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Antarctic marine biology - two centuries of research

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Abstract: Whilst interest in the economic exploitation of the Southern Ocean resources dates back to the last part of the 18th century scientific research into elements of the marine ecosystem only began in the mid 19th century. As far as plankton and benthos are concerned the great exploratory voyages and expeditions laid a firm taxonomic foundation on which later work was built. The most outstanding expedition contribution was from the *Discovery* Investigations. Concern about uncontrolled exploitation stimulated the SCAR BIOMASS programme which in turn led to CCAMLR with its modelling programmes and top predator monitoring. Recent research on pack ice communities has been aided by dedicated ice-capable research vessels whilst unmanned photographic techniques as well as SCUBA diving and experimental research facilities in the Antarctic have encouraged major research on benthos. International collaboration, interdisciplinary research and good ideas suggest Antarctic marine biology has a bright future.

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Biologists' interest in the Antarctic

Curiosity and economical interests have both made the Antarctic attractive to biologists for more than two hundred years. But why? Biologists like rarities and extremes - so of course they look at the few terrestrial species and the life in permanently frozen lakes, in cryoconite habitats, on bare rocks and in the frozen and ornithogenic soils. The cold deserts on the mainland are small oases amidst the ice sheet. In fact, in the decades from the 1960s to 1980s Antarctic places like the McMurdo Dry Valleys and the Schirmacher Oasis were studied in more detail than many less remote places on earth.

The greatest attraction, however, to polar biologists lies in the seas around the Antarctic continent and its islands. There is a rich spill-over from the sea onto the few ice free coastal places from birds and mammals looking for rookeries and moulting places. This nutrient input is a vital link in supporting terrestrial ecosystems. Since James Cook's voyage in the late 18th century explorers and naturalists, followed by sealers, have been reporting on the rich mammalian and avian fauna of the Antarctic, stimulating the interest of scientists. In the early days of the Scientific Committee on Antarctic Research (SCAR) the study of the recovery of the over-exploited stocks of fur seals was an important topic. Over more than five decades, the Antarctic seals, penguins, and flying birds such as skuas, albatrosses and petrels have been studied intensively, both on land and more recently also at sea where we have witnessed a methodological revolution from the introduction of a rich array of recording devices. However, there has been growing interest in the seas and their communities for much longer than the past 50 years and it is this I wish to survey.

The exploratory phase of 120 years

My review of past Antarctic biology will concentrate on plankton and benthos in the sea. It will by no means be a proper historical account. The first papers on Antarctic diatoms in the pack ice were published by Ehrenberg (1844, 1854) and Hooker (1847) on material collected by Hooker during the *Erebus* and *Terror* Expedition of 1839–1843 led by James Clark Ross, and the reconnaissance investigation of Antarctic plankton and benthos was continued by various scientific exploratory expeditions until World War I. The great series of scientific volumes of the expeditions by the research vessels *Challenger* 1872–1876, *Belgica* 1897–1898, *Valdivia* 1898/1899, *Gauss* 1901–1903, *Pourquoi Pas?* 1908–1910, *Nimrod* 1908 and others are still the backbone of taxonomic literature in Antarctic phyto- and zooplankton and benthos.

On some expeditions, such as e.g. *Discovery* (1901–1904) and *Endurance* (1914–1917), biological work was largely limited to observations of birds and mammals. Edward Wilson (1966) provided a wonderfully illustrated diary of his work as an ornithologist on RRS *Discovery* as well as some of the finest illustrations of Antarctic birds (Wilson 1967). The *Terra Nova* (1910–1912) expedition provided more marine biology with several volumes describing new marine invertebrates from many groups.

The *Discovery* phase

After World War I, the *Meteor* and *Discovery* cruises, both starting in 1925, were the first expeditions in the Southern Ocean to focus on studies of marine phenomena rather than undertaking such work as an ancillary to geographical exploration and geophysical observations. The *Meteor*

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Fig. 1. RRS *Discovery* on the Danco Coast, Antarctic Peninsula, during the Discovery Investigations. [Photo: British Antarctic Survey Archives]

expedition (1925–1927) touched the Southern Ocean and provided detailed information on the zonation of plankton and biogenic sediments in the Southern South Atlantic. More important for the study of Southern Ocean biology was the long series of cruises by *Discovery* and *Discovery II* between 1925 and 1950. The results were compiled in the famous Discovery Reports and, for the general public, summarized by Sir Alister Hardy (1967) in his book *Great Waters*, one of the best pieces of popular marine biological literature ever written.

The Discovery Investigations were essentially concerned with a better understanding of all the different aspects of the ocean affecting the distribution of the whales. Therefore research into krill was of prime importance. Hardy & Gunther (1935) created the belief in the key role of krill in the Southern Ocean ecosystem whilst Marr (1962) published the monumental monograph on the natural history and geography of *Euphausia superba* Dana which was to prove the cornerstone of much later work. The larval development of krill from nauplius through various calyptopis and furcilia stages to adult krill was described and well illustrated by F.C. Fraser (1936) and Helene Bargmann (1945). She also analysed in great detail the very complicated reproductive system of krill (Bargmann 1937), working only on fixed material as women were not allowed on board *Discovery* in those days.

In the 1930s and immediately after World War II the economic interest in whales ensured the funding of research in the Southern Ocean. The Discovery Investigations were financed out of the levies on the oil produced by whaling industry. Consequently research in whales and their food chain, primarily krill and diatoms, were at the top of the agenda. Studies on dinoflagellates and other phytoplankton were traditionally less well favoured. Nevertheless, Hart (1934, 1941) described zonal distribution and seasonal periodicity of phytoplankton in quantitative terms and pointed to the Antarctic paradox. Both he and Gran (1931) speculated about the role of trace elements, like iron, in controlling phytoplankton growth. Zooplankton other than krill was studied particularly by Mackintosh (1934, 1937) and after World War II by Foxton (1956) who later specialised in salps (Foxton 1961, 1966).

Other whaling nations, particularly Norway, also had biologists working in the Southern Ocean, partly in the whaling industry and partly on research and survey vessels - but the Discovery Reports remained outstanding in their wealth of scientific information.

In the 1950s and 1960s research into standing stock and primary production of phytoplankton expanded greatly because of the new techniques for chlorophyll *a* determination and the radio-carbon method, both published in 1952. New expeditions provided high estimates of phytoplankton biomass and production, mostly at the edge of the pack ice in spring and summer. Extrapolation of those high local figures to larger parts of the Southern Ocean and to other seasons led to the false assumption of a highly productive ocean which should support enormous amounts of krill. Important in this research were the expeditions of

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the Soviet vessels *Ob* and *Vitiaz*, and the USNS *Eltanin*. But the Argentinean, French and Japanese research vessels also assembled large datasets whilst Norway focussed on whales and on notothenoid fish.

Research in the 1960s

In the 1960s after 120 years of surveying, reconnaissance, and collecting, the need for new lines of research was recognized. The proceedings of three symposia provide important indications of how the new ideas were developed.

In 1966 SCAR organized a Symposium on Antarctic Oceanography in Santiago, Chile. The list of participants included famous names in physical oceanography like Stommel, Mosby and Kort, and Ewing in geology. The invited papers in biology were given by Knox, Andriashev, El-Sayed and Nemoto. Old hands of the Discovery Investigations like Hardy and Mackintosh were present, but also the next generation including Holdgate and Hureau. Chilean and Argentinean marine biology was represented by *inter alia* Szidat, Etcheverry, and Esteban Boltovskoy, but only one female author Irene Bernasconi, a sea urchin specialist from Buenos Aires, appears to have been present.

The Symposium was supposed to stimulate "inter-disciplinary discussion, particularly between the fields of physical and biological oceanography" - for the sake of science and for optimizing the use of logistics. In an attempt "to highlight the unresolved but more approachable problems in each subject", specific recommendations were made for the various "regimes" of the Southern Ocean:

For the upper pelagic zone the participants wanted better knowledge of the life history of key species and "a better assessment of the structure and interrelationships of the living communities" - in relation to the physical and chemical driving forces. For the deep waters the study of physical and chemical parameters should be given priority to time consuming biological observations. The study of the distribution and dynamics of benthic communities called for better sampling devices. Deep sea floor photography was in its infancy at this point. For sea floor microbiology the need for uncontaminated and pressurized sampling was mentioned. Not only was Antarctic deep sea benthos virtually unknown in those days but also the inshore benthos including the vertical zonation, autecology, and physiology of its key members. The Symposium stressed "the need for more taxonomic facilities", which were seen as a limiting factor in the whole field of Antarctic marine biological research. Further questions were raised regarding sea ice communities and about biochemical processes within and right under sea ice. Sensors developed for clinical research should be adopted for *in situ* observations. Some biologists wanted to know: "Who is living beneath the floating ice shelves?" There was a plea for the standardisation of biological methods in plankton and benthos research in Antarctic waters.

The systematists working on Antarctic material wanted to see the material of certain expeditions in for example the Weddell Sea, Ross Sea and Bouvet Island waters to be pooled.

And on logistics, scientists in 1966 were not willing to accept any longer that most of their work had to be done from supply vessels. Nearly all workers asked for more flexible programmes, "so that opportunity could be taken of sampling unusual occurrences or investigating unusual phenomena."

The pre-BIOMASS phase

In the early years of SCAR rather little came out of all those recommendations of 1966. The balance of interest within Antarctic biology ten years later is reflected in the proceedings of a two-day discussion meeting - "Scientific Research in Antarctica" of the Royal Society of London (Fuchs & Laws 1977). The volume contains almost fifty pages on terrestrial and limnological studies, and a further thirty on seals and whales. Marine primary and secondary production and cold adaptation covered only 20 pages.

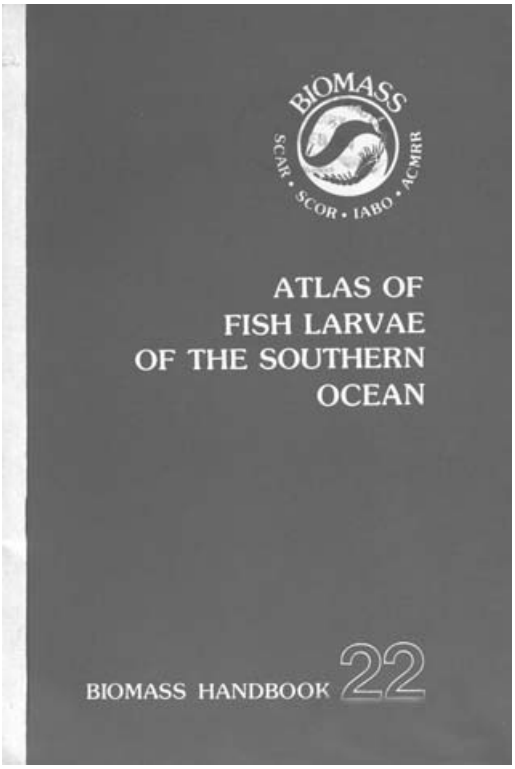
G.M. Dunnet, a zoologist from Aberdeen University, in his contribution wanted more marine biology in SCAR. He spoke about the marine environment with its richness in nutrients and productivity, but low biodiversity. "The understanding of ecological processes and trophic relations in such systems is of fundamental importance, and is essential before technology is developed to exploit the vast biological resources of the Southern Ocean" (Dunnet 1977).

Antarctic marine biology still did not follow the mainstream of biological sciences, as it largely ignored molecular and evolutionary biology. With the introduction of the large Exclusive Economic Zones (EEZ) of coastal states and with the warnings of the Club of Rome, the 1970s saw a growing economic interest in Antarctic krill and fin fish. They replaced whales in their role as public justification for marine research in the Southern Ocean in the 1970s and 1980s.

Already at the 1966 Symposium Hardy had mentioned the potential of the krill resource. He expected it to be harvested on a very large scale for fish meal or direct human consumption. He warned against uncontrolled exploitation prior to careful international studies and proposed: "An international commission should appoint scientists, organize expeditions and then make recommendations. Without such guidance man is most likely to blunder again" (Hardy in Anon 1968). That was two decades before the Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR).

In those days the biomass of all baleen whales, except minke whales, was very low due to chronic over-exploitation and so the marine resources industry thought they might start taking the krill which was not being used by whales. This was an alarming prospect. Early estimates of

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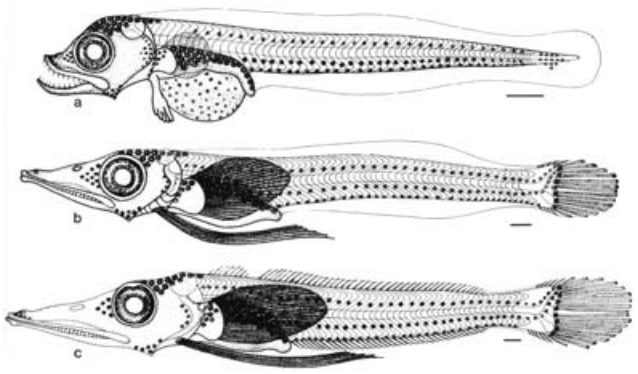


Fig. 2. One of the series of practical handbooks produced for BIOMASS cruises with an illustration of the larval forms of *Chaenocephalus aceratus* (Lönnberg, 1906).

krill biomass and potential yield were based on both bottom-up and top-down approaches using primary production and the supposed krill consumption by higher trophic levels. The assumptions on transfer efficiencies were weak. Early Soviet estimates of annual krill production amounted to two billion tonnes. In a study for FAO we brought the annual krill production estimates down to 150 million tonnes (Hempel in Gulland 1972). The difference of more than an order of magnitude called in to question all assumptions and made a strong case for direct measurements of total krill biomass, combined with environmental data and estimates of primary production and krill predator abundance.

In his review of the history of primary productivity studies of the Southern Ocean, El Sayed (2005) paid tribute to the US Polar Programs which had already anticipated in the late 1960s the impending commercial exploitation of Antarctic marine living resources. Three *Eltanin* cruises in 1969–1971 opened the phase of system-oriented studies, focussing on pathways of nutrients and on energy flow through the pelagic lower trophic levels from nanoplankton to krill. Integrated datasets were collected as a basis for the first computer models. El Sayed, McWhinnie and Holm-Hansen were the key scientists in the marine biological part of the US Program. From 1978 the Nimbus-7 coastal zone colour scanner provided good seasonal and geographic coverage of the near-surface phytoplankton distribution in areas and at times where and when direct ship borne observations were virtually impossible. Continuous remote sensing of sea surface temperature and ice cover helped us to understand the year to year biological variations in the distribution and dynamics of plankton. Twenty years later SeaWiFS provided an even wider field of view and higher resolution.

The BIOMASS Programme

The Biological Investigations of Marine Antarctic Systems and Stocks (BIOMASS) started in 1976, primarily thanks to the initiative of S.Z. El Sayed. It was directed towards the understanding of structure and functioning of the ecosystem of the Southern Ocean as a basis for the future management of its potential living resources (El Sayed 1977). BIOMASS viewed the pelagic system as krill dominated. Therefore large-scale multi-ship hydro-acoustic and fishing surveys were initiated, called the First and Second International BIOMASS Experiments - FIBEX 1980/1982 and SIBEX 1983/1984 and 1985/1986. Many supporting research activities were carried out, mostly on fish and seals as predators of krill and all data were accumulated in the BIOMASS Data Base for international use and analysis.

BIOMASS provided much detailed information on the biological variability at different scales of space and time in all parts of the ecosystem. There was no longer much belief in the global figures of total biomass, production and energy budget. It was felt that any new research strategy should include studies of metabolism at the levels of organisms and communities, and aim for rates rather than stocks, fluxes rather than compartments and for variations rather than average steady states. The ecosystem approach, and the

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network of international cooperation developed in BIOMASS, helped the establishment of CCAMLR as the world's first ocean-wide international convention for the conservation of the marine resources and their environment. By its close in 1991, El Sayed (1994) praised BIOMASS as the largest and most comprehensive international biological programme in the Southern Ocean. BIOMASS served the divergent interests of its parent organisations SCAR, SCOR, and FAO by producing a wealth of information on the biology of the Southern Ocean and its living resources and provided the scientific basis for the establishment of a sustainable management regime over 10% of the world's oceans - no mean feat.

So far no large-scale fishery for krill has developed. The main reasons then were the hesitation of industry to invest in the exploitation of a resource which was so far away from the established markets, and posed difficulties both in processing and sale. Furthermore industry realized the high variability in accessibility of krill and the conservative attitude of CCAMLR and of consumers being worried that krill fishing might detrimentally compete with penguins, seals and whales in their respective foraging areas. Such abstention may not continue for much longer with new processing facilities being built and a much wider product range - including pharmaceuticals - now being developed from krill.

Southern Ocean-GLOBEC - krill again

Since BIOMASS, no further cooperative projects in Antarctic marine biology have been of the same scale, but several projects covering major parts of the Southern Ocean picked up certain aspects of BIOMASS (Hempel 1994). Remote sensing substituted for simultaneous multi-ship surveys. CCAMLR initiated an ecosystem monitoring programme and encouraged studies in the variability of Southern Ocean circulation and its influence on primary production, zooplankton, and krill predators (Sahrhage 1988). Joint Global Ocean Flux Studies (JGOFS) and Global Ocean Ecosystem Dynamics (GLOBEC) finally connected the biological processes in the ice free upper pelagic zone with the life in deeper layers and at the seafloor as well as in the sea ice.

At the end of the 1980s, industry and most Antarctic researchers had become tired of krill. It took another decade before interest in krill popped up again as source of natural products like chitin and pigments and as luxury food for men and salmon. Krill research became re-vitalized first in USA and subsequently in Europe.

Southern Ocean GLOBEC focuses on questions related to krill abundance, stock identity (is there only a single krill population in the Southern Ocean?) and on the survival of krill and krill larvae in winter. The advancements in population genetics, under ice studies, and metabolic measurements have meant great steps forward in elucidating the life history, population dynamics and fluctuations of krill, particularly in relation to sea ice cover (Siegel 2005). Integrated analyses of the ecosystem around South Georgia, in Bransfield Strait, Antarctic Peninsula waters, Prydz Bay and in parts of the Ross Sea have shown the great differences and variations in the relative importance of krill in each of those regions. Most of these studies were under the umbrella of national programmes but often with participation of scientists from other countries, particularly in Europe. Outstanding was EPOS in 1988/89 as a pan-European project initiated and largely financed by Germany (Hempel 1993).

JGOFS and the iron issue

The Joint Global Ocean Flux Study of the 1980s and early 1990s was a long term programme to understand the role of the World Ocean in the global carbon budget. The study of the polar oceans as sinks for atmospheric CO_2 started relatively late in JGOFS, as employing sediment traps for long-term data collections in the sea ice zone is not an easy task. Because the microbial loop is relatively weak and remineralization rates in the water column are low, much of the organic matter produced in the euphotic zone reaches the sea floor. The spring bloom of phytoplankton at the edge of the melting sea ice produces a very strong seasonal signal. The combination of remote sensing and ship-borne observations demonstrated the dynamics of frontal zones with their eddies and up- and down-welling processes, which determine nutrient supply and mixed layer depth and hence primary production and subsequent grazing, remineralization and sedimentation.

In JGOFS the Antarctic Paradox, i.e. the low primary production relative to rather high nutrient contents in the euphotic zone, finally attracted the full attention of the scientific community. This paradox is typical for most of the Southern Ocean. John Martin postulated that the low production for those areas was due to a limitation by iron instead of the otherwise common limitation by phosphorus and nitrogen compounds, and he related the iron deficits to low airborne supply of iron in dust (Martin & Fitzwater 1988).

Artificial iron fertilization as means to counteract the anthropogenic CO_2-increase was a logical step for a society which believes in man's capacity to find medicine for all man made disorders of Nature. In 1992 Martin initiated the first iron fertilization experiment in the equatorial Pacific (Coale 1998), followed by SOIREE 1999 in sub-Antarctic waters south of New Zealand and more recently the SoFEX cruise down towards the Ross Sea (Boyd 2004).

RV *Polarstern* conducted EISENEX 2000 in the Polar Front south of Africa (Strass *et al.* 2001). The fertilization effect was striking but the observation period was too short to show an increased flux to the sea floor. This was achieved only at the second, longer experiment in 2004 which

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Fig. 3. The German research vessel *Polarstern* has provided a major international platform for Southern Ocean marine research for over twenty years. [Photo: British Antarctic Survey]

witnessed an increase in zooplankton and large amounts of fresh organic material at the seabed six weeks after fertilization of the surface water (Smetacek 2006).

Those experiments were riding the wave of public concern about Global Change, but it seems clear at present that this approach will not help to stop atmospheric CO_2 increase and global warning. By close international and multidisciplinary cooperation of biologists and biogeochemists they have however provided important insights into the dynamics of the pelagic food web of the open ocean.

The *Polarstern* phase - studies in the sea ice zone

Until the 1980s biological studies on Antarctic sea ice biota, and in the water-column and sea bed in the zone of more or less permanent sea ice, were largely restricted to opportunistic sampling done en route by ships focussed on other tasks like supplying Antarctic stations. In Arctic sea ice, however, considerable biological work had been carried out since the early studies by Fridtjof Nansen, as summarized recently by Thomas & Dieckmann (2003).

Since 1983 RV *Polarstern* has been serving as a platform for international teams studying the physical, chemical and biological properties of sea ice itself and of the water column below. Those year-round studies of the sea ice zone of the Antarctic - both its seasonal and permanent parts - have provided some of the most important advances in polar biology over the past 25 years. They demonstrated that the sea ice itself is a temporary habitat, only full of life for the months between ice formation around March/April and ice melt in November/December. Sea ice determines the stability of the water column, and the exchange of heat, water and gases between ocean and atmosphere. All those physical and chemical parameters affect the sea ice biota. The sea ice is vertically structured with an epifauna and flora on its underside and with an interstitial endofauna and flora inhabiting the brine channels. Many sea ice organisms belong to what are otherwise benthic taxa. The detection of the pivotal role of sea ice in the life history of krill was one of the major contributions to BIOMASS. The knowledge of the interaction between the sea ice flora and the plankton blooms at the ice edge helped us to understand the dynamics of phytoplankton communities (Thomas 2004).

The findings of the past 25 years since the onset of BIOMASS have drastically changed our basic picture of the pelagic web. In particular:

- The Southern Ocean is not tightly confined by the Polar Front,
- Overall primary production is not as high as earlier assumed nor is it confined to the ice edge spring bloom,
- The pelagic system is not generally dominated by krill and it is not just a simple food chain of diatoms-krill-whales but a complex food web with a high variability

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which goes much beyond alternations of krill and salps,

- Winter is not a dead season, nor is the pack ice completely hostile to life.

Compared with vertebrates and plankton, benthos had been rather neglected in Southern Ocean studies until the early 1980s. As with sea ice studies a major impetus came from RV *Polarstern*. In 1983–1996 major exploratory studies were carried out in the Weddell Sea and Bransfield Strait. Then SCAR launched its programme on the Ecology of the Sea Ice Zone (EASIZ). It became the framework and umbrella for a set of very comprehensive studies including three international *Polarstern* expeditions in 1996 to 2000, several cruises of other polar research vessels and numerous shore based studies in Peninsula region, Weddell Sea and Ross Sea.

EASIZ linked, for the first time, all aspects of Antarctic marine ecology from microbiology to mammal research, from the surface of sea ice to the deep sea bed, from the shore line to the open ocean, year round and looking into the geological past as well as into the future under climate change. A large set of EASIZ results was presented at a mid term symposium in 1999 (Arntz & Clarke 2002) reflecting a wide range of problems tackled by EASIZ in an area which 30 years ago was virtually a *mare incognitum* - at least in the permanent sea ice zone.

Never before had so much emphasis been given to ecophysiological observations and experiments elucidating the potential hazards of high UV irradiance due to the ozone hole, and to studying the adaptive processes to life near freezing and to highly intermittent food supplies. Metabolic cold adaptation suggests that animals in cold water exhibit rates of physiological processes similar to rates in warmer environments. Altogether the number of benthic species with planktotrophic larvae is small compared to the many brooding species or those with lecithotrophic larvae. Accordingly the reproduction period in most species is not restricted to spring and summer only. Similarly it had been postulated that Antarctic suspension feeders feed primarily during and right after the phytoplankton blooming in early summer. That does not hold true anymore as the majority of the vagil species prove to be saprophages or omnivores and find food anytime, independent of plankton blooms.

The study of benthos was very high on the agenda of EASIZ. Many new species were found and the species distribution, horizontal/vertical zonation, biodiversity at different spatial scales and along latitudinal gradients were described. The present distribution was interpreted by evolutionary processes governed by plate tectonics and changes in currents and glaciation. Stepping stones like the Scotia Arc and Bouvetøya (Arntz 2006) were intensively visited. The benthic fauna of the Antarctic Peninsula region was compared in detail with the benthos of the Magellan Region. Detailed analyses recognized dissimilarities between Arctic, Antarctic and deep sea faunas. Some species have pelagic larvae and their development and metabolism is slow, showing little indication of temperature adaptation.

Obviously the Antarctic benthic biodiversity is considerably higher than was hitherto known. The ANDEEP expeditions in 2002 studied the benthic deep water communities in selected parts of the Scotia and Weddell Sea. Its results published collectively in *Deep-Sea Research II* (Brandt & Hilbig 2005) are the most comprehensive accounts so far of biodiversity in Antarctic deep sea benthos.

All those studies demonstrated the partial validity of the early paradigms of Antarctic and deep sea benthos: bipolarity in some groups, brooding fairly common and year round, lecithotrophy prevailing in pelagic larvae. Low metabolic rates seem to be themselves adaptations to Antarctic conditions.

Driving forces, tools, and international cooperation

The driving forces, logistics, tools and institutions of Antarctic marine biological research have undergone great changes over the past two centuries and particularly in the second half of the twentieth century.

In the nineteenth century marine biology was a by-product of other interests in the Antarctic since Cook's search for the *terra incognita australis*. Marine biology was done sporadically and en route during the explorers' voyages and later on the supply cruises. Marine biology was not a major issue for most of the Antarctic expeditions of the nineteenth century.

Three sets of driving forces followed each other in the twentieth century: sealing and whaling until 1950s, fishing for krill and fish in the 1960s to 1980s, worries about global climate change and biodiversity since the 1990s. Each of those drivers prompted a particular suite of lines of research on mammals, krill and plankton, biogeochemistry, sea ice, and benthos. Ornithologists had always their special niche so that bird research seems to have gone on regardless of the drivers.

Each of the main drivers were directly related to global demands. Seals and right whales helped to bring candlelight to Europe and other parts of the world in pre-petroleum times. After the two World Wars, margarine made from whale blubber helped to save millions of people from starvation. The Club of Rome postulated that overexploitation of the limited world's resources would spell disaster and the Law of the Sea closed most fishing grounds to foreign distant water fleets. The Southern Ocean, with its fish and krill, was considered heaven by the Eastern Bloc fishermen. The concern about climate change and the hope for a CO_2 sink that would painlessly solve the squandering of fossil fuels by the developed world brought the Southern Ocean and its biota into the sharp focus of

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researchers and now of politicians. Finally the worry about the rapid loss of biodiversity reached the sea and at last the Antarctic deep sea floor. Antagonistically to the economic interests environmentalists called for studies on the impact of man on the Antarctic biota, particularly birds, seals and whales.

At the same time research moved from the study of individual species to food chains and food webs and, in the waters around South Georgia, to an ecosystem analysis. Today ecophysiology and taxonomy are again deemed important and population genetics and evolutionary biology have become promising fields for Antarctic researchers.

Antarctic marine biology is greatly dependent on logistics. Large dedicated research vessels like *Polarstern, James Clark Ross*, and *Nathaniel Palmer* have meant a break through in what can be achieved not least because the cruises are determined by science requirements and not logistic needs. Sampling devices, sensors, ROVs and landers have greatly advanced as well as satellite tracking and telemetry and year-round satellite imaging. SCUBA diving has been successfully employed for direct nearshore and under-ice observations

Antarctic biology is no longer carried out in isolation either from the rest of the oceans or the rest of the discipline. It profits greatly from automation in chemistry and molecular biology as well as in image analysis and statistics. Shore stations which can be visited relatively easily provide excellent platforms for broad multidisciplinary and multinational cooperation and for transdisciplinary communication. Their number has increased from the original twelve Antarctic treaty nations to include almost 30 nations from all parts of the world.

Meanwhile many institutes have started programmes in Antarctic marine biology and introduced new approaches. In Europe that was particularly noticeable with the eco-physiological work done by Italian researchers and with Spanish benthos studies - just to name two examples. Polish groups profited from their earlier work in Spitsbergen. In Germany many “ordinary” marine biologists wanted to work in the Antarctic at least once. Wheels were re-invented by the newcomers but they enjoyed the support of old hands in Antarctic research and, in turn, helped the next group entering the Antarctic science community.

Joint projects under the umbrella of SCAR, SCOR and CCAMLR as well as the SCAR Antarctic Biology Symposia brought biologists of different nations and backgrounds together and provided young scientists with the opportunity to become acquainted with multinational cooperation and make themselves internationally known. Automated data bases and networks will hopefully continue to facilitate the exchange of personnel and data.

In several countries, such as France, Germany, Norway, USA, and in the European Polar Board, Antarctic and Arctic research are combined in one institution competing for the same funds and logistics.

In the 1980s two major international journals were established to serve Antarctic biologists - *Polar Biology* and *Antarctic Science*. Editorial policy and very cooperative peer reviewers helped greatly to develop and maintain quality standards for these scientific publications in the rapidly expanding community. Both now provide key outlets for some of the best Antarctic marine biology.

The end of the Cold War and the opening of the Arctic Ocean to international studies resulted in more comparisons than ever before between Arctic and Antarctic biota (Hempel & Hempel 1995).

Summary and conclusions

The Southern Ocean with its Antarctic shelves, coasts and islands remains unique for marine biologists in many respects: The sea is fairly pristine and is inhabited by both gigantic as well as sluggish organisms living in the sea ice zone. Its seasonal sea ice cover undergoes the most dramatic seasonal change of any part of the World’s Ocean.

At present, and in the foreseeable future, the Southern Ocean is the only major part of the World Ocean rich in life where economic interests in the living resources are low. Evidence of exploitation elsewhere makes it imperative that these resources must be kept under permanent surveillance. Conservationists’ interests will hopefully ensure continued political and financial support for Antarctic biological research from many countries.

There is widespread scientific interest in old and new questions in Antarctic biology: How do the organisms defend themselves against the extreme cold? How did continental drift and past climate change bring about the present biodiversity? What will happen to the Antarctic ecosystem and its biodiversity under global warming? Many questions will now be addressed by the new SCAR programme on Evolution and Biodiversity in the Antarctic (EBA).

Antarctic marine biology is increasingly contributing to biology in general. Studies on whales, penguins, icefish and krill have entered common textbooks of biology and are particularly interesting and attractive to the public. Indeed, Antarctic biologists have been good in selling their science and have been used by other disciplines as drivers for their own projects. There are substantial feedbacks in terms of multidisciplinary studies and transdisciplinary thinking.

Antarctic marine biology is nowadays global in scope and participation. It benefits form strong public interest and from a large array of modern logistics and sophisticated tools. It is carried by a strong international community of dedicated scientists from universities and other research institutions round the World and has a bright future.

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References

ANON. 1968. *Symposium on Antarctic oceanography*. Cambridge: Scott Polar Research Institute, 268 pp.

ARNTZ, W.E. & CLARKE, A. 2002. *Ecological studies in the Antarctic sea ice zone*. Berlin: Springer, 277 pp.

ARNTZ, W.E. *ed*. 2006. Macrobenthic studies at Bouvet Island. *Polar Biology*, **29**, 81–151.

BARGMANN, H.E. 1937. The reproductive system of *Euphausia superba*. *Discovery Reports*, **14**, 325–350.

BARGMANN, H.E. 1945. The development and life-history of adolescent and adult krill (*Euphausia superba*). *Discovery Reports*, **23**, 103–176.

BOYD, P. 2004. Ironing out algal issues in the Southern Ocean. *Science*, **304**, 396–397.

BRANDT, A. & HILBIG, B., *eds*. 2005. ANDEEP (Antarctic benthic DEEP sea biodiversity. Colonization history and recent community patterns). *Deep-Sea Research II*, **51**, 1457–1919.

COALE, K. 1998. The Galapagos iron experiments: a tribute to John Martin. *Deep Sea Research II*, **45**, 915–918.

DUNNET, G.M. 1977. The place of the Antarctic in biological sciences. *Philosophical Transactions of the Royal Society London*, **B279**, 105–112.

EHRENBERG, C.G. 1844. Vorläufige Resultate seiner Untersuchungen der ihm von der Südpolarreise des Captain Ross, so wie der Herren Schrayer und Darwin zugekommenen Materialien über das Verhalten des kleinsten Lebens in den Oceanen und den grössten bisher zugänglichen Tiefen des Weltmeeres. *Abhandlungen der königlichen Akademielder Wissenschaften zu Berlin*, 182–207.

EHRENBERG, C.G. 1854. *Mikrobiologie. Das Erden- und Felsenschaffende Wirken des unsichtbar kleinen selbständigen Lebens auf der Erde*. Leipzig: Leopold Voss, 374 pp. (continued 1856 88 pp.)

EL-SAYED, S.Z., *ed*. 1977. *Biological investigations of marine Antarctic systems and stocks.* vol. 1. Cambridge: Scott Polar Research Institute, 79 pp.

EL-SAYED, S.Z. *ed*. 1994. *Southern Ocean ecology: the BIOMASS perspective*. Cambridge: Cambridge University Press, 399 pp.

EL-SAYED, S.Z. 2005. History and evolution of primary productivity studies of the Southern Ocean. *Polar Biology*, **28**, 423–438.

FOXTON, P. 1956. The distribution of the standing crop of zooplankton in the Southern Ocean. *Discovery Reports*, **28**, 191–236.

FOXTON, P. 1961. *Salpa fusiformis* Cuvier and related species. *Discovery Reports*, **32**, 1–32.

FOXTON, P. 1966. The distribution and life history of *Salpa thompsoni* Foxton with observations on a related species *Salpa gerlachei* Foxton. *Discovery Reports*, **34**, 1–116.

FRASER, F.C. 1936. On the development and distribution of the young stages of krill (*Euphausia superba*). *Discovery Reports*, **14**, 1–192.

FUCHS, V. & LAWS, R.M., *eds*. 1977. Scientific research in Antarctica. *Philosophical Transactions of the Royal Society London*, **B279**, 1–288.

GRAN, H.H. 1931. On the conditions for the production of plankton in the sea. *Rapports et Proces-Verbaux des Reunions du Conseil Permanent International pour l'Exploration de la Mer* (ICES), **75**, 37–46.

GULLAND, J.A. 1972. *The fish resources of the ocean*. West Byfleet, Surrey: Fishing News (Books), 255 pp.

HARDY, A. 1967. *Great waters*. London: Collins, 541 pp.

HARDY, A.C. & GUNTHER, E.R. 1935. The plankton of South Georgia whaling grounds and adjacent seas. *Discovery Reports*, **11**, 1–456.

HART, T.J. 1934. On the phytoplankton of the South-West Atlantic and the Bellingshausen Sea, 1929–1931. *Discovery Reports*, **8**, 1–268.

HART, T.J. 1941. Phytoplankton periodicity in Antarctic surface waters. *Discovery Reports*, **21**, 261–356.

HEMPEL, G. *ed*. 1993. *Weddell Sea ecology, results of EPOS European "Polarstern" study*. Berlin: Springer, 333 pp.

HEMPEL, G., 1994. The legacy of BIOMASS. *In* EL SAYED, S.Z., *ed*. *Southern Ocean ecology: the BIOMASS perspective*. Cambridge: Cambridge University Press, 377–381.

HEMPEL, J. & HEMPEL, G., *eds*. 1995. *Biologie der polarmeer*. Jena: Gustav Fischer, 365 pp.

HOOKER, J.D. 1847. *Diatomaceae. The botany of the Antarctic voyage of H.M. Discovery ships Erebus and Terror in the years 1839–43*, vol. 56. London: Reeve Brothers.

MACKINTOSH, N.A. 1934. Distribution of the macroplankton in the Atlantic sector of the Antarctic. *Discovery Reports*, **9**, 65–160.

MACKINTOSH, N.A. 1937. The seasonal circulation of the Antarctic macroplankton. *Discovery Reports*, **16**, 365–412.

MARR, J.W.S. 1962. The natural history and geography of the Antarctic krill (*Euphausia superba* Dana). *Discovery Reports*, **32**, 33–464.

MARTIN, J.H. & FITZWATER, S.E. 1988. Iron-deficiency limits phytoplankton growth in the Northeast Pacific Subarctic. *Nature*, **331**, 341–343.

ROBERTS, B. 1967. *Birds of the Antarctic*. London: Blandford Press, 316 pp

SAHRHAGE, D., *ed*. 1988. *Antarctic Ocean and resources variability*. Berlin: Springer, 304 pp.

SIEGEL, V. 2005. Distribution and population dynamics of *Euphausia superba*: summary of recent findings. *Polar Biology*, **29**, 1–22.

SMETACEK V. 2006. Eisendüngung - Grossexperimente im offenen Ozean. *In* HEMPEL, G. *et al*., *eds. Faszination Meeresforschung*. Bremen: Hauschild, 263–267.

STRASS, V.H., LEACH, H., CISEWSKI, B., GONZALEZ, S., POST, J., DA SILVA DUARTE, V. & TRUMM, F. 2001. The physical setting of the Southern Ocean iron fertilization experiment. *Berichte zur Polar- und Meeresforschung*, **400**, 94–130.

THOMAS, D.N. & DIECKMANN, G.S., *eds*. 2003. *Sea ice: An Introduction to its physics, chemistry, biology and geology.* Oxford: Blackwells, 416 pp.

THOMAS, D.N. 2004. *Frozen oceans: the floating world of pack ice*. London: Natural History Museum, 224 pp.

WILSON, E. 1966. *Diary of the Discovery expedition to the Antarctic 1901-1904.* London: Blanford Press, 416 pp.

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