Antarctic Science 15 (3): 333–338 (2003) © Antarctic Science Ltd Printed in the UK DOI: 10.1017/S0954102003001342

Annual warming episodes in seawater temperatures in McMurdo Sound in relationship to endogenous ice in notothenioid fish

BEN M. HUNT, KEVIN HOEFLING and CHI-HING C. CHENG*

Department of Animal Biology, University of Illinois, Urbana, IL 61801, USA
**corresponding author: c-cheng@uiuc.edu*

Abstract: We obtained two years (1999–2001) of continuous, high resolution temperature and pressure data at two near-shore shallow water sites in McMurdo Sound, Ross Sea. Contrary to the long-held assumption of constant freezing conditions in the Sound, these records revealed dynamic temperature fluctuations and substantial warming during January to March reaching peak water temperatures of about -0.5°C. They also revealed that excursions above -1.1°C, the equilibrium melting point of ice in Antarctic notothenioid fish, totalled 8–21 days during the summer. Microscopic ice crystals are known to enter these fish but ice growth is arrested by antifreeze proteins. Prior to this study there were no known mechanisms of eliminating accumulated endogenous ice. The warm temperature excursions provide for the first time a possible physical mechanism, passive melting, for ice removal. The continuous records also showed a correlation between tidal pressures and cold temperature episodes, which suggests the influx of cold currents from under the Ross Ice Shelf may provide a mechanism for ice crystal nucleation as the source of the ice in McMurdo Sound fish. The accumulation of anchor ice on one logger caused it to float up which was recorded as a decrease in pressure. This is the first evidence for the time of onset of anchor ice formation in McMurdo Sound.

Received 4 September 2002, accepted 14 January 2003

Key words: annual temperature records, Antarctica, dynamic temperature excursions, endogenous ice disposal

Introduction

The waters of McMurdo Sound are among the coldest and iciest in the world, because of the extremely high latitude (78°S) of the Sound and its immediate proximity to the massive Ross Ice Shelf which is a source of freezing shelf water (Jacobs *et al*. 1979). The endemic Antarctic notothenioid fish have evolved antifreeze glycoproteins (AFGPs) to survive in this freezing environment (Chen *et al*. 1997, Cheng & Chen 1999). These fish acquire ice crystals from the ambient water, but ice growth within the fish is arrested by the binding of AFGPs to these crystals, so that the body fluids do not freeze (DeVries & Cheng 1992). Whether AFGP-bound ice crystals are eliminated from the fish, and if so by what mechanism, has been a long-standing question in Antarctic fish physiology. To date, no biochemical or physiological mechanisms for endogenous ice removal have been documented. Physical (thermal) melting of endogenous ice appears impossible because the water of McMurdo Sound is believed to be perennially at or near its freezing point (-1.9°C), which is below the equilibrium melting point of ice in the fish (-1.1°C, based on the concentration of colligative solutes in their blood and body fluids). This means that the ambient water temperature has to rise above -1.1°C for endogenous ice to melt. Prior annual water temperature measurements (Littlepage 1965) indicated that McMurdo Sound water is frozen year round, which suggests that endogenous ice crystals in the local fish could never melt. However, these measurements were intermittent and confined to certain times of the year when annual sea ice was accessible for deploying the instruments for data collection. To obtain continuous high resolution temperature profiles, we started long-term monitoring of McMurdo Sound water temperatures in December 1999 by deploying continuously recording loggers on the sea floor at two shallow water, near-shore sites (Fig. 1) with an abundance of local fish. Logger data were supplemented by periodic conductivity, temperature, and depth (CTD) profiler casts, which give vertical profiles of water temperatures versus depth. The first two years of data reveal unexpected seasonal temperature changes with large warm temperature excursions during the summers that are highly pertinent to the fate of endogenous ice crystals in the fish resident at those sites.

Materials and methods

Temperature/pressure loggers (SBE-39, Sea-Bird Electronics, Washington, USA) were deployed on the sea floor by divers at Cape Armitage (77°51'42"S, 166°40'45"E, 9 m deep) and at the McMurdo Station salt water intake jetty (77°51'05"S, 166°39'39"E, 40 m deep, see Fig. 1). The two logging sites are about 1.5 km apart. The Cape Armitage and jetty sites are about 3 km and 5 km respectively from the Ross Ice Shelf. The loggers were

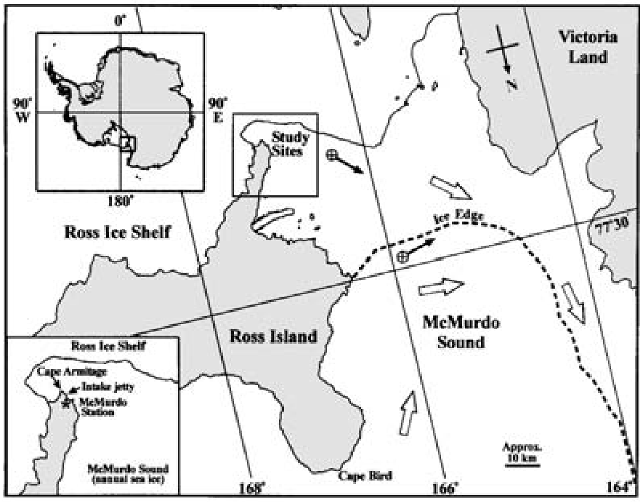

Fig. 1. Map of Ross Island and McMurdo Sound, created from GIS data available online (Antarctic Digital Database Consortium 2000). Rectangle (in top left inset) shows the McMurdo location with respect to Antarctica. Bottom left inset (enlargement of rectangle in map) shows the logger locations at Cape Armitage and the salt water intake jetty at the tip of Hut Point Peninsula, Ross Island. McMurdo Station is indicated by asterisk. The location of ice edge is based on satellite image of McMurdo Sound on 27/01/01 provided by the Arctic and Antarctic Research Center, Scripps Institution of Oceanography. Solid vector arrows indicate the mean current vectors at 200 m over a month (October–November 1982) measured by Lewis & Perkin (1985). Hollow arrows indicate surface water circulation as described by Heath (1977).

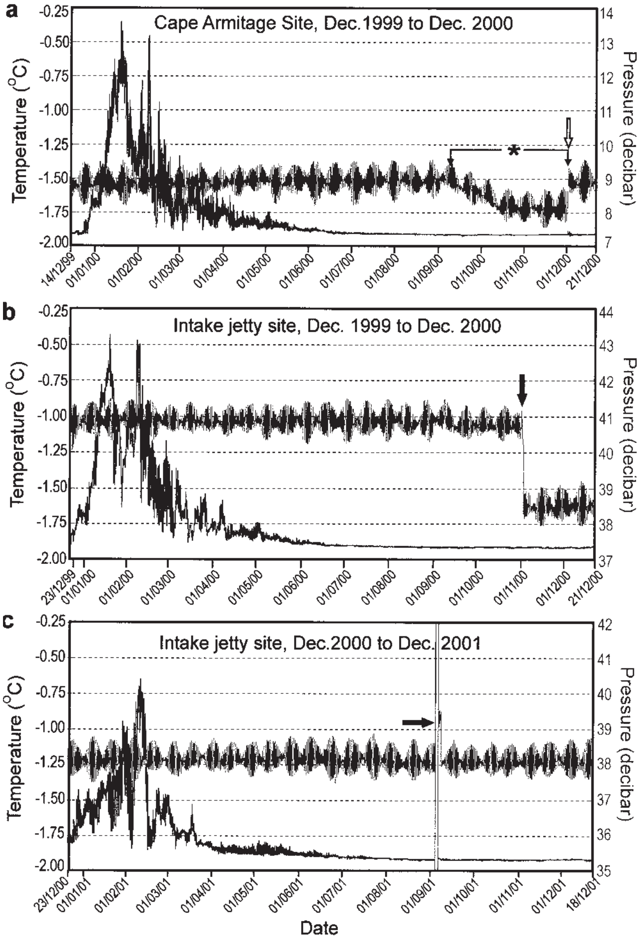

Fig. 2. Full year sea water temperatures (black trace) and benthic pressures (grey trace) recorded every 15 min from two McMurdo Sound inshore sites. **a.** Cape Armitage site at 9 m in 1999–2000. The depression in the pressure record (*) was caused by ice accumulation on the logger which caused it to float, and dislodging the ice (⇓) returned the logger to its original depth. **b**. The McMurdo Station salt water intake jetty site at 40 m in 1999–2000, and **c**. the same site in 2000–01. In **b**, (↓) indicates when the logger was repositioned by divers, and in **c**, (➜) indicates the logger was retrieved for downloading and then repositioned**.**

attached to 15 kg lead weights with 60 cm nylon webbing straps. Loggers recorded water temperature and pressure every 15 minutes. Temperature measurements have an initial accuracy of ± 0.002°C and maximum drift of 0.0002°C per month, and pressure measurements have an initial accuracy of ± 0.35 decibars and maximum drift of 0.02 decibars per month (Sea-Bird specifications). Loggers were retrieved by divers for data download once, during the summer field season, and redeployed the next day to the same site. CTD casts were made with an SBE-25 (Sea-Bird Electronics, Washington, USA), which has accuracies of 0.002°C, 0.00004 S/m (conductivity), and 1 decibar (Sea-Bird specifications), and was factory calibrated yearly.

In situ freezing point (f.p.) is the temperature at which ice and seawater are in equilibrium at the ambient salinity and pressure. *In situ* f.p. was calculated for each data point in the CTD cast by a data analysis program written by the authors, according to the UNESCO equation (1983).

Power spectrum analysis of the logger data was carried out using custom routines written with MATLAB software (MathWorks, Natick, MA). Fast Fourier Transforms were performed in a moving 5-day Hanning window with one day displacement, and then averaged across the data set. This method kept large baseline fluctuations with > 5-day period from dominating the power spectrum, and minimized edge-of-window effects. Temperature and pressure frequency analyses were also carried out with the T_TIDE package written for MatLab (Pawlowicz *et al.* 2002).

Results

Temperature

Continuous temperature and pressure records were obtained for one year (December 1999–December 2000) at the Cape Armitage site (Fig. 2a), and for two consecutive years (December 1999–December 2001) at the McMurdo Station

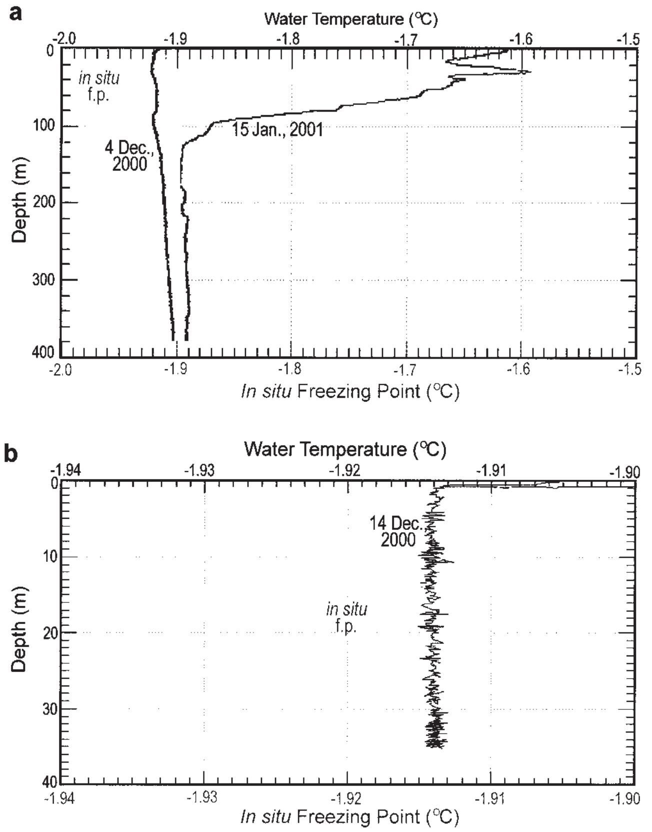

Fig. 3. Data from conductivity, temperature, and depth (CTD) profiler casts showing water temperature (black trace), and calculated *in situ* freezing point (*in situ* f.p., grey trace), which is largely dependent on depth. **a.** Two casts from a deep-water location 4 km from the logger sites. The left-hand black trace is from a cast on 4 December 2000, and shows water temperature fairly constant with respect to depth. The right-hand trace is from a cast taken six weeks later, 15 January 2001, at a slightly deeper location 1 km away. It measured substantial warming of surface waters, and consistent thermal stability (within 0.02°C) in water deeper than 150 m, both of which are typical traits of the CTD casts taken in eastern McMurdo Sound. **b.** A cast taken at the jetty site on 14 December 2000, showing water temperature (black trace) and calculated *in situ* freezing point (grey trace) versus depth. The water temperature was nearly constant (-1.913 to -1.915°C) at all depths, while *in situ* f.p. decreased with depth. Above the intersection of the two traces, the water is slightly supercooled, and therefore may contain microscopic ice crystals.

salt water intake jetty (Fig. 2b & c). We were unable to locate the logger at Cape Armitage in 2001 during the diving operations. We suspect that it accumulated a large mass of platelet ice, becoming sufficiently buoyant to float upwards with weight attached, and then became embedded in the platelet layer beneath the annual sea ice. The temperature and pressure data in Fig. 2 are the first continuous records of this duration, resolution and accuracy to come from McMurdo Sound. The annual temperature profiles of the two sites for year 1999–2000 appear similar and synchronous (Fig. 2a & b), and a similar pattern was observed for year 2000–01 (Fig. 2c). Water temperatures stayed at freezing from early July to December, warmed slightly in late December, then began to rise sharply in early January. Large temperature fluctuations occurred from January through mid-March, and smaller ones continued until the water temperature reached freezing again in early July. In year 1999–2000, there appeared to be two prominent episodes of warming, around mid-January and early February, that raised water temperatures above -0.5°C (Fig. 2a & b). Maximum water temperatures occurred in mid-January, reaching -0.347°C at the Cape Armitage and -0.436°C at the jetty site. Second year (2000–01) maximum temperature at the jetty site was -0.648°C, cooler than prior year's maximum, and occurred in February (Fig. 2c). Also in contrast to year one, the amount of warming in January of the second year was much less extensive, and the peak water temperatures were only slightly above -1.0°C (Fig. 2c).

Excursions above -1.1°C, the equilibrium melting point of notothenioid fish body fluids, occurred between early January and mid-February for a total 15 days at the Cape Armitage site (1999–2000), and 21 and 8 days respectively for year 1999–2000 and 2000–01 at the jetty site. CTD casts early in the season (August through early December) showed highly stable water temperature at these sites (and nearby, deeper locations), varying by less than 0.01°C from the surface to at least 400 m (Fig. 3). Casts later in the season (January and February) showed warming, but only in the top 100 m to 200 m (Fig. 3a). Water deeper than 100 m to 200 m was thermally stable and remained below -1.8°C for every cast in this study.

Pressure

Pressure records show prominent diurnal and fortnightly tidal cycles (Fig. 2). The maximum tidal exchange recorded was 1.26 m. The depression in the pressure trace at Cape Armitage between early September and 1 December 2000 (* in Fig. 2a) was due to accumulation of platelet ice on the logger, which caused it to gradually float upward until its mooring strap was fully extended. The incipient pressure drop on about 10 September 2000 is the first definitive record of the onset time of platelet ice formation at this depth in McMurdo Sound. We found the logger encased in a column of platelet ice 30 cm in diameter on 1 December 2000, dislodged the ice, and the logger returned to the sea floor, resulting in the sharp pressure increase (Fig. 2a, ⇓). The abrupt drop in the jetty pressure record (Fig. 2b, ↓) on 1 November 2000 resulted from the logger being repositioned by divers to 2.5 m above its prior depth. The interruption in data in early September 2001 (Fig. 2c, →) occurred when the logger was retrieved for data download. No platelet ice accumulated on the jetty logger because it

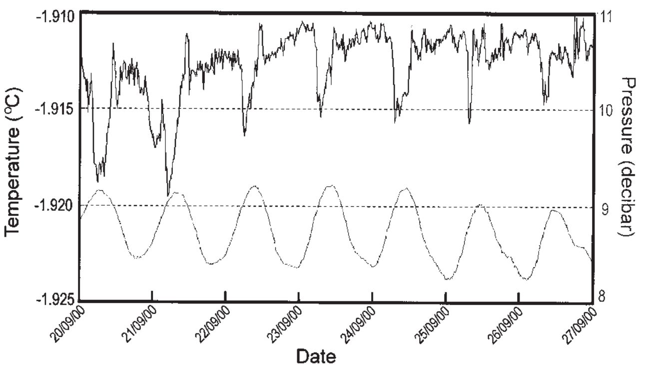

Fig. 4. Water temperature (upper trace) and pressure (lower trace) over one week (20–27 September 2000) at the Cape Armitage site. Cold water episodes occurred with approximately the same period as the tidal cycle. These periodic cold-water spikes are characteristic of the entire data set (both sites, both years) during the time of year in which the water is at or near its freezing point (early July to mid-December).

was placed below the freezing isotherm at the jetty site. Freezing isotherm is the depth above which freezing and ice formation occur. Figure 3b shows *in situ* freezing point (light trace) and actual temperature (dark trace) versus depth at the jetty site. The two temperature traces cross at 13 m, which is the freezing isotherm. Water above 13 m is supercooled by as much as 0.01°C, and this supercooling is the driving force for sea ice formation above the freezing isotherm. The lowest observed crossover depth at the jetty site during this study was 25 m, which means that the logger, located at 40 m, was always below the zone of ice formation.

A prominent feature of the data is that temperature and pressure often appeared to vary with the same period (Fig. 4). Power spectrum analysis confirmed this observation. This co-variation is only discernible in the winter months, when the water temperature is extremely stable. In the summer months it is presumably masked by the large amplitude temperature changes. Although the winter water temperature deviations are low amplitude (usually < 0.01°C), they nonetheless constitute distinct low temperature spikes on already freezing temperatures, and the regularity is striking (Fig. 4). For the one month period from 30 July–28 August 2000 in the Cape Armitage data, 99% of the pressure variability has a period of 1 ± 0.3 days, and 67% of the temperature variability has the same period. The period is one day, not half a day, because in the polar regions the tilt of the Earth's axis out of the ecliptic results in diurnal tides, rather than the semi-diurnal tides that occur on most of the rest of the Earth. Analysis of the temperature data with the T_TIDE package also revealed significant ($P < 0.05$) power spectrum peaks with a period of one day, and several significant peaks with shorter periods (including several shallow water constituents). However, since T_TIDE was written to analyse data with tidal periodicity, it found several falsely significant ($P < 0.05$) tidal peaks in a computer-generated white noise signal which was analysed as a control. These falsely significant peaks were not present in the Fast Fourier Transform analysis.

Discussion

The only prior published annual records of near-shore shallow water temperatures of McMurdo Sound were those of Littlepage (1965), which were collected in McMurdo Sound several kilometres from our logger sites, from 2 January–21 February 1961, and from 29 April–31 December 1961. These records showed temperatures ranging from -1.40°C to -2.15°C, indicating little deviation from freezing. However, water temperatures could not be sampled for parts of February, and all of March and April because the Sound was open water and thus the sampling sites were inaccessible (Littlepage 1965). Temperature data we collected over recent field seasons (generally from August through the end of January, when sea ice access was possible) by individual CTD casts at various McMurdo Sound locations also showed stable freezing water temperatures (unpublished data) consistent with Littlepage's observations. This had led to the general belief that McMurdo Sound water temperatures are perennially at or near the freezing point of seawater. The limitations of the intermittent nature of the prior measurements, and the confinement of sampling to summer has not provided an accurate picture of the thermal history of McMurdo Sound. Our continuous, high resolution temperature records show the complete annual pattern and existence of dynamic thermal variations with time.

The sharp rise in water temperature beginning in early January and the large temperature fluctuations through mid-March in the past two years at these two shallow water (9 m and 40 m), near-shore logger sites (Fig. 2) were completely unexpected, and contrary to the existing expectation of thermal stability in the Sound. Even less expected were the repeated warming episodes during these three months to temperatures (-0.648°C to -0.347°C) substantially above the equilibrium melting point of the body fluids of the notothenioid fishes (-1.1°C). These warm temperature excursions have important implications on the disposal of ice crystals that accumulate in the local notothenioid species during the freezing months of the year.

Invertebrates and fishes (predominantly teleosts and a few cartilaginous skates and rays) are the only ectothermic animals that inhabit the frigid Antarctic marine environments. The body fluids of marine invertebrates and cartilaginous fishes are isosmotic (same solute concentration) with seawater (Prosser 1973), so their equilibrium freezing point is same as that of the latter (about -1.9°C). Thus unless their habitats completely freeze over, which does not happen even in the frigid Antarctic coastal marine environment because water and ice are in equilibrium, these organisms are in no danger of freezing. In contrast, teleost fishes are hyposmotic (much less solutes in their blood and body fluids) to seawater (Prosser 1973), and thus have an equilibrium freezing point much higher than that of seawater, about -1.1°C in the case of the notothenioid fishes (DeVries 1982). In the presence of ice crystals in ambient seawater, the fish cannot avoid freezing by supercooling. Most of the McMurdo Sound notothenioids are localized, shallow benthic species that frequently contact and acquire ice crystals from their ice-laden environment. They do not freeze because the antifreeze glycoproteins in their blood and body fluids recognize and bind to ice crystals that enter and inhibit ice growth, further depressing the organismal freezing temperature to a few tenths below -1.9°C (DeVries 1982, DeVries & Cheng 1992).

Presence of ice crystals on and within the fish can be assayed by immersing tissue or fluid samples from wild-caught fish in supercooled saline; samples carrying ice crystals will rapidly nucleate and freeze the supercooled saline solution into solid ice (DeVries & Cheng 1992). By using this method on McMurdo notothenioid fishes, ice is found to be associated with the skin, gills, intestinal fluid (acquired through ingestion of ice-laden seawater and food) (DeVries & Cheng 1992), as well as in the spleen (Tien 1995) which indicates ice entry into the blood circulation since spleen filters blood and serves as a reservoir of blood cells in teleost fish. The ice that enters the gastrointestinal tract with diet presumably could be eliminated with the faeces. However, no physiological or biochemical mechanisms have been definitively identified that would remove endogenous ice crystals from the blood or spleen. Although the AFGPs of the fish can arrest ice growth, without the means of ice removal the accumulation of ice crystals in the small blood vessels and spleen over time conceivably could lead to circulatory blockage or tissue damage. The confinement of notothenioid fish to the Antarctic region, and the assumed constancy of freezing conditions in these waters prior to this study also mean endogenous ice in fish could never melt. The current results reveal that the amount of time when McMurdo water temperature rose above the equilibrium freezing point of the fish body fluids (-1.1°C) is substantial, totalling 15 days at the Cape Armitage site for year 1, and 21 and 8 days for years 1 and 2 respectively at the jetty site in January and February, during which time endogenous ice crystals in fish could theoretically be melted. The fish would then remain ice-free until early July, when water reached freezing and ice could again form in the water column (Fig. 2a, b & c). These continuous temperature data thus allow us for the first time to assign a purely physical means - thermal melting - as a mechanism to eliminate endogenous ice in notothenioid fish, at least for the endemic populations at and near these two McMurdo locations. However, this should not be generalized to other years or other sites, since year-to-year and site-to-site summer hydrodynamic, thickness of sea ice cover, water temperatures and many other oceanic factors may vary greatly. An indication of such variations is seen in the data of the jetty site, where, although the temperature profiles of the two years are very similar, the highest temperature reached in the second year was substantially lower than the first year (-0.648°C versus -0.436°C), and the total duration of above -1.1°C temperature was much shorter, 8 days versus 21 days, indicating a colder water regime in the summer of the second year. The annual ice cover over the Sound has not broken up during the summers of several years including the two year logging period, thus the ice cover of the second year is multiyear fast ice which may have contributed to the overall cooler summer temperatures in the second summer than the first summer. In addition, although the cumulative duration in days of above -1.1°C water temperature appears substantial, the warm temperatures are not continuous, and whether these periodic temperature rises last long enough for sufficient heat transfer to melt the internal ice of the entire resident fish population remains to be determined. Our preliminary sampling of fish in January indicated not all individuals are ice-free, suggesting endogenous ice crystals may either be melted later in the summer, or persist till the next summer, assuming there are no biological means of removing them.

An interesting question is what is the source of ice crystals in the Sound. Currents at the study sites are known to be dominated by tidal exchanges (Tressler & Ommundsen 1962, Littlepage 1965, Lewis & Perkin 1985). Taken together with the strong tidal periodicity observed in the temperature data (Fig. 4), this suggests that the observed diurnal water temperature variations are caused by tidal currents, and that the regular low temperature spikes (Fig. 4) might be the result of tidally entrained frigid shelf water. Shelf water is formed by melting of the underside of the ice shelf at depth, which lowers the temperature of the seawater below its surface freezing point by several tenths of a degree (Jacobs *et al*. 1979). This cold water could conceivably be advected by tidal currents from under the nearby Ross Ice Shelf and forced to the surface by the bathymetry of the Cape Armitage Shoal. Pressure release during the upwelling raises the freezing point of the shelf water without changing the water temperature appreciably, leading to ice nucleation in the water column, which presumably is one of the sources of endogenous ice in fish. Seawater cooled at the surface is only cooled to its surface freezing point, which means that shelf water can be much colder than other seawater layers. During the winter months the water at our study sites is constantly at its freezing point, as measured (Fig. 2) and evidenced by active surface ice formation. As seen in Fig. 3b, surface waters can even be slightly supercooled, which can act as the driving force for ice formation. The cold temperature spikes we observed in water that is already at its freezing point (Fig. 4) suggest the influx of still colder water, and the likely source is shelf water from the nearby Ross Ice Shelf. This is implicated by the north-west mean current direction at 200 m at a near-Shelf site west to our logger sites (Fig. 1, solid arrow) determined by Lewis & Perkin (1985), and similarly by Heath (1977) for surface water (Fig. 1, open arrow). Water at sites farther from the influence of major ice shelves (e.g. farther offshore in Antarctica, or in the Arctic Ocean) would presumably be warmer, and fish in other locations would therefore be exposed to less environmental ice.

The high resolution, long-term temperature records obtained in this study showed for the first time that the in-shore McMurdo waters could undergo dramatic temperature fluctuations in January to March. The maximum amplitude of temperature rise for 1999–2001 was about 1.57°C (from -1.915°C to -0.347°C). This amount of warming can be considered large for the endemic Antarctic notothenioid fish on the basis of its potential in melting the endogenous ice crystals the fish accumulate during the freezing months. However, this 1.57°C change is very small when compared to the coastal water of the north polar or subpolar oceans inhabited by other antifreeze-bearing fishes where large scale seasonal changes of water temperature occur and peak summer temperatures reach 14°C to 16°C (Petzel *et al.* 1980, Fletcher *et al.* 1985). Whether in relative terms or absolute terms, the McMurdo Sound water is extremely thermally stable and cold. The north polar and subpolar coastal fishes probably acquire ice crystals in the winter analogous to their Antarctic counterparts, but their endogenous ice undoubtedly can be melted by the large scale seasonal warming.

Both temperature and pressure loggers continue to record data year-round. We hope to recover the logger at the Cape Armitage site in the field season of 2002–03 to obtain multiyear data from that site. In addition, a third logger has been placed at Cape Bird, near the northern boundary of McMurdo Sound (Fig. 1). This logger site is much farther from the Ross Ice Shelf, and may allow us to determine whether the cold water spikes are indeed Ice Shelf water by analysing the temporal relationship of these spikes at all three sites. These high resolution long-term temperature and pressure data provide valuable information on the dynamics of inshore Antarctic continental waters, which are not only useful for addressing the questions regarding the fate of endogenous ice crystals in the resident notothenioid fishes, but for other biological or physical studies which require a knowledge of the annual thermal histories of McMurdo Sound or of a representative high latitude Antarctic marine environment.

Acknowledgements

This research was supported by National Science Foundation Grant OPP 99-09841 to Arthur L. DeVries and Chi-Hing C. Cheng. We thank the three referees, Dr Mike Meredith, Professor Andrew Clarke and an anonymous reviewer, for their valuable input, especially those of Dr Meredith.

References

Antarctic Digital Database Consortium. 2000. *Antarctic Digital Database, Version 3.0. Database, manual and bibliography*. Cambridge: Scientific Committee on Antarctic Research, 93 pp. Data available online at http://www.nerc-bas.ac.uk/public/magic/add_main.html.

Chen, L., DeVries, A.L. & Cheng, C.-H.C. 1997. Evolution of antifreeze glycoprotein gene from a trypsinogen gene in Antarctic notothenioid fish. *Proceedings of the National Academy of Sciences,* **94**, 3811–3816.

Cheng, C.-H.C. & Chen, L. 1999. Evolution of an antifreeze glycoprotein. *Nature,* **40**, 443–444.

DeVries, A.L. 1982. Biological antifreeze agents in coldwater fishes. *Comparative Biochemistry and Physiology,* **73A**, 627–640.

DeVries, A.L. & Cheng, C.-H.C. 1992. The role of antifreeze glycopeptides and peptides in the survival of cold water fishes. *In* Somero, G.N., Osmond, C.B. & Bolis, C.L., *eds. Water and life: comparative analysis of water relationships at the organismic, cellular, and molecular levels.* Berlin: Springer, 303–315.

Fletcher, G.L., Hew, C.L., Li, X., Haya, K. & Kao, M. 1985. Year-round presence of high levels of plasma antifreeze peptides in a temperate fish, ocean pout (*Macrozoarces americanus*). *Canadian Journal of Zoology*, **63**, 488–493.

Heath, R.A. 1977. Circulation across the ice shelf edge in McMurdo Sound, Antarctica. *In* Dunbar, M.J., *ed. Polar oceans.* Montreal: Arctic Institute of North America, 129–139.

Jacobs, S.S., Gordon, A.L. & Ardai Jr, J.L. 1979. Circulation and melting beneath the Ross Ice Shelf. *Science*, **203**, 439–443.

Littlepage, J.L. 1965. Oceanographic investigations in McMurdo Sound, Antarctica. *Antarctic Research Series*, **5**, 1–37.

Lewis, E.L. & Perkin R.G. 1985. The winter oceanography of McMurdo Sound, Antarctica. *Antarctic Research Series*, **43**, 145–165.

Pawlowicz, R., Beardsley, B. & Lentz, S. 2002. Classical tidal harmonic analysis including error estimates in MATLAB using "T_TIDE". *Computers and Geosciences*, **28**, 929–937.

Petzel, D.H., Reisman, H.M. & DeVries, A.L. 1980. Seasonal variation of antifreeze peptide in the winter flounder, *Pseudopleuronectes americanus*. *The Journal of Experimental Zoology,* **211**, 63–39.

Prosser, C.L. 1973. Water: osmotic balance; hormonal regulation. *In* Prosser, C.L., *ed. Comparative animal physiology*. Philadelphia, PA: Saunders, 1–78.

Tien, R. 1995. *Freezing avoidance and the presence of ice in shallow water Antarctic fishes.* PhD thesis, University of Illinois at Urbana-Champaign, 146 pp. [Unpublished.]

Tressler, W.L. & Ommundsen, A.M. 1962. Seasonal oceanographic studies in McMurdo Sound, Antarctica. *US Navy Hydrographic Office Technical Report TR–125.*

UNESCO. 1983. Algorithms for Computation of Fundamental Properties of Seawater. *UNESCO Technical Papers in Marine Science*, **44**.