 000 (Gutt *et al.* 2004). Therefore, species richness of the Antarctic continental shelf is comparable to the shelf faunas of Hawaii or north-west Europe, and more diverse than that of the Arctic (Clarke 2008). Species richness of the Southern Ocean benthos vary across major taxonomical groups. Pycnogonids, polychaetes, ascidians, amphipods and some echinoderm groups are well represented, whereas gastropods, isopods, sponges and bivalves are relatively poorly represented (Clarke and Johnston 2003).

Particularly striking features of the Southern Ocean are the lack of decapods, high level of endemism and vertical zonation of benthic communities. Outside Antarctica decapods such as crabs or lobsters comprise a key component of the shallow waters (Gili *et al.* 2006). In the Antarctic their role is played by numerous sea stars and nemerteans (Dayton *et al.* 1974, McClintock 1994, Gibson 1983). High endemism of Southern Ocean benthos is a key biogeographic and evolutionary feature, with the percentage of endemic species especially high in groups such as



pycnogonids and amphipods (90% and more) or polychaetes, holothurians and bryozoans (>50%) (Clarke 1996). The lack of significant littoral or intertidal fauna in the Antarctic and strong vertical zonation in subtidal benthic communities is the consequence of different ice phenomena (e.g. sea ice, anchor ice, ice foot, growlers, icebergs) (Dayton *et al.* 1974).

Antarctic benthic invertebrates are characterized by physiological rates, such as metabolic, growth, development or activity rates, being considerable lower than in temperate species (e.g. Pearse et al. 1991, Brey and Clarke 1993, Arntz et al. 1994, Peck and Robinson 1994, Chapelle and Peck 1995, Peck et al. 2000, Peck 2002, Peck et al. 2004a, McClintock et al. 2008). Growth and development rates of Antarctic benthic organisms are about five times slower than of similar species from lower latitudes (Arntz et al. 1994, Peck et al. 2000, Pearse et al. 1991, Peck Robinson 1994). In many species (e.g. caridean shrimp *Chorismus antarcticus*, bivalve *Lissarca* miliaris, sea urchin Sterechinus neumayer) a strongly seasonal pattern of growth was observed, with organisms ceasing to feed during austral winter due to limited food supply (Clarke 1996, Brockington, Clarke 2001). In consequence, Antarctic benthic invertebrates have extended life spans. Brachiopod Liothyrella uva lives to over 50 years and does not reproduce until it is 20 years old (Peck, Holmes 1990), sea star *Odontaster validus* lives to 100 years (Pearse 1969), and bivalve *Yoldia* eightsi to over 40 years (Nolan, Clarke 1993). The metabolic rates in Antarctic bottom invertebrates are 8 to 27 times lower than in species living in 20°C, resulting in extreme low levels of activity (long periods of rest, slower walking, swimming or burrowing) and ability to stay 4–7 months without food (Peck 2005, Klages, Gutt 1990; Brockington et al. 2001, Barnes, Clarke 1995; Dayton et al. 1974).

The other feature typical to the Antarctic benthic invertebrates is the significantly wider depth ranges in comparison with temperate or tropical fauna (Brey *et al.* 1996).

These characteristics of Antarctic benthic invertebrates are the effect of adaptation to conditions prevailing in extreme environment (low temperature, intermittent food supply), as well as unique past history of Southern Ocean ecosystem.

PAST HISTORY OF ANTARCTIC BENTHIC FAUNA

The Southern Ocean fauna has evolved *in situ* over a long period of time, during which it has been subject to the fragmentation of Gondwana, variation in glacial extent, isolation (both geographical and climatic) from the outside oceans and a substantial decline in temperature of ca 15–20°C (Clarke 1996).

In late Jurassic period southern latitudes were dominated by the supercontinent of Gondwana surrounded by temperate waters (Clarke 1990). By the late Cretaceous Gondwana had started to fragment with South America, Africa, India and Australia

separating and drifting north. The separation of the Tasman Ridge and opening of the Drake's Passage (about 34 Myr ago) lead to the establishment of Antarctic Circumpolar Current, isolating the Southern Ocean and initiating cooling processes (Aronson, Blake 2001; Rogers 2009, Gili et al. 2006). Fossils from Seymour Island and James Ross Island suggest that at that time shallow-water communities were similar to those from lower latitudes (Aronson, Blake 2001). One of the consequences of the Antarctic cooling was a dramatic change in the biodiversity of marine ecosystems, with the loss of major top predators (e.g. sharks, crabs, lobsters) and a reduction in the biodiversity of such groups as bivalve mollusks and gastropods with calcareous shells (Thatje et al. 2005). It seems likely that extinction of crabs and lobsters was caused by their inability to adapt physiologically to very low water temperatures (Thatje et al. 2005), although the rapid onset of seasonality of primary production may have also played a role (Clarke 1990). The reduction in the diversity of large calcareous gastropods and bivalves may be explained by the extra energetic costs of precipitating calcium carbonate from seawater at lower temperatures (Clarke 1990).

Mean sea-water temperature decreased from about 15°C in the early Tertiary to the present range of +2°C to -1.8°C with several periods of rapid temperature changes (Clarke 1990). A large ice mass covered Antarctic continent. It was very dynamic and in the last 2 Myr it has cyclically advanced and retreated (Barnes, Conlan 2007). In glacial maxima ice edge advanced across the continental shelf erasing benthic fauna. In consequence, the shelf habitats have to be repeatedly colonized during ice retreat, resulting in repeated shifts in the distribution of species (Rogers 2009; Barnes, Conlan 2007). Survival of the benthic fauna was possible in the deep sea (hence the eurybathy – Brey *et al.* 1996) or in refugia on the continental shelf resulting from the diachronism in maximum ice extant (Thatje *et al.* 2005).

The loss or diversity reduction of many taxonomical groups resulted in the evolutionary radiation and endemism of others (e.g. pycnogonids, isopods, amphipods, predatory gastropods, notothenioid fishes), which may be driven by periodic advances and retreats of the Antarctic ice sheet (Clarke *et al.* 2004).

The extinction of active skeleton breaking (durophagous) top predators such as crabs or teleost fishes, decreased the predation pressure and allowed dense crinoid and ophiuroid populations to flourish at shallow depths (Aronson, Blake 2001). Shallow-water communities of epifaunal suspension feeders were typical for Paleozoic marine environments before the evolution of durophagy (Aronson, Blake 2001). Outside the Southern Ocean such benthic communities are at present observed only in the deep-sea (Gili *et al.* 2006).

In consequence of long history of isolation, glacial oscillation and cooling, modern Antarctic shelf fauna is characterized by endemic species with metabolism and lifestyle adapted to low temperatures and seasonality of primary production, forming peculiar benthic communities distinctly differing from those living outside the Southern Ocean.

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GLOBAL CLIMATE CHANGES ALONG THE ANTARCTIC PENINSULA

The Antarctic Peninsula is one of the areas of the globe that are currently experiencing rapid regional climatic change (King 1994, Vaughan *et al.* 2003).

Throughout the twentieth century global air temperatures increased by 0.3–0.6°C (Hughes 2000), and current climatic models predict further warming (IPCC 2001, 2007). Global seawater temperatures have risen by 0.06°C during the last half century (Levitus *et al.* 2000) with a predicted increase of 2°C over the next 100 years (IPCC 2001, 2007). Especially rapid changes were observed along the Antarctic Peninsula, with air temperatures having risen by ca 3°C in the last 50 years at some localities, and winter minimums by over 5°C (King *et al.* 2003). There is no significant trend, either warming or cooling, in East Antarctica, and data collected in some sites suggest a cooling trend (Turner *et al.* 2005). The warming observed in the region of the Antarctic Peninsula has had a significant impact on the terrestrial ice sheet. The majority (87%) of glacier termini retreated during the past 50 years (Cook *et al.* 2005). In the same time, loss of seven ice shelves were noted (Vaughan, Doake 1996).

Antarctic seawater temperatures are also rising, both in sub-surface water masses (Gille 2002, Robertson *et al.* 2002), and in shallow waters along the Western Antarctic Peninsula (Meredith, King 2005) and around South Georgia (Whitehouse *et al.* 2008), with measured or calculated changes since 1950s ranging from 0.17°C to 1°C, depending on depth or region.

Some indications of sea ice extent reductions are also observed (Curran *et al.* 2003), with especially significant changes in the Bellingshausen and Amundsen seas (Zwally *et al.* 2002, Clarke *et al.* 2007). Data for the western Antarctic Peninsula showed 40% reduction in annual mean sea ice extent over a 26-year period (Smith, Stammerjohn 2001).

Localized instances of lowered shallow waters salinities resulting from melted freshwater discharge were also noted (Nihashi *et al.* 2005; Kidawa, Janecki personal observations), although the overall trend shows a significant increase in the salinity of the summer ocean surface (Meredith, King 2005).

On the basis of current evidence, it seems probable that the warming of the Antarctic Peninsula region will continue, but without more comprehensive data and a firm understanding of all interrelated mechanisms controlling regional climate change, it is impossible to predict future changes with any degree of certainty (Clarke *et al.* 2007).

ECOLOGICAL CONSEQUENCES OF CLIMATE CHANGE FOR ANTARCTIC MARINE BIOTA

Climate change is already having significant impact on some components of the Antarctic food web. Changes in phytoplankton concentration and composition along the western shelf of the Antarctic Peninsula associated with long-term climate modification were noted (Montes-Hugo *et al.* 2009) as well as significant shifts in bird and seal populations sizes in the Southern Ocean (Barbraud, Weimerskirch 2001; Croxall *et al.* 2002, Weimerskirch *et al.* 2003). There are also indications that populations of *Pleuragramma antarcticum*, a key fish species of the trophic web, whose reproduction is closely associated to sea ice, declined locally, to be replaced by myctophids, a new food item for predators (after SCAR Report 2009).

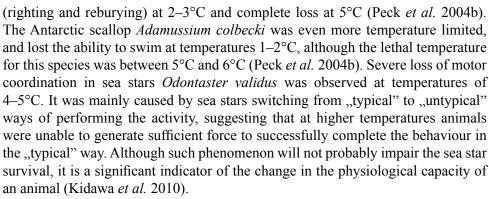
There are very few long-term studies of Antarctic benthic invertebrates, and currently it is impossible to detect potential effects of climate change (Clarke *et al.* 2007), but there were some experimental evidence and field observations done which may help to ascertain future fate of the bottom fauna.

Seawater warming

All currently tested Antarctic benthic invertebrates are highly strongly stenothermal (Peck *et al.* 2004b, Peck 2005, Young *et al.* 2006). Many die in temperatures between 5°C and 10°C (Peck 1989, Peck *et al.* 2002, Peck *et al.* 2004b). The most sensitive are brachiopod *Liothyrella uva* and bivalve *Limopsis marionensis* which die at temperature of 4°C (Pörtner *et al.* 1999, Peck 1989). Other, such as the bivalve *Laternula elliptica* (Peck *et al.* 2002) and the limpet *Nacella concinna* (Peck 1989) survived in experiments to temperatures of about 10°C.

Temperature sensitivity of Antarctic benthic invertebrates can be explained by the oxygen limitation hypothesis (Pörtner 2002, Pörtner *et al.* 2007). In a given temperature range all functions of an organism can be completed using solely aerobic metabolism. Outside this range, organism progressively loses aerobic scope and need to use anaerobic pathways to provide the required energy (Pörtner 2002). Data collected for some Antarctic benthic invertebrates (bivalve *Laternula elliptica*, isopod *Glyptonotus antarcticus*, limpet *Nacella concinna*, brachiopod *Liothyrella uva*) suggest that at higher temperatures oxygen demand can rapidly outstrip oxygen supply mechanism (Robertson *et al.* 2001, Peck 2002, Peck *et al.* 2002, Peck 2005).

The environmental range in which growth and normal physiological functioning can occur is usually narrower than the tolerance limits of any species (Newell, Branch 1980; Peck *et al.* 2004b, Rupp, Parsons 2004). Current research showed that activity (e.g. locomotion, swimming, reburying) of Antarctic benthic invertebrates is sensitive to temperature rise. Limpet *Nacella concinna* and the large bivalve *Laternula elliptica* suffered 50% failure in vital biological functions



Antarctic marine species may have some of the most restricted scopes of any fauna (Barnes, Peck 2008). Acclimation experiments showed that species such as scallop *Adamussium colbecki*, bivalve *Laternula antarctica* and brittle star *Ophionotus victoriae* are unable to acclimate to 3°C (Barnes, Peck 2008; Peck *et al.* 2009b). But other species, sea star *Odonatser validus* was shown to be acclimated to higher temperatures, righting itself when turned over at temperatures up to 8°C and feeding up to 7°C (Peck *et al.* 2008).

Factors that can influence thermotolerance of Antarctic benthic invertebrates are individual size (Peck *et al.* 2009a) and geographical location (Morley *et al.* 2009). When temperatures were raised acutely smaller individuals belonging to several taxa survived to higher temperatures than large animals, which can strongly affect the species' reproductive potential (Peck *et al.* 2009a). It was also established that limpets *Nacella concinna* from South Georgia have a lower critical limit (5.1–10.0°C) than *Nacella concinna* from the colder environments of Signy Island and Adelaide Island (10.0–12.5°C) (Morley *et al.* 2009).

Although most individuals were sensitive to warming, some degree of diversity was observed in sea stars *Odontaster validus* and ispods *Serolis polita*, with a small proportion of animals able to perform successfully even at higher temperatures (Janecki *et al.* 2010, Kidawa *et al.* 2010). Such phenomenon implies the existence of considerable variability within these species, which can make them less vulnerable to future warming trends.

At present, data from the laboratory experiments suggests that temperature increase will impair the ability of Antarctic benthic invertebrates to perform vital biological function critical for their long term survival. Therefore, it can be assumed that their ability to cope with future environmental change is limited, and they can successfully perform only in a narrow range of temperatures.

On the other hand, some field observations show that the geographic range of many Antarctic species extends to locations (e.g. South Georgia) with higher summer and winter sea temperatures than elsewhere in the Southern Ocean (Barnes *et al.* 2006, Barnes, Peck 2008). Substantial population of species shown in experiments to be vulnerable to small temperature variations (e.g. *Nacella concinna, Laternula*

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elliptica, *Odontaster validus*) were found on South Georgia living at 2–3°C above typical temperatures for higher latitude Antarctic shallow waters (Barnes *et al.* 2006, Barnes, Peck 2008).

Salinity changes

There is only scant data on the effect of salinity decline on Antarctic marine invertebrates. Small salinity changes slowed development rate, decreased the percentage of embryos reaching morula stage and reduced viability of embryos of sea urchin *Sterechinus neumayeri*, suggesting its greater stenohaline limitation in comparison to tropical and temperate species of sea urchins (Cowart *et al.* 2009). Significant behavioural responses to meltwater (Davenport 2001) and increased mortality in lowered salinity (Davenport, Macalister 1996) were observed in limpets *Nacella concinna*. Interactive effects between temperature and salinity on vital biological functions of *Serolis polita* were observed, so that isopods were more vulnerable to lower salinities when exposed to higher temperatures (Janecki *et al.* 2010).

Seawater acidification

The sharp increase of carbon dioxide in the atmosphere results in more CO₂ dissolving in surface sea water leading to its acidification, and – in consequence – to increase of calcium carbonate solubility, which Antarctic benthic invertebrates precipitate to produce shells or skeletons (Barnes, Peck 2008). With increasing acidity many organisms will face a greater energetic cost to build and maintain their shells or skeletons. Thinning of shells makes them more susceptible to predators or mechanical damage typical for shallow waters (Barnes, Conlan 2007), which may result in depletion of thin-shelled sessile species (Barnes, Peck 2008).

Increased ice disturbance

Ice disturbance by icebergs is one of the major factors structuring Antarctic benthic communities (Teixidó *et al.* 2004, Lee *et al.* 2001, Peck *et al.* 1999, Gutt, Starmans 2001). Grounded or scouring icebergs severely damage large areas of sea floor, changing its topography, altering sediments, modifying bottom current flow and destroying whole benthic communities (Peck *et al.* 1999, Gutt, Starmans 2001; Barnes, Conlan 2007).

Although, it was estimated that every square meter of the Antarctic shelf down to 600 m will be scoured by an iceberg once in every 340 years (Gutt 2001), some areas are impacted more often. For example, frequency of iceberg scouring at Signy Island was estimated at once every 50–75 years (Peck, Bullough 1993). Video transects from the eastern Weddell Sea recorded that in intensively scoured areas about 80% of seafloor was disturbed (Gutt Starmans 2001). Current data

show that scouring lead to almost compete removal of bottom macrofauna and >90% of meiofauna (Peck et al. 1999, Lee et al. 2001). Recovery rates of Antarctic benthic communities are very slow (Brown et al. 2004). Recolonisation begins with an invasion of mobile organisms, many of them scavengers exploiting organisms killed by the scouring, followed by pioneer species with a fast recruitment and growth rates (ascidians, bryozoans, polychaetes, gorgonians). The next stage begins with the arrival of slow growing and reproducing taxa such as sponges, and ends with extremely slow-growing hexactinellid glass sponges attaining the height of ca 40 cm, forming three-dimensional structures and providing a special habitat for an associated fauna (Gutt et al. 1996, Johst et al. 2006, Teixido et al. 2007). Recovery time of such benthic communities was estimated to be even 250-500 years (Gutt 2000). The recovery is not deterministic but follows highly complex pathways of succession (Gutt, Starmans 2001; Teixido et al. 2007, Teixido et al. 2004). The local removal of benthic fauna by ice scouring and subsequent recolonisation creates a patchy pattern on sea floor, generating a community mosaic and increasing the total variability of Antarctic benthos (Gutt 2000, Teixido et al. 2007).

Regional warming observed in the region of Antarctic Peninsula is likely to increase the breaking up of ice shelves and – in consequence – scouring frequency of the seafloor, so bottom fauna living in one of the most highly disturbed environment may suffer even more disturbance (Brown *et al.* 2004). But on the other hand, ice disturbance is considered a common event in the evolutionary history of the Southern Ocean, with significant fluctuations in the intensity of ice scouring (Clarke *et al.* 2007), and Antarctic benthic species seem well adapted to such events (Peck *et al.* 1999)

Invasion by alien species

The evolution of Antarctic marine biota has taken place relatively unaffected by biotic exchange (Clarke *et al.* 2007). The Southern Ocean is isolated from the outside seas by the complex barrier of Antarctic Circumpolar Current and Polar Front. Pelagic larvae of potential invading species would have to survive the large and abrupt temperature (4–5°C) and salinity (>0.5) changes across the Polar Front (Kim, Thurber 2007). However, a few larvae of decapod crustaceans and adults of others (e.g. spider crab *Hyas araneus* from boreal and subarctic waters) have recently been found around South Shetland Islands (Thatje, Arntz 2004). Small populations of lithodid crabs, long known from South Georgia, are now present in deep waters off the continental shelf in the Bellingshausen Sea at temperatures >1°C (Thatje *et al.* 2005). It is unknown if they have recently colonized this area or been there for some time (Barnes 2005). Lithodid crabs occur frequently in the Subantarctic Region, although they are limited by physiology and life history from living and breeding in waters permanently below 0°C (Thatje *et al.* 2005). Future warming may enable them to reconquer the Southern Ocean after about 15 Myr of

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absence. The return of durophagous (shell crushing) top predators would reshape Antarctic benthic communities. Such invasion would probable affect crinoids and ophiuroids, flourishing in the Antarctic due to the disappearance of crabs after global cooling, as well as thin shelled molluscs, and asteroids currently playing the role of benthic top predators (Aronson, Blake 2001; Thatje *et al.* 2005).

Three possible gateways to the Southern Ocean are proposed: migration through the abyssal depths in case of eurybathic species, migration through the shelves of the Scotia Arc Islands, or transport of larvae with eddies forming in the Antarctic Circumpolar Current (Clarke *et al.* 2005).

Disruption of food webs

Changes in phytoplankton concentration and composition along the Antarctic Peninsula were already observed (Montes-Hugo *et al.* 2009). The warming of the surface waters accompanied by large reductions in the extent and duration of sea ice cover may potentially result in further changes (e.g. disappearance of sea algae). That may cause a cascade through higher trophic levels, both in the water column and on the sea bottom (after SCAR Report 2009).

Similarly, the potential reduction in number or even removal of any of the key species from the benthic ecosystem, may disrupt ecological interactions which stabilize benthic communities, and may reduce functional diversity in the Antarctic food-web, especially if different species or different functional groups (e.g. prey *versus* predator) will be affected to a different degree (Clarke *et al.* 2007).

At present there are no data showing disruption in benthic food-web, although some observation suggesting the switch in dominance of krill and salps along the western coast of the Antarctic Peninsula were noted (Ross *et al.* 2008). The complexity of interactions between the environmental factors (e.g. temperature, salinity, sea ice, currents, mixing) and biological processes makes it impossible to predict the outcome of climate change observed in the area of Antarctic Peninsula (Clarke *et al.* 2007).

CONCLUSIONS – VULNERABILITY *VERSUS* ROBUSTNESS OF ANTARCTIC BENTHIC FAUNA

Antarctic Peninsula is experiencing rapid regional climatic change which may significantly change benthic environment, although it is impossible to predict the scope and speed of changes. No trend of climate change is observed in East Antarctic.

Current research suggests that Antarctic benthic fauna can successfully perform only in a narrow range of environmental factors and have only a limited ability to withstand future environmental change, but geographic range of many Antarctic species extends to locations with higher sea temperatures than elsewhere in the Southern Ocean.

Future warming will make Antarctic open to invasive species. Benthic fauna, having evolved in isolated, stable and cold environment, is vulnerable to alien predators and /or competitors.

Past history of ca 30 Myr show Antarctic benthic biota to be resilient to major temperature and ice changes, able to recolonise the continental shelf after each glacial maximum

REFERENCES

- Arntz W.E., Brey T., Gallardo V.A., 1994, *Antarctic zoobenthos*, Oceanogr. Mar. Biol. Annu. Rev., 32, 241–304.
- Aronson A.B., Blake D.B., 2001, Global climate change and the origin of modern benthic communities in Antarctica, Amer Zool, 41, 27–39.
- Barbraud C., Weimerskirch H., 2001, *Emperor penguins and climate change*, Nature, 411,183–186.
- Barnes D.K.A., 2005, Changing chain: past, present and future of the Scotia's Arc and Antarctica's shallow benthic communities, Scientia Marina, 69, 65–89.
- Barnes D.K.A., Clarke A., 1995, Seasonality of feeding activity in Antarctic suspension feeders, Polar Biol., 15, 335–340.
- Barnes D.K.A., Conlan K.E., 2007, *Disturbance, colonization and development of Antarctic benthic communities*, Phil. Trans. Soc. Lond. B, 36, 11–38.
- Barnes D.K.A., Linse K., Waller C., Morley S., Enderlein P., Fraser P.P., Brown M., 2006, Shallow benthic fauna communities of South Georgia Island, Polar Biol., 29, 223–228
- Barnes D.K.A., Peck L.S., 2008, Vulnerability of Antarctic shelf biodiversity to predicted regional warming, Clim. Res., 37, 149–163.
- Brey T., Clarke A., 1993, *Population dynamics of marine benthic invertebrates in antarctic and subantarctic environments*, Antarctic Science, 5, 253–266.
- Brey T., Dahm C., Gorny M., Klages M., Stiller M., Arntz W.E., 1996, *Do Antarctic benthic invertebrates show an extended level of eurybathy?* Ant. Sci., 8, 3–6.
- Brockington S., Clarke A., 2001, *The relative influence of temperature and food on the metabolism of a marine invertebrate*, J. Exp. Mar. Biol. Ecol., 258, 87–99.
- Brockington S., Clarke A., Chapman A.L.G., 2001, Seasonality of feeding and nutritional status during the austral winter in the Antarctic sea urchin Sterechinus neumayeri, Mar. Biol., 139, 127–138.
- Brown K.M., Fraser K.P.P., Barnes D.K.A., Peck L.S., 2004, Links between the structure of an Antarctic shallow-water community and ice-scour frequency, Oecol, 141, 121–129.
- Chapelle G., Peck L.S., 1995, The influence of acclimation and substratum on the metabolism of the Antarctic amphipods Waldeckia obesa (Chevreux 1905) and Bovallia gigantea (Pfeffer 1888), Polar Biol., 15, 225–232.

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- Clarke A., 1990, Temperature and evolution: Southern Ocean cooling and the Antarctic marine fauna, [in:] K.R. Kerry, G. Hempel (eds), Antarctic ecosystems. Ecological change and conservation, Springer Verlag Berlin Heidelberg, 9–22.
- Clarke A., 1996, *The distribution of Antarctic marine benthic communities*, Antarctic Research Series, 70, 219–230.
- Clarke A., 2003, Evolution, adaptation and diversity: global ecology in an Antarctic context, [in:] A.H.I. Huiskes, W.W.C. Gieskes, J. Rozema, S.M. van der Vies, W.J. Wolff (eds), Antarctic Biology in a global context, Backhuys Publishers, Leiden, The Netherlands, 3–17.
- Clarke A., 2008, *Antarctic marine benthic diversity: patterns and processes*, J. Exp. Mar. Biol. Ecol., 366, 48–55.
- Clarke A., Aronson R.B., Crame J.A., Gili J.M., Blake D.B., 2004, Evolution and diversity of the benthic fauna of the Southern Ocean continental shelf, Antarctic Sci., 16, 559–568.
- Clarke A., Barnes D.K.A., Hodgson D.A., 2005, *How isolated is Antarctica?* Tree, 20, 1–3,
- Clarke A., Johnston N.M., 2003, *Antarctic marine benthic diversity*, Oceanogr. Mar. Biol. Ann. Rev., 41, 47–114.
- Clarke A., Johnston N.M., Murphy E.J., Rogers A.D., 2007, *Introduction. Antarctic ecology from genes to ecosystems: the impact of climate change and the importance of scale*, Phil. Trans. R. Soc. B, 362, 5–9.
- Clarke A., Murphy E.J., Meredith M.P., King J.C., Peck L.S., Barnes D.K.A., Smith R.C., 2007, *Climate change and the marine ecosystem of the western Antarctic Peninsula*, Phil. Trans. R. Soc. B., 362, 149–166.
- Cook A.J., Fox A.J., Vaughan D.G., Ferrigno J.G., 2005, Retreating Glacier Fronts on the Antarctic Peninsula over the Past Half-Century, Science, 308, 541–544.
- Cowart D.A., Ulrich P.N., Miller D.C., Marsh A.G., 2009, Salinity sensitivity of early embryos of the Antarctic sea urchin, Sterechinus neumayeri, Polar Biol., 32, 435–441.
- Croxall J.P., Trathan P.N., Murphy E.J., 2002, *Environmental change and Antarctic seabird populations*, Science, 297,1510–1514.
- Curran M.A.J., van Ommen T.D., Morgan V.I., Phillips K.L., Palmer A.S., 2003, *Ice core evidence for Antarctic sea ice decline since 1950s*, Science, 302, 1203-1206.
- Davenport J., 2001, *Meltwater effects on intertidal Antarctic limpets, Nacella concinna*, J. Mar. Biol. Ass. UK, 81, 643–649.
- Davenport J., Macalister H., 1996, Environmental conditions and physiological tolerances of intertidal fauna in relation to shore zonation at Husvik, South Georgia, J. Exp. Mar. Biol. Ecol., 76, 985–1002.
- Dayton P.K., Robilliard G.A., Paine R.T., Dayton L.B., 1974, *Biological accommodation in the benthic community at McMurdo Sound, Antarctica*, Ecol. Monog., 44, 105–128.
- Gibson R., 1983, Antarctic nemerteans: the anatomy, distribution and biology of Parborlasia corrugatus (McIntosh, 1876) (Heteronemertea, Lineidae), Antarct. Res. Ser., 29, 289–316.
- Gili J.M., Arntz W.E., Palanques A., Orejas C., Clarke A., Dayton P.K., Isla E., Teixido N., Rossi S., Lopez-Gonzales P.J., 2006, *A unique assemblage of epibenthic sessile suspension feeders with archaic features in the high-Antarctic*, Deep-Sea Res. II, 53, 1029–1052.

- Gille S.T., 2002, Warming of the Southern Ocean since the 1950s, Science, 295, 1275–1277.
- Gutt J., 2000, Some "driving forces" structuring communities of sublittoral Antarctic macrobenthos, Antarctic Science, 12, 297–313.
- Gutt J., 2001, On the direct impact of ice on marine benthic communities, a reviw, Polar Biol., 24, 553–564.
- Gutt J., Starmans A., 2001, Quantification of iceberg impact and benthic recolonisation patterns in the Weddell Sea (Antarctica), Polar Biol., 24, 615–619.
- Gutt J., Sirenko B.I., Smirnov I.S., Arntz W.E., 2004, *How many amcrozoobenthic species might inhabit the Antarctic shelf?* Ant. Sci., 16, 11–16.
- Gutt J., Starmans A., Dieckmann G., 1996, *Impact of iceberg scouring on polar benthic habitats*, Mar. Ecol. Prog. Ser., 137, 311–316.
- Hughes L., 2000, Biological consequences of global warming: is the signal already? Tree, 15, 56–61.
- IPCC, 2001, Climate change: synthesis report, Cambridge University Press, Cambridge.
- IPCC, 2007, Climate change: synthesis report, Cambridge University Press, Cambridge.
- Janecki T., Kidawa A., Potocka M., 2010, *The effects of temperature and salinity on vital biological functions of the Antarctic crustacean Serolis polita*, Polar Biol., 33, 1013–1020.
- Johst K., Gutt J., Wissel C., Grimm V., 2006, Diversity and disturbances in the Antarctic megabenthos: feasible versus theoretical disturbance ranges, Ecosystems, 9, 1145–1155.
- Kidawa A., Potocka M., Janecki T., 2010, *The effects of temperature on the behaviour of the Antarctic sea star Odontaster validus*, Polish Pol. Res., 31, 271–284.
- Kim S., Thurber A., 2007, Comparison of seastar (Asteroidea) fauna from across island groups of the Scotia Arc, Polar Biol., 30, 415–425.
- King J.C., 1994, *Recent climate variability in the vicinity of the Antarctic Peninsula*, Int. J. Climatol., 14, 357–369.
- King J.C., Turner J., Marshall G.J., Connolley W.M., Lachlan-Cope T.A., 2003, *Antarctic Peninsula climate variability and its causes as revealed by instrumental records*, Antarctic Res. Series, 79, 17–30.
- Klages M., Gutt J., 1990, Comparative studies on the feeding behaviour of high Antarctic amphipods (Crustacea) in laboratory, Polar Biol., 11, 73–79.
- Lee H.J., Vanhove S., Peck L.S., Vincx M., 2001, Recolonisation of meiofauna after catastrophic iceberg scouring in shallow Antarctic sediments, Polar Biol., 24, 918–925.
- Levitus S., Antonov J.I., Boyer T.P., Stephens C., 2000, Warming of the World Ocean, Science, 287, 2225–2229.
- McClintick M.A., DeMaster D.J., Thomas C.J., Smith C.R., 2008, *Testing the FOODBANCS hypothesis: Seasonal variations in the near-bottom particle flux, bioturbation intensity, and deposit feeding based on* ^{234Th} measurements, Deep Sea Res. II, 55, 2425–2437.
- McClintock J.B., 1994, *Trophic biology of Antarctic shallow-water echinoderms*, Mar. Ecol. Prog. Ser., 111, 191–202.
- Meredith M.P., King J.C., 2005, Rapid climate change in the ocean west of the Antarctic Peninsula during the second half of the 20th century, Geophys. Lett., 32, L19604–L19609.

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- Montes-Hugo M., Doney S.C., Ducklow H.W., Fraser W., Martinson D., Stammerjohn S.E., Schofield O., 2009, *Recent changes in phytoplankton communities associated with rapid regional climate change along the western Antarctic Peninsula*, Science, 323, 1470–1473.
- Morley S.A., Hirse T., Pörtner H.O., Peck L.S., 2009, *Geographical vatiation in thermal tolerance within Southern Ocean marine ectotherms*, Comp. Biochem. Physiol. A, 153, 154–161.
- Newell R.C., Branch G.M., 1980, *The effects of temperature on the maintenance of metabolic energy balance in marine invertebrates*, Adv. Mar. Biol., 17, 329–396.
- Nihashi S., Ohshima K.I., Mo Jeffries, Kawamura T., 2005, Sea-ice melting processes inferred from ice-upper ocean relationships in Ross Sea, Antarctica, J. Geophys. Res., 110, C02002.
- Nolan C.P., Clarke A., 1993, *Growth in the bivalve Yoldia eightsi at Signy Island, Antarctica, determined from internal shell increments and calcium-45 incorporation*, Mar. Biol., 117, 243–250.
- O'Loughlin P.M., Paulay G., Davey N., Michonneau F., 2011, *The Antarctic region as a marine biodiversity hotspot for echinoderms: Diversity and diversification of sea cucumbers*, Deep-Sea Res., II, 58, 264–275.
- Pearse J.S., 1969, Antarctic sea star, Austr. Nat. Hist., 16, 234–238.
- Pearse J.S., McClintock J.B., Bosch I., 1991, Reproduction of Antarctic benthic marine invertebrates tempos, modes, and timing, Am. Zool., 31, 65–80.
- Peck L.S., 1989, Temperature and basal metabolism in two Antarctic marine herbivores, J. Exp. Mar. Biol. Ecol., 127, 1–12.
- Peck L.S., 2002, *Ecophysiology of Antarctic marine ectotherms: limits to life*, Polar Biol., 25, 31–40.
- Peck L.S., 2005, Prospects for survival in the Southern Ocean: vulnerability of benthic species to temperature change, Antarctic Sci., 17, 497–507.
- Peck L.S., Bullough L.W., 1993, *Growth and population structure in the infaunal bivalve Yoldia eightsi in relation to iceberg activity at Signy Island*, Antarctica, Mar. Biol., 117, 235–241.
- Peck L. S., Holmes L. J., 1990, Seasonal and ontogenetic changes in tissue size in the Antarctic brachiopod Liothyrella uva (Broderip, 1983), J. Exp. Mar. Biol. Ecol., 134, 25–36.
- Peck L.S., Robinson K., 1994, *Pelagic larval development in the brooding Antarctic brachiopod Liothyrella uva*, Mar. Biol., 120, 279–286.
- Peck L.S., Ansell A.D., Webb K.E., Hepburn L., Burrows M., 2004a, *Movements and burrowing activity in the Antarctic bivalve molluscs Laternula elliptica and Yoldia eightsi*, Polar Biology, 27, 357–367.
- Peck L.S., Brockington S., Vanhove S., Beghyn M., 1999, Community recovery following catastrophic iceberg impacts in a soft-sediment shallow-water site at Signy Island, Antarctica, Mar. Ecol. Prog. Ser., 186, 1–8.
- Peck L.S., Clark M.S., Morley S.A., Massey A., Rossetti H., 2009a, *Animal temperature limits and ecological relevance: effects of size, activity and rates of change*, Funct. Ecol., 23, 248–256.
- Peck L.S., Colman J.G., Murray A.W.A., 2000, Growth and tissue mass cycles in the infaunal bivalve Yoldia eightsi at Signy Island, Antarctica, Polar Biol., 23, 420–428.

- Peck L.S., Massey A., Thorne M.A.S., Clark M.S., 2009b, *Lack of acclimation in Ophionotus victoriae: brittle stars are not fish*, Polar Biol., 32, 399–402.
- Peck L.S., Pörtner H.O., Hardewig I., 2002, *Metabolic demand, oxygen supply, and critical temperatures in the Antarctic bivalve Laternula elliptica*, Physiol. Biochem. Zool., 75, 123–133.
- Peck L.S., Webb K.E., Bailey D.M., 2004b, *Extreme sensitivity of biological function to temperature in Antarctic marine species*, Functional Ecol., 18, 625–630.
- Peck L.S., Webb K.E., Miller A., Clark M.S., Hill T., 2008, *Temperature limits to activity, feeding and metabolism in the Antarctic starfish Odontaster validus*, Mar. Eco.l Prog. Ser., 358, 181–189.
- Pörtner H.O., 2002, Climate variations and the physiological basis of temperature dependent biogeography: systemic to molecular hierarchy of thermal tolerance in animals, Comp. Biochem. Physiol. Part A, 132, 739–761.
- Pörtner H.O., Hardewig I., Peck L.S., 1999, *Mitochondrial function and critical temperature* in the Antarctic bivalve, Laternula elliptica, Comp. Biochem. Physiol. A., 124, 179–1889
- Pörtner H.O., Peck L.S., Somero G., 2007, *Thermal limits and adaptation in marine Antarctic ectotherms: and integrative view*, Phil. Trans. R. Soc., B 362, 2233–2258.
- Robertson R., El-Haj A.J., Clarke A., Peck L.S., Taylor E.W., 2001, The effects of temperature on metabolic rate and protein synthesis following a meal in the isopod Glyptonotus antarcticus Eights (1852), Polar Biol., 24, 677–686.
- Robertson R., Visbeck M., Gordon A.L., Fahrbach E., 2002, *Long-term temperature trends in the deep waters of the Weddell Sea*, Deep Sea Res., 49, 4791–4806.
- Rogers A.D., 2009, Evolution and biodiversity of Antarctic organisms: a molecular perspective, Phil. Trans. R. Soc. B., 362, 2191–2214.
- Ross R.M., Quetin L.B., Martinson D.G., Iannuzzi R.A., Stammerjohn S.E., Smith R.C., 2008, Palmer LTER: patterns of distribution of five dominant zooplankton species in the epipelagic zone west of the Antarctic Peninsula, 1993-2004, Deep-sea Res. II, 55, 2086–2105.
- Rupp G.S., Parsons G.J., 2004, Effects of salinity and temperature on the survival and byssal attachment of the lion's paw scallop Nodipecten nodosus at its southern distribution limit, J. Exp. Mar. Biol. Ecol., 309, 173–198.
- SCAR Report, 2009, *Antarctic Climate Change and the Environment*, Turner J., Bindschadler R.A., Convey P., Di Prisco G., Fahrbach E., Gutt J., Hodgson D.A., Mayewski P.A., Summerhayes C.P. (eds), Cambridge, p. 360.
- Smith R.C., Stammerjohn S., 2001, Variations of surface air temperature and sea ice extent in the Western Antarctic Peninsula (WAP) region, Ann. Glaciol., 33, 493–500.
- Teixido N., Garrabou J., Gutt J., Arntz W.E., 2004, Recovery in Antarctic benthos after iceberg disturbance: trends in benthic composition, abundance and growth forms, Mar. Ecol. Prog. Ser., 278, 1–16.
- Teixido N., Garrabou J., Gutt J., Arntz W.E., 2007, *Iceberg disturbance and successional spatial patterns: the case of the shelf Antarctic benthic communities*. Ecosystems, 10, 142–157.
- Thatje S., Arntz W.E., 2004, *Antarctic reptant decapods: more than a myth?* Polar Biol., 27, 195–201.

- Thatje S., Hillenbrand C.D., Larter R., 2005, On the origin of Antarctic marine benthic community structure, TREE, 20, 534–540.
- Turner J., Colwell S.R., Marshall G.J., Lachlan Cope T.A., Carleton A.M., Jones P.D., Lagun V., Reid P.A., Iagovkina S., 2005, *Antarctic climate change during the last 50 years*, Int. J. Climatol., 25, 279–294.
- Vaughan D.G., Doake C.S.M., 1996, Recent atmospheric warming and retreat of ice shelves on the Antarctic Peninsula, Nature, 379, 328–331.
- Vaughan D.G., Marshall G.J., Conneley W.M., Parkinson C., Mulvaney R., Hodgson D.A., King J.C., Pudsey C.J., Turner J., 2003, *Recent rapid regional climate warming on the Antarctic Peninsula*, Climatic Change, 60, 243–274.
- Weimerskirch H., Inchausti P., Guinet C., Barbraud C., 2003, *Trends in bird and seal populations as indicators of a system shift in the Southern Ocean*, Ant. Sci., 15, 249–256.
- Whitehouse M.J., Meredith M.P., Rothery P., Atkinson A., Ward P., Korb R.E., 2008, *Rapid warming of the ocean around South Georgia, southern ocean, during the 20th century: forcings, characteristics and implications for lower trophic levels*, Deep Sea Res. I, 155, 1218–1228.
- Young J.S., Peck L.S., Matheson T., 2006, *The effects of temperature on walking and righting in temperate and Antarctic crustaceans*, Polar Biol., 29, 978–987.
- Zwally H.J., Comiso J.C., Parkinson C.L., Cavalieri D.J., Gloersen P., 2002, *Variability of Antarctic sea ice 1979–1998*, J. Geophys. Res., 107, C5, 3041.