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Tackling fundamental issues in Southern Ocean plankton ecology—Japan and Australia's collaborative achievements

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Abstract: The international BIOMASS (Biological Investigation of Marine Antarctic System and Stocks) program was the formal start of Japan and Australia working together to understand the role of plankton in the waters around Antarctica. Exchange of scientists began soon afterwards, under the support of the National Institute of Polar Research (NIPR) and Australian Antarctic Division (AAD), slowly at first, then rapidly increased through the 1990's with a corresponding increase in the number of collaborative projects at a scientist-to-scientist level. This was eventually formally recognised at an institutional level with an agreement of collaboration between NIPR and AAD signed in 2001. Notable collaborative projects have been the study of krill biology, especially the development and maintenance of live krill, the impact of salps in the region, the importance of marine snow in vertical flux and trophodynamics, composition of nano- and picoplankton, microzooplankton grazing, and the establishment of a long-term time series study of zooplankton patterns, essentially using the sensitivity of plankton to environmental change as indicators of ecosystem health. These collaborative studies culminated recently in the highly successful multiship survey of the seasonal ecology of the sea ice zone along longitude 140°E. These projects have involved a large number of plankton scientists and institutes in both countries, including many graduate students. The success of these projects and the volume of papers that have been generated are testimony that we have achieved more in Antarctic plankton research by working together and sharing resources and ideas, than could be achieved by working in isolation.

Key words: Collaboration, Antarctica, monitoring, microbial ecology, krill

Introduction

The international BIOMASS Program (Biological Investigation of Marine Antarctic Systems and Stocks) marked the formal start of collaboration between Australia and Japan in plankton research when both countries surveyed the Prydz Bay region of eastern Antarctica during the first and second international BIOMASS experiments, FIBEX (1980/81) and SIBEX (1982/83 and 1983/84). The main objective of BIOMASS was to gain a deeper understanding of the structure and function of the Antarctic marine ecosystem (El-Sayed 1977, 1994). The main focus was the Antarctic krill *Euphausia superba*, viewed as the central component of the Antarctic marine food web, but research on phyto- and zooplankton also formed a major component of these surveys in order to properly understand interactions within the ecosystem, especially in relation to future management of living resources. Prior to BIOMASS, Japan already had an established program of plankton research in the region, including a long term monitoring program since 1972 using NORPAC nets from icebreakers *Fuji* and later *Shirase* of the Japanese Maritime Self-Defence Force during supply voyages to Syowa station (Fukuchi & Tanimura 1981; Takahashi et al. 1997, 1998). By comparison, Australian plankton research was sporadic and limited often to mainly descriptive surveys of distribution and taxonomy of a few key groups such as copepods and euphausiids through the Southern Ocean (Brady 1918; Sheard 1953; Vervoort 1957), or to a few coastal studies near stations (Bunt 1960, 1964; Ealey & Chittleborough 1956). The

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main target areas during BIOMASS was the western Atlantic sector of the Southern Ocean, near the Antarctic Peninsula, the Indian Ocean sector and parts of the Pacific sector (El-Sayed 1994). Japan made a strong commitment to BIOMASS surveying the Pacific sector alone, joining several other nations, in the Atlantic survey, and also joining with Australia in the survey of part of the eastern Indian Ocean sector, known as the Prydz Bay region. South Africa and France surveyed the adjoining western part of the Indian Ocean sector during BIOMASS. The former Soviet Union had conducted a number of studies around Prydz Bay before and after BIOMASS, but in later years Russia, France and South Africa have participated less in studies in the Indian Ocean sector leaving Japan and Australia as the only nations conducting regular plankton surveys in eastern Antarctica.

While Japan and Australia jointly surveyed the same area during BIOMASS, there was no exchange of scientists at that time. This changed with the appointment of Prof. Tsutomu Ikeda to the Australian Antarctic Division (AAD) in 1982. Although not really an exchange, his appointment at AAD served as a focus or catalyst for future exchanges and collaboration in krill and plankton research, which was initiated by inviting Prof. Mitsuo Fukuchi, National Institute of Polar Research (NIPR), as the first visiting Japanese plankton scientist to the AAD in 1983. This perhaps marks the true practical start of collaboration between Japan and Australia. Prof. Fukuchi's visit was also strongly supported by Prof. Takao Hoshiai, the Director of NIPR at the time, who actively promoted collaboration between Japan and Australia. Prof. Fukuchi has since become a frequent visitor to the AAD, developing a number of collaborative programs culminating with the successful Japan-Australia collaborative multi-ship survey of the sea-ice zone along 140°E longitude in the 2001/02 season (Odate et al. 2001; Fukuchi & Odate 2002). Other exchange of scientists and development of collaborative projects was slow at first but gained considerable momentum in the 1990's with a corresponding increase in the number of collaborative projects at a scientist-to-scientist level. This eventually lead to a formal recognition of collaboration at an institutional level when the directors of NIPR and AAD signed an agreement of collaboration in 2001.

The collaborative projects have covered a diverse range of subjects in Antarctic and Southern Ocean plankton ecology. These projects have involved a large number of plankton scientists from numerous institutes in both countries, including many graduate students (Table 1). There have also been numerous short term visits, workshops and planning meetings in both countries. The 50th anniversary of the Japanese Plankton Society coincides with 20 years of collaboration and exchange between Japan and Australia, and therefore seems an appropriate opportunity to review the achievements of our collaborations. It is beyond the scope of this paper to review every single project. Instead, a selection of projects will be reviewed as examples of successful collaboration in understanding fundamental issues in krill ecology through live krill experiments, marine microbial ecology, specifically microbial loop processes and understanding long-term patterns of zooplankton variation and their value as indicators on environmental change.

Live Krill Research

Antarctic krill *Euphausia superba* is a key central species in the food web of the Antarctic sea-ice zone. Many vertebrate predators are dependant on this species and it is also the target of a fishery. In order to properly understand the role of krill in the sea-ice zone, and to manage and protect both the fishery and dependent ecosystem, fundamental information of the species' biology and life history is required, notably its growth, developmental and moulting rates, reproduction and fecundity, survival/mortality rates, metabolism and energy budget, and behaviour. We also need to determine its longevity and develop methods of accurately aging the species. Most of this information can only be obtained or confirmed through experiments with live krill. Surprisingly, there is still very little live research conducted, with much of the research focussed on gathering, or in reality inferring information, from preserved krill collected by nets (Nicol 2000, 2003). Most of the live krill research conducted by Prof. Ikeda at the AAD in the 1980's still comprises a substantial amount of the relevant information on the biology of the species, and the techniques he developed in maintaining live krill are the foundation of today's live krill facilities.

Prior to Prof. Ikeda's appointment at the AAD, Australian krill research was restricted to surveys of distribution and abundance. Prof. Ikeda established an enhanced krill research group with a strong focus on live krill research, conducted on board ship as well as in laboratory at the AAD headquarters. The initial live krill facilities were quite simple and conducted in very small cold rooms. Krill were usually kept as one animal per experimental bottle, or in buckets of <20 litres, there being limited space for keeping krill en masse. Despite the limited facilities, the research conducted was highly productive, with Prof. Ikeda authoring some 30 refereed publications. He showed for the first time that krill were capable of shrinking and successfully maintained krill for 211 days without food, demonstrating a potential overwintering strategy when food might be limiting during the Antarctic winter (Ikeda & Dixon 1982; Ikeda 1985; Thomas & Ikeda 1987). Consequently, we could no longer assume that a larger krill was older than a smaller specimen. Prof. Ikeda was also the first person to successfully collect eggs from females in the field and raise krill through to mature adults. This provided valuable information on growth rates and development times of larval stages (Ikeda 1983, 1987). These data were used to develop a number of models for different growth/non-growth periods, and together with successfully keeping krill alive in vitro for many years showed that Antarctic krill have a

Table 1. Japanese and Australian scientists and students who have undertaken extended visits to the other nation's laboratories or participated in their expeditions.

Name	Home Institute	Host Institute or Expedition	Year	Purpose
Mitsuo Fukuchi	NIPR	AAD	1983*	Phytoplankton ecology
Harvey Marchant	AAD	NIPR	1988*	Visiting Professor–choanoflagellate ecology
Atsushi Tanimura	NIPR	*Aurora Australis*	1990/91	Copepod distribution and abundance
Kentaro Watanabe & Hiroshi Sasaki	NIPR	*Aurora Australis*	1991/92	Sediment trap mooring
Atsushi Tanimura	NIPR	AAD	1992	Copepod ecology
Harvey Marchant	AAD	JARE 35 summer	1993/94*	Marine snow
Graham Hosie	AAD	NIPR	1995*	Zooplankton community ecology
Graham Hosie	AAD	NIPR/Mie University	1997*	Analysis of JARE NORPAC samples
So Kawaguchi	NRIFSF	AAD	1998	Gregarine parasites in Antarctic krill
Sanae Chiba	Tokyo U. of Fisheries	*Aurora Australis*	1998/99	Salp ecology
Haruko Umeda	Mie University/NIPR	AAD	1998	Zooplankton community patterns
Graham Hosie	AAD	NIPR	1999*	Visiting Professor–zooplankton monitoring
Akira Ishikawa	Mie University	AAD/*Aurora Australis*	1999/2001	Ecology of nano and picoplankton
Graham Hosie & John Kitchener	AAD	NIPR	2000	Continuous plankton recorder analysis workshop
Tsuneo Odate	NIPR	*Aurora Australis*	2000/01	Primary productivity in the sea ice zone
Osamu Yoshida	Hokkaido University	*Aurora Australis*	2000/01	Methane production by bacteria in zooplankton guts
Yoshinari Endo	Tohoku University	AAD	2001	Krill ecology and management
Kunio Takahashi	NIPR	*Aurora Australis*	2001/02	Copepod life cycles in the sea ice zone
Sandric Leong	Soka University	*Aurora Australis*	2001/02	Effect of light and UV on phytoplankton
Nobuaki Ohi	Soka University	*Aurora Australis*	2001/02	Diel variability in light absorption on phytoplankton
Andrew McMinn	IASOS	NIPR	2004	Visiting Professor–sea ice ecology

AAD—Australian Antarctic Division
IASOS—Institute for Antarctic and Southern Ocean Studies, University of Tasmania
JARE—Japanese Antarctic Research Expedition
NIPR—National Institute of Polar Research, Tokyo
NRIFSF—National Research Institute of Far Seas Fisheries, Shimizu
* Plus numerous short visits.

potential longevity of 11 years and not 2 years as originally thought (Mackintosh 1972; Ikeda 1985; Ikeda & Thomas 1987). This had ramifications for the management of the krill fishery as a longer life span and hence a longer regeneration time meant that krill could not be fished as hard as one with a faster turnover. Prof. Ikeda was not successful in completing the life cycle but his work was fundamental in the later successes at the Port of Nagoya Public Aquarium (Hirano & Matsuda 2003; Hirano et al. 2003).

The first AAD facility was limited to just 100–200 krill, studies on group behaviour were not possible and with experimental specimens kept one per jar, the possibility of "bottle effect" could not be ignored. A new facility was built in 1992 under the direction Dr Stephen Nicol. The second facility was designed with a carrying capacity of >2000 live krill. Krill could be kept in holding tanks varying between 90 to 1300 litres within a closed 4000 l circulation system (Fig. 1). The whole system, including mechanical and biological filters, were housed inside a large cold room maintained at 0°C (King et al. 2003). The new system greatly improved our ability to conduct dedicated long term experiments, but also allowed a reserve of krill to be kept, the largest outside of Antarctica, in order to conduct experiments at short notice to test new theories. This lead to increased usage by graduate students and visitations by overseas scientists.

Dr So Kawaguchi from the National Research Institute of Far Seas Fisheries, Shimizu, with support from the Science and Technology Agency, was one Japanese scientist to make use of the new facility to study the biology of gregarines recently found living in the digestive tract of Antarctic krill. He was able to show that the gregarines, a group normally parasitic in insects, was also parasitic in krill. He showed that the gregarines caused damage to the hepatopancreas and gut of krill, especially the microvilli, which can result in a considerable impact on the growth and development. Use of the AAD live krill facility also allowed him to determine the complete life cycle of the gregarine and show how krill become infected. Dr Kawaguchi is now project leader of krill research at the AAD.

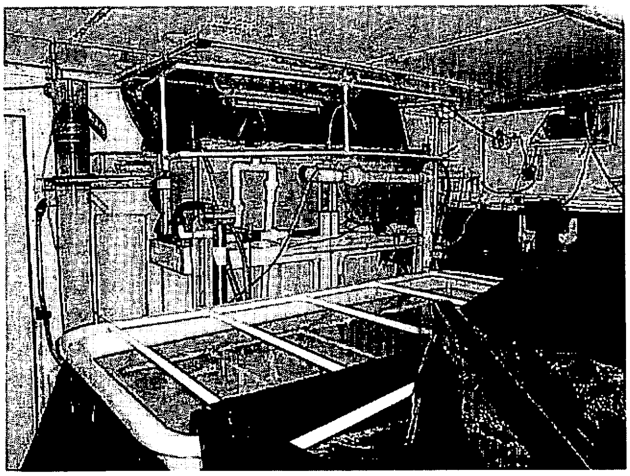

Fig. 1. Second live krill facility at the AAD. Carrying capacity is about 2000 krill but the facility was very cramped and the biofilters operated at 0°C.

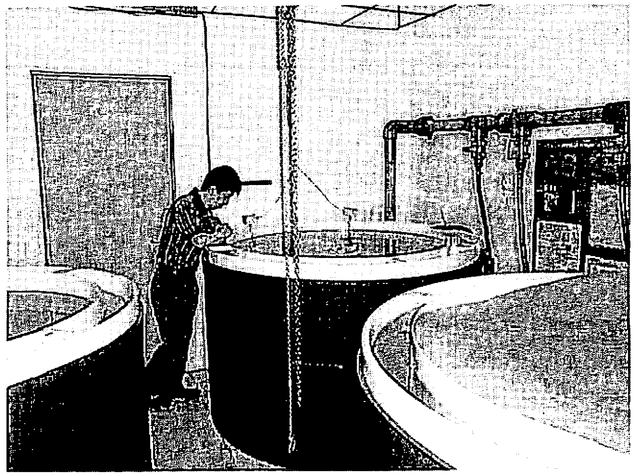

Fig. 2. Dr So Kawaguchi at 1200 litre insulated krill holding tanks in the new AAD Antarctic Marine Research Aquarium. Krill are kept at 0°C, while staff can work at 18°C.

The increased holding capacity of krill also permitted export of fresh specimens or live krill to external institutes. Several shipments of live krill, 100–200 at a time, were sent to the Tokyo Sea-Life Park during the 1990's and later to the Port of Nagoya Public Aquarium (PNPA) in 2000. The krill were primarily for display to the public, but the Antarctic curating team at PNPA, Yasuo Hirano, Tsuyoshi Matsuda and Kakuro Watanabe, also conducted experiments to improve the system for the exhibition and maintenance of live krill (Hirano & Matsuda 2003), and to induce reproduction in captive krill (Hirano et al. 2003). Collaboration on krill experiments started between the AAD and PNPA, with the AAD providing regular advice, during a number of visits to PNPA, on the development of the krill aquarium, maintenance and feeding of live krill, and suggested experiments to induce reproduction. This included the use of varying light : dark regimes to simulate changes in the Antarctic seasons. The team at PNPA subsequently succeeded in developing a superior holding facility with a biological filter operating at 10°C greatly improving the ability of nitrifying bacteria to remove ammonia waste. They experimented with a mixed feeding regime of diatom and haptophyte phytoplankton, and animal product (minced clam) simulating an omnivorous diet which resulted in maturation of ovaries (Hirano et al. 2003). This feeding regime coupled with a change from a spring time light : dark cycle to full 24 hour light resulted in mating and subsequently the first spawning of viable eggs outside of Antarctica. Larvae have continued to develop in the PNPA system.

The second AAD krill facility that had been in operation since 1992, eventually become too small. Scientists had to work in very cold and cramped conditions for long periods and the biological filters worked inefficiently in the 0°C environment (Fig. 1). In particular, they could not cope with the heavy load of phytoplankton required as food to maintain large stocks of krill. The experiences gained PNPA were imported into the design of the new AAD Antarctic Marine Research Aquarium (AMRA) commissioned in May 2003 (King et al. 2003). The ambient air temperature of the new aquarium is maintained at 18°C, much more comfortable for staff, and the seawater is maintained at 0°C by chilling through heat exchanges (Fig. 2). Biological filters operate at 20°C allowing a more efficient removal of ammonia than previously possible (Fig. 3), and thus allowing higher feeding loads for krill (King et al. 2003). Krill can be kept in insulated tanks of 1200 litres (Fig. 2) and a new experimental tanks of 150 litres have been constructed to allow experiments to be run at different temperatures. The carrying capacity of the AMRA is now >5000 krill and other invertebrates can be kept. The major outcome of the collaboration between PNPA and AAD is enhanced live krill research facilities in both countries which are world best standard. This also lead to PNPA hosting the Interna-

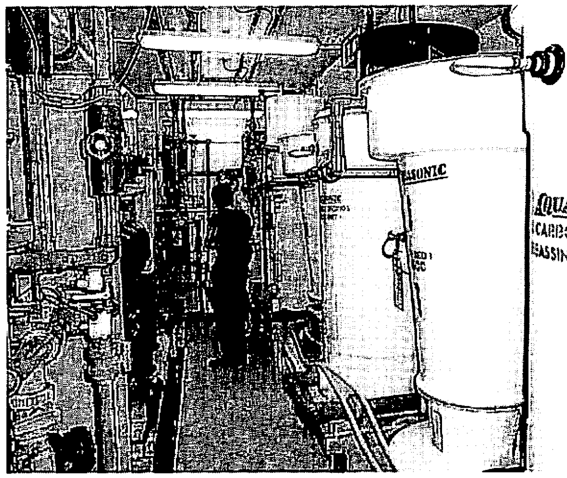

Fig. 3. Bank of filtration units in the new AMRA, which operate at 20°C before chilling by heat exchange back to 0°C.

tional Workshop on Understanding Living Krill for Improved Management and Stock Assessment in October 2002 (Kawaguchi & Nicol 2003).

Marine Microbial Ecology

The Antarctic marine food web has often been portrayed as a simple linear food chain comprising large diatoms-krill-predators (Marchant & Murphy 1994). In fact, prior to the BIOMASS program little was known about the importance of the smaller autotrophic nano- and picoplankton, or about the role of heterotrophic protozoa and flagellates, bacterioplankton and marine viruses in the accumulation and transfer of carbon and nutrients via the microbial loop (El-Sayed 1983, 1984; Fogg 1994; Marchant & Murphy 1994). Prof. Harvey Marchant AAD had a particular interest in determining the importance of the microbial loop in Antarctic waters. Notably, he had an interest in the role of choanoflagellate protozoa and conducted part of his research on this group at NIPR and Saroma-ko, Hokkaido, during a 4 month visit to NIPR in 1988.

Choanoflagellates are very abundant and conspicuous in marine pelagic systems (Marchant 1990), and form a large component of the biomass of Antarctic microheterotrophs (Buck & Garrison 1983, 1988). In turn, they are a conspicuous component in the diet of Antarctic krill (Marchant & Nash 1986; Tanoue & Hara 1986). Choanoflagellates are known to consume bacteria and possibly also pico- and nanoplankton, detritus and high molecular weight dissolved organic matter, however, little was known about ingestion rates or feeding selectivity, especially the size of food particles (Marchant 1990). In order to understand the role of choanoflagellates in ice-covered marine environment, Prof. Marchant conducted feeding experiments on *Diaphanoeca grandis* living in the ice covered marine lake, Saroma-ko in northern Hokkaido in March 1988. *Diaphanoeca grandis* is common in many marine environments, including Antarctic lakes, coastal sites and in the sea-ice zone (Marchant 1985, 1990; Marchant & Perrin 1986, 1990; Garrison & Buck 1989), and Saroma-ko served as a convenient analogy for the Antarctic zone for experimental studies.

Prof. Marchant used fluorescent latex microspheres to measure size selection and ingestion rates. He showed that *D. grandis* could only eat particles smaller than 1 μm, equivalent in size range to bacteria and picoplankton. Together with experiments he had conducted in Antarctica showing *D. grandis* capable of consuming polysaccharides with a molecular weight as low as 4000, Prof. Marchant concluded that choanoflagellates could short circuit the microbial loop by consuming DOM that would normally be eaten by bacteria prior to consumption by choanoflagellates. He further concluded that choanoflagellates could play a significant role as direct links between metazoan grazers such as krill and high molecular weight DOM and picoplankton (Marchant 1990).

The second next phase of Prof. Marchant's collaborative

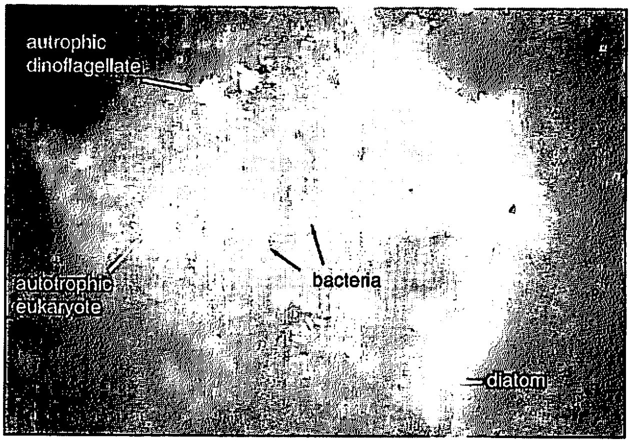

Fig. 4. Marine snow collected in Antarctic waters: a micro-okonomiyaki of mucilage, phytoplankton, bacteria and heterotrophic protists. (Photo by Harvey Marchant, AAD)

Fig. 5. The JARE 35 diving team collecting marine snow at Kita-no-seto Strait near Syowa station, January 1994. (Photo by Harvey Marchant, AAD)

research was on the role of marine snow in Antarctic waters (Fig. 4). Marine snow is an aggregate of organic and inorganic material colonized by prokaryotic and eukaryotic micro-organisms at concentrations and associated biological activity much higher than the surrounding water (Alldredge & Silver 1988; Caron 1991; Marchant et al. 1996). Marine snow can play an important role in the energy flow through marine ecosystems (Alldredge & Silver 1988). Prof. Marchant hypothesized that marine snow could potentially be a major source of food for Antarctic krill and other zooplankton grazers based on previous analysis of gut contents and faecal pellets (Marchant & Nash 1986). Marine snow is very fragile and therefore best collected and observed by divers. At the time, the Australian Antarctic Division did not have a diving program in Antarctica. Instead, Prof. Marchant joined the Japanese Antarctic Research Expedition JARE 35 for summer 1993/94 to study marine snow collected by divers at Kita-no-seto Strait near Syowa Station (Fig. 5). This work was conducted in collaboration

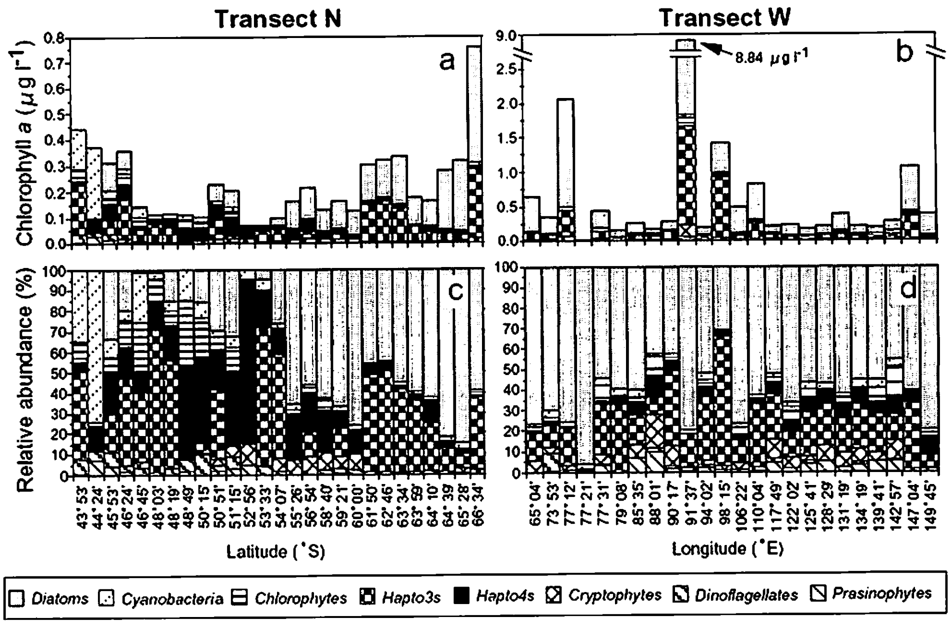

Fig. 6. Variation in surface distributions and contributions (a, b) of various phytoplankton classes to total chlorophyll *a* concentrations, plus percent relative abundance, with change in latitude (Transect N) and longitude (Transect W) through the Southern Ocean. (Reproduced from Ishikawa et al. 2002)

with Drs Kentaro Watanabe NIPR and Masanobu Kawachi, Marine Biotechnology Institute Co. Ltd, Kamaishi, and was the first report on the composition of marine snow in Antarctic waters and its potential importance as food for krill and other grazers (Marchant et al. 1996).

Marchant et al. (1996) reported concentrations of marine snow particles >1 mm as high as $10\,l^{-1}$ and these aggregations were found to be derived either from diatoms and mucilage from the sea-ice community or from the colonial *Phaeocystis*. The marine snow had accumulated bacteria 10 times above the concentration in the surrounding water, while the enrichment factor for eukaryotic protists was between 200 to 600 times. Marchant & Nash (1986) had already demonstrated the presence of organisms $<5\,\mu m$ in size in the gut and faeces of Antarctic krill, comprising diatoms, Parmales, flagellates and choanoflagellates, which were also typical abundant components of the marine snow aggregations collected near Syowa. However, McClatchie & Boyd (1983) reported that Antarctic krill have difficulty feeding on organisms $<5\,\mu m$ in size. Prof. Marchant and his colleagues concluded that krill probably consume the smaller organisms through grazing on marine snow. They also noted that concentration of chlorophyll *a* in Antarctic waters is generally too low to meet the daily food requirements of an adult krill, but krill could meet their requirements by consuming only 30 marine snow particles per day containing $500\,\mu g$ C. Marine snow are thus likely to be a significant source of food for krill as well as other zooplankton grazers.

Phytoplankton $<20\,\mu m$ comprise a significant and consistently high proportion of the phytoplankton community in Antarctic waters, usually dominating both the biomass and autotrophic production (Weber & El-Sayed 1987; Marchant 1993; Marchant & Murphy 1994; Waters et al. 2000; Ishikawa et al. 2002). The nanophytoplankton comprise a range of taxonomic groups, prasinophytes, chrysophytes, cryptophytes, dinoflagellates, diatoms and haptophytes in Antarctic waters with the last two groups dominant (Marchant 1993; Marchant & Thomsen 1994; Ishikawa et al. 2002). Studies of the ecology of the Antarctic marine microbial systems has tended to be biased towards the Scotia Sea and large embayments of the Weddell and Ross Seas (Jacques & Fukuchi 1994; Waters et al. 2000), with a noticeable paucity of data from the Indian Ocean sector despite representing approximately 40% of the total Antarctic Ocean (Waters et al. 2000). Most of the data in that area has come from Japanese and Australian expeditions. Our most recent information on the ecology of nano- and pico-phytoplankton has come from Dr Akira Ishikawa, Mie University, working in collaboration with the Marine Microbial Ecology Group at the AAD.

Dr Ishikawa undertook a two year postdoctoral fellowship at the AAD, 1999–2001, funded by the Japanese Society for the Promotion of Science, to study the abundance, size structure and composition of phytoplankton, plus interactions between phytoplankton groups, across the Southern Ocean latitudinally as well longitudinal zonation along the eastern Antarctic coast (Fig. 6) (Ishikawa et al. 2002). His experimental studies were conducted both in the AAD's laboratories and during two research cruises in the 1999/2000 and 2000/01 seasons. His shipboard experiments included the use of incubation tanks to measure grazing rates on phytoplankton, especially by heterotrophic plankton, and how grazing influences phytoplankton community composition. Dr Ishikawa demonstrated that grazing by microheterotrophs, particularly dinoflagellates, is important in packaging small cells as larger faster sinking faecal pellets, which has relevance to estimates of carbon flux. His other studies confirmed that cyanobacteria are rare south of the Antarctic Polar Front (APF). South of the APF, nanophytoplankton are most abundant, and greater than picophytoplankton. The composition of phytoplankton changed markedly across the Southern Ocean especially in the abundances of diatoms and haptophytes in relation to the APF. Dr Ishikawa suggested that such changes, including the decline of cyanobacteria at the APF, means that carbon flow through the ecosystem may vary latitudinally. Moreover, the paucity of picophytoplankton and absence of cyanobacteria are key features of Antarctic waters and thus the microbial community in those waters functions and interacts differently compared with warmer waters where picoplankton and cyanobacteria are considerably more abundant (Ishikawa et al. 2002). Dr Ishikawa's research on picoplankton is continuing, but his work so far has become the most comprehensive study of the species composition of this group in Antarctic waters. While, picoplankton may occur in low abundances in the region, this work together with his studies on nanoplankton composition, will form the essential foundation in future studies on any change in phytoplankton composition in response to global warming (Marchant et al. 1987), especially in relation to krill and other grazers which are better adapted to a diet of nano- and microplankton.

The major outcomes in the collaboration between Japan and Australia in marine microbial ecology are that we now have a much greater understanding of the microbial composition, interactions, spatial and temporal patterns and processes in the Southern Ocean and Antarctic waters. Further, we have improved our knowledge of the importance of some of the smaller groups and marine snow aggregations as food source for krill and other grazers. The data gathered are fundamental in the development of models to understand and predict the role of the microbial loop in ocean-atmospheric exchange processes, such as CO_2-carbon flux and DMS production.

Zooplankton Ecology

There have been a number of collaborations in zooplankton research. Dr Atsushi Tanimura, NIPR and now Mie University, participated in an Australian research cruise in 1990/91 on RSV *Aurora Australis*, to study the abundance and fine scale distribution patterns of copepods. Dr Sanae Chiba, Tokyo University of Fisheries, conducted studies on spatial-temporal variability in zooplankton communities, and copepods in particular, in the western Pacific sector (Chiba et al. 2001, 2002). She also conducted essential research on distribution and changes in population structure of the Antarctic salp *Salpa thompsoni*. This group has been much neglected despite their high abundance and impact as a grazer. Dr Chiba planned further experimental studies during an *Aurora Australis* voyage in 1998/99, but ship problems curtailed that work. This was unfortunate as this work would have greatly enhanced Dr Chiba's previous studies, which had shown that salps, normally restricted to the Antarctic Circumpolar Current (ACC), can extend south of the Antarctic Divergence into the colder waters normally inhabited by Antarctic krill (Chiba et al. 1998, 1999, 2000). How well salps survive in this colder region is still to be determined. However, the main focus of this section will be on the joint Australia-Japan zooplankton monitoring program, which has become the largest and most detailed collaborative plankton project to date in terms of area surveyed, intensity of sampling, and the number of personnel and ships involved.

The Southern Ocean Continuous Plankton Recorder (SO–CPR) Survey commenced in 1990 with the purposes of mapping spatial and temporal variation in zooplankton patterns, and then to use the sensitivity of plankton to environmental change (Reid et al. 1998a, b, 2001; Beaugrand et al. 2002) as early warning indicators of the health of the Southern Ocean (Hosie et al. 2003). At the same time, the survey will serve as a reference of the general status of the Southern Ocean for comparison with other monitoring programs as the CCAMLR-Ecosystem Monitoring Program (Agnew 1997) and the Regional Sensitivity to Climate Change in Terrestrial Ecosystems (RiSCC) program (www.riscc.aq).

The principal survey area extends from 60 to 160°E and south of approximately 46°S to the Antarctic coast—an area>14 million km^2 or just under 30% of the Southern Ocean (Fig. 7). CPRs are towed on all voyages of the *Aurora Australis* on route to from the Antarctic stations and on dedicated marine science voyages, from early spring to autumn and occasionally in winter. This forms the core of the data, both geographically and temporally. This wide spatial coverage is ideal for mapping biodiversity, but there was concern, with the survey extending over much of the year, that distinguishing temporal from spatial variation in patterns could become difficult. This would complicate the task of identifying seasonal and long-term interannual changes in zooplankton patterns. The establishment of fixed routine transects surveyed regularly would solve this problem but this has proved infeasible in the extensive and demanding Australian Antarctic shipping schedule. Consequently collaboration was sought with NIPR to tow CPR's from *Shirase* and take advantage of that ship's fixed route and time schedule as a temporal reference for measuring long-term annual variability and to help interpret the Australian data.

NIPR had the foresight to establish a long-term routine zooplankton sampling program on JARE voyages commencing with JARE 14 in the 1972/73 austral summer, initially on icebreaker *Fuji* and later *Shirase*. Zooplankton samples were usually taken once a day using a twin NORPAC net (0.16 m^2 mouth area each, 110 and 330 μm mesh)

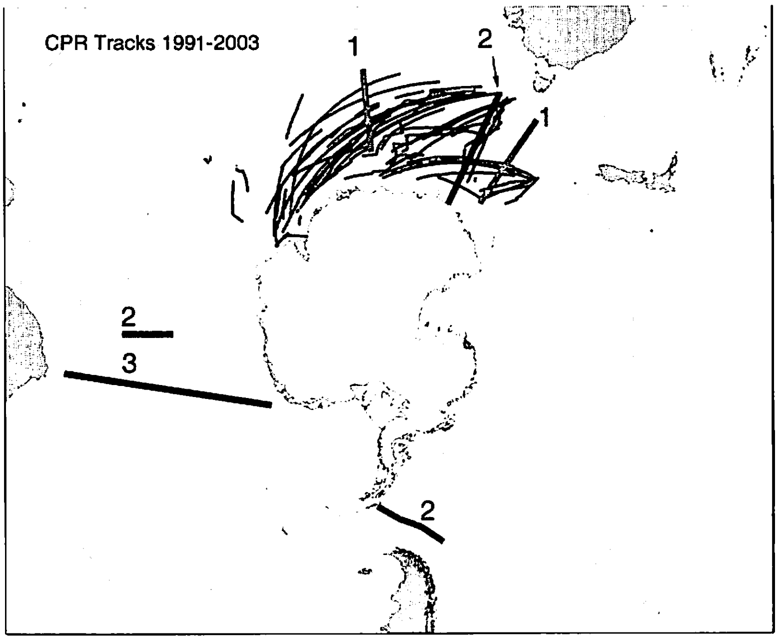

Fig. 7. Routine CPR tracks through the Southern Ocean January 1991 to March 2003. (1) fixed transects of *Shirase*, (2) dedicated tows for studying spatial and temporal variation, (3) planned new *Polarstern* transect.

to estimate the mean biomass of zooplankton and time/space variation in the uppermost 150 m of the Indian Ocean sector of the Southern Ocean (Fukuchi & Tanimura 1981; Takahashi et al. 1997, 1998). Other oceanographic measurements are taken at the same site, such as CTD (conductivity-temperature-depth) profiles. Initial analyses of total zooplankton biomass from 1972/3 to 1995/6 seasons (JARE 14 to 37) showed some cyclic variation in abundance with a 4–6 year periodicity, which may be related to physical processes such as sea-ice extent or the Antarctic Circumpolar Wave (Takahashi et al. 1998). This was particularly so in the case of the zooplankton community in the Antarctic Zone south of the Polar Front. The NORPAC stations were widely spaced, 300 nautical miles (555 km) in an area of numerous oceanographic fronts (Orsi et al. 1995; Sokolov & Rintoul 2003). During a visit to NIPR and Mie University in 1997, supported by JSPS, I conducted more detailed analysis of the dataset in collaboration with Drs Atsushi Tanimura and Sanae Chiba. We studied a smaller area just north of Syowa station and this also identified a correlation between zooplankton biomass and temperature (Tanimura et al. 1999). However, because of the small size of the net coupled with net avoidance problems, and the large distances between sampling sites, it was noted that the NORPAC net was not ideal for long-term mapping and monitoring of changes in distribution or abundance in relation to the various oceanographic boundaries in the Southern Ocean. We enthusiastically agreed that CPR tows from *Shirase* would benefit both national programs, enhancing their existing plankton monitoring program, while providing the much needed fixed transects. A schedule of collaboration was agreed between myself and Prof.

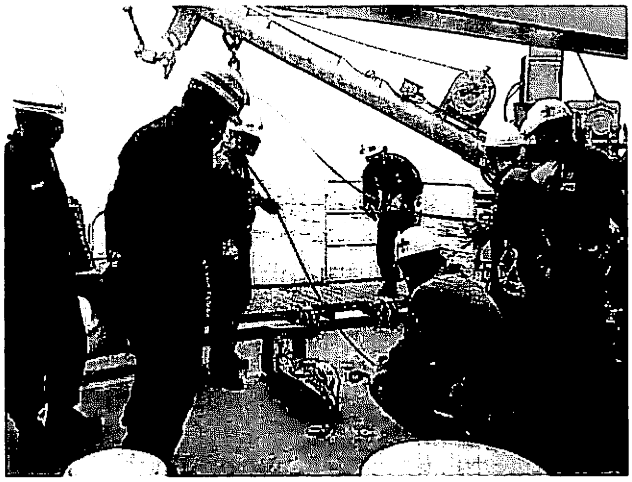

Fig. 8. Preparing the CPR for its first deployment from *Shirase* during sea trials in the Sea of Japan, September 1999. (Photo by Dr Toru Hirawake, NIPR)

Mitsuo Fukuchi, Director of the Centre of Antarctic Environment Monitoring at NIPR, and Australian CPR units have been operating on *Shirase* since the 1999/2000 season, JARE 41 (Fig. 8).

The collaboration between Australia and Japan also provided the opportunity of occasionally using other Japanese vessels conducting plankton research around Antarctica, *Kaiyo Maru* (National Research Institute of Far Seas Fisheries), *Hakuho Maru* (Ocean Research Institute, Tokyo University), *Umitaka Maru* (Tokyo University of Fisheries, now Tokyo University of Marine Science and Technology) and *Tangaroa* (on charter to NIPR from National Institute

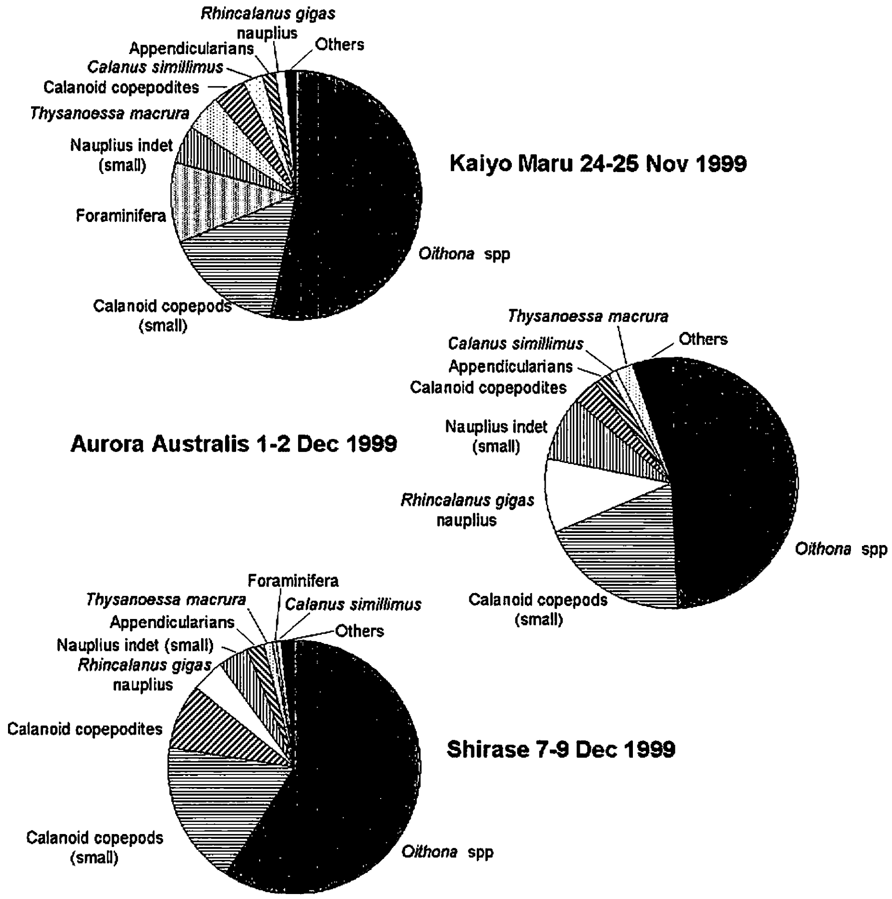

Fig. 9. Relative abundance of major taxa recorded on each transect of the three-ship survey, November–December 1999. (Redrawn from Hosie et al. 2003)

of Water & Atmospheric Research, New Zealand). These vessels have not only supplied a large amount of routine data, but also allowed a number of unique experiments to be conducted. The first of these was a set of almost simultaneous tows across the Antarctic Circumpolar Current in late November/early December 1999, along three widely spaced transects below Africa (*Kaiyo Maru*), Fremantle (*Shirase*) and Macquarie Island (*Aurora Australis*) to test for similarities in zooplankton patterns across the frontal zones of the ACC. In theory, because the ACC flows uninterrupted around Antarctica, the species composition of zooplankton should be the same within any part of the current, and the three ship survey subsequently found the hypothesis to be true. The Sir Alister Hardy Foundation for Ocean Science (SAHFOS), based in Plymouth UK, became involved through the supply of a CPR for *Kaiyo Maru*. The *Kaiyo Maru* voyage also provided the opportunity to replicate one of Hardy's early CPR transects across Drake Passage and to compare species composition between 1927 and 2000.

The three ships commenced sampling within 14 days of each other, which is as close to simultaneous sampling as possible given the different scientific and logistic priorities of the vessels (Takahashi et al. 2002; Umeda et al. 2002; Hosie et al. 2003). *Kaiyo Maru* and *Shirase* started sampling north of the Polar Front (PF), and *Aurora Australis* just on the PF. The results showed little difference in abundances between the three transects south of the PF. Species composition and the relative proportions were similar between transects for the ten most abundant taxa (Fig. 9). The composition and proportions were similar to those obtained from other CPR tows through the same zone. The similarity in abundance and composition between the transects, as well as consistency with previous tows, strongly indicates minimal spatial variation (Hosie et al. 2003).

The complementary experiment examining variation within a season along a single transect was conducted during the 2001/02 summer (November and March) when CPR's were towed repeatedly by four ships, *Aurora Australis*, *Hakuho Maru*, *Tangaroa* and *Shirase*, along longitude 140°E. Much of the analysis is still being conducted, but results to date have identified a number of plankton assemblages with strong north-south zonation in association with the various oceanographic fronts across the Southern Ocean (Sokolov & Rintoul 2003). The northern edge of the ACC, the Sub-Antarctic Front (SAF), marks a distinct change in salinity and temperature, and is a major biogeographic boundary separating communities of different zooplankton composition. South of the SAF, physical charac-

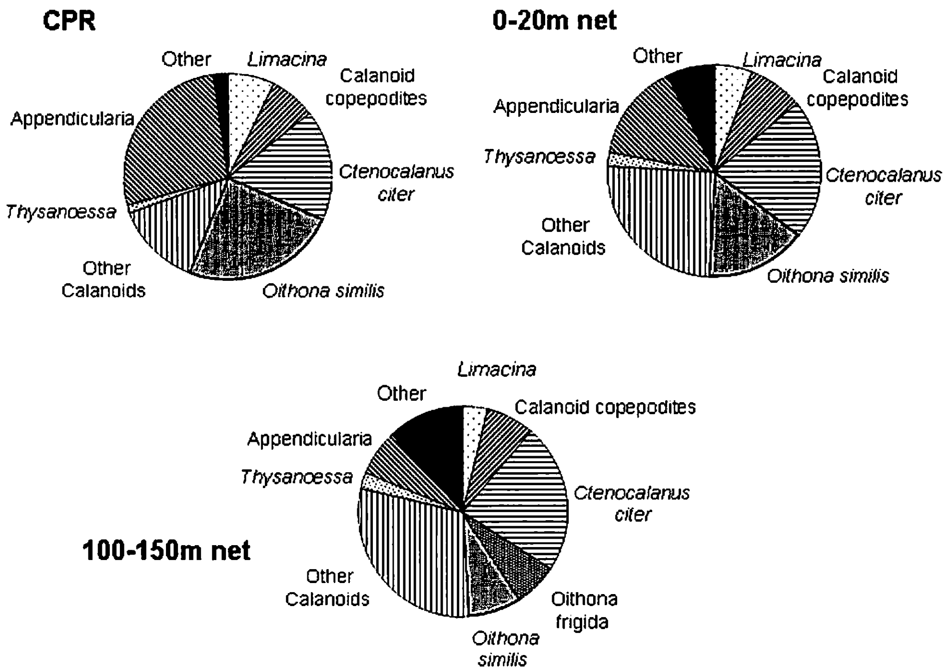

Fig. 10. Relative abundance of major taxa caught by CPR, and in the 0–20 m NORPAC net hauls during Aurora Australis voyage on 140°E, November–December 2001. 100–150 m net samples also shown for comparison with surface samples. (Redrawn from Hunt & Hosie 2003).

teristics such as temperature change gradually and the fronts within the ACC can only be properly defined by deep, detailed and time consuming oceanographic profiling. However, multivariate analysis of the CPR data from the multiship survey have revealed quite discrete and easily definable zooplankton assemblages in each of the zones between the fronts. While the physical characteristics of the fronts can be subtle, the demarcation between zooplankton communities was clear, with the plankton effectively amplifying cross-frontal physical changes. Further, analysis of samples across the Sub-Antarctic Front and Polar Front in the north of the ACC showed that while these fronts vary in position significantly during the season the various zooplankton assemblages kept their integrity in relation to each front and strongly correlated with temperature. Congruence between zooplankton communities and the physical environment highlights the value of plankton as indicators of environmental change and their utility in monitoring programs.

It was noted above that the NORPAC net is perhaps not ideal for monitoring zooplankton patterns across the Southern Ocean. Nonetheless, it is the longest running zooplankton survey in the region and can provide useful data to help identify long-term changes. Consequently, routine NORPAC net sampling is continuing on *Shirase* voyages with the CPR towed between sampling sites. This raises the question, can the CPR and NORPAC net samples be compared quantitatively to allow back comparison of the two datasets? During the *Aurora Australis* voyage of the multiship survey of longitude 140°E, we had the opportunity to conduct a detailed quantitative comparison of NORPAC net and CPR samples (Hunt & Hosie 2003). On the south leg in November 2001, 19 stations were sampled using a twin NORPAC net between 47 and 61°S. The transect was then sampled by CPR on the return leg in early December. JARE NORPAC nets are fitted with 110 and 330 μm mesh nets. On the *Aurora Australis* survey the twin NORPAC nets were fitted with 270 and 330 μm mesh allowing comparison with the CPR which also uses 270 μm mesh and also with the previous JARE NORPAC samples. The nets were towed through four depth strata, 0–20 m, which corresponds with the sampling depth of the CPR, plus 20–50, 50–100 and 100–150 m at each station to determine if the CPR samples are representative of zooplankton patterns deeper in the water column. The CPR samples showed most similarity with the 0–20 m NORPAC samples, in relation to species richness, diversity and abundance (Fig. 10). Species richness and diversity increased with depth, whereas the measure for dominance was highest in the CPR sample and decreased with depth. Increase in biodiversity measures were due mainly to increase in the number of rare species with depth. There was little variation in abundance estimates between the four Norpac depth zones, but the CPR produced higher abundances, mainly due to appendicularians, the cyclopoid copepod *Oithona similis* and larvae of the calanoid copepod *Rhincalanus gigas*. This was compensated in part by undersampling of other components, such as pteropods, polychaetes and other soft-bodied species. However, the CPR provided sufficient taxonomic resolution to identify biogeographic zones in the Southern Ocean, which were similar to those identified using NORPAC samples (Hunt and Hosie, 2003). Further, we are now able to make a direct quantitative comparison and calibration between the CPR and NORPAC 270 μm samples. Quantitative comparison can also be made between the 270 and 330 μm NORPAC samples, which in turn will allow quantitative comparison between the CPR and previous JARE NORPAC data. This will be of considerable use for the SCOR-Working Group 115 on "Standards for the Survey and Analysis of Plankton", which is developing methods for intercomparison of data collected by sampling methods.

Another significant collaborative experiment involved *Kaiyo Maru* later in the 1999/2000 season, after the 3-ship spatial survey, when the ship closely followed Sir Alister Hardy's April 1927 CPR transect across Drake Passage (Takahashi et al. 2002). Sir Alister Hardy first conducted trials of his Mark I continuous plankton recorder (CPR) in Antarctic waters during the 1925–1927 voyages of the RRS Discovery and RRS William Scoresby (Hardy 1936). Initial tows across the southern Atlantic Ocean were not always successful, but he was successful with a series of tows across Drake Passage producing the first continuous trace of Antarctic plankton abundances for nearly 300 nautical miles (555 km). We are still looking for Sir Alister's original raw data in order to make a full comparison, but *prima facie* comparison with his published descriptions of the 1927 data suggests a major change in plankton patterns has occurred between 1927 and 2000. Chaetognaths were particularly common in the 1927 CPR samples (Hardy 1936), and their changes in abundance corresponded with changes in the abundances of large calanoid copepods in those tows. Modern CPR samples are dominated by small calanoid and cyclopoid copepods and there is a general paucity of chaetognaths (Hosie et al. 2003). The possible decline in the abundance of large copepods concurs with the suggestion of Prof. Kawamura that the Antarctic marine ecosystem had changed (Kawamura 1986, 1987).

The collaboration between Australia and Japan has greatly improved the rate of routine data acquisition for the CPR survey through the additional tows. Further, the specific experimental tows to study spatial and seasonal patterns of variation, and to compare methodologies would not have been possible without the involvement of a number of Japanese scientists, students and ships. To date, the SO-CPR Survey has completed 235 tows, covering more than 74,000 nautical miles (>137,000 km) representing nearly 14,800 samples with associated environmental data. Approximately a quarter of those data have been collected by Japan. The success of the collaboration in the survey, and the quality of the results has attracted the attention of other Antarctic nations. Subsequently, CPR tows will be conducted in March and May 2004 from the German research *Polarstern* south of South Africa. Success with these tows will lead to the German Antarctic program joining the SO-CPR Survey and the establishment of a new fixed route between Cape Town and Georg von Neumayer station covering the eastern Atlantic sector of the Southern Ocean.

The Future

There is no doubt overall, that Japan and Australia have gained a much better understanding of the Antarctic marine ecosystem by working together, sharing ideas, skills, personnel, equipment, and logistics, than by working in isolation. Japan and Australia both have world best standard live krill research facilities. We have a greater understanding of the marine microbial food web, especially the role of nano- and picoplankton, and a well established monitoring program second only to the original SAHFOS CPR Survey in relation to the size of the area surveyed and volume of the database. These collaborations culminated in the 2001/02 Japan-Australia time-series multi-ship survey, a joint project developed and coordinated by Prof. Fukuchi NIPR, which involved numerous Japanese and Australian scientists, students and institutions, in the study of the seasonality of protists, zooplankton, krill ecology, and physical and chemical oceanography of the sea ice zone along 140°E. New Zealand was involved with the supply of the vessel *Tangaroa*, to support *Aurora Australis*, *Hakuho Maru* and *Shirase*. The result of this project will be presented in different forums in due course. It is not appropriate to review that work now, other than to highlight that the success of the multi-ship survey was due in part to the foundations laid by the previous krill, protistan and zooplankton collaborations which subsequently formed integral components of the multi-ship survey.

The success of our joint projects can also be attributed to the frequent collaborative workshops conducted in Japan and Australia. These workshops provide the opportunity to review the latest results, assess progress with existing studies, and to identify and develop new collaborative programs. One of the next major initiatives will involve a set of collaborative projects in support of The International Polar Year to be held from 2007, and this may include a contribution to the international Census of Marine Life project which is attempting to understand the diversity, distribution, and abundance of marine life. However, numerous other specific gaps in our knowledge have been identified that would benefit from continued collaborative efforts:

- Most plankton surveys have been confined to the summer period when access to the region is easier for research vessels. Consequently, we know little about the biodiversity of plankton in winter, in the sea ice zone, in polynyas (permanently open pools of water in the sea ice) or in the permanent open ocean zone (POOZ) north of the sea ice.
- We still know little about the importance of the smaller meso-zooplankton. For example, the cyclopoid *Oithona similis*, and small calanoid copepods *Calanus simillimus*, *Ctenocalanus* spp are particularly abundant in the open waters of the ACC (Hosie et al. 2003; Hunt & Hosie 2003) but it is suspected that they are major consumers of non-autotrophic carbon.
- Similarly, appendicularians are extremely abundant through the region (Hosie et al. 2003; Hunt & Hosie 2003),

but largely have been overlooked because they are poorly sampled by conventional nets. In oligotrophic conditions or when autotrophic production is suppressed, e.g through winter, appendicularians may play a key role in the food web through their potentially high grazing impact on heterotrophic and nano-, picoplankton autotrophic production, and production of marine snow from their discarded houses.

• Dr Sanae Chiba initiated important research on the role of salps *Salpa thompsoni* in the waters of eastern Antarctica (Chiba et al. 1998, 1999, 2000). Continued research on salps was an important component of the multi-ship survey of 140°E longitude, but further work is still required, particularly in relation to grazing impact on the protistan community and interactions with other grazers.

• Most studies on Antarctic plankton have been restricted to surface waters. Very few recent studies have been undertaken on the ecology of meso-bathypelagic species and their possible effect on vertical carbon flux and predation of Antarctic krill larvae during their deep water developmental ascent to the euphotic zone.

• The role of carnivorous zooplankton in general requires further study in their top down control of plankton community structure, and not just the role of omnivorous and predatory copepods but also chaetognaths, polychaetes and gelatinous zooplankton such as medusae which are generally ignored.

• The CPR survey has demonstrated clear changes in zooplankton patterns in relation to the various fronts across the Southern Ocean. A very clear marked decline in abundance is regularly recorded in the vicinity of the Southern Antarctic Circumpolar Current Front (Hosie et al. 2003). What exactly happens at these fronts can only be determined by a sampling strategy at a finer scale than can be achieved by CPR with its 5 nautical mile resolution. This is perhaps best achieved through the use of an undulating recording/sampling systems designed for samplings at finer scales of kilometres to 10's of meters (Reid et al. 2003).

Finally, it needs to be acknowledged, that a considerable amount of the success of our current collaborations can be attributed to the strong friendships that have been established amongst Japanese and Australian colleagues. This has resulted in a significant understanding of each other's research interests and expertise, which in turn has allowed faster development and easier co-ordination of projects. Perhaps just as important, though, these friendships and participation in collaborative projects has lead to a much greater appreciation of, and interest in, the cultural heritage of each nation. However, the success of future collaboration in Antarctica depends on our students and their involvement in collaborative research should continue to be actively encouraged and supported, especially exchange visits to work in the laboratories of the other nation or participate in their field work.

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