Scientific Polar Ice Diving

Adam G. Marsh, Amy L. Moran, and James B. McClintock

ABSTRACT. Early ecological descriptions of under-ice benthic communities in McMurdo Sound were made over 40 years ago by wetsuit divers Paul Dayton and John Pearse, resulting in seminal papers. Polar diving equipment has evolved since then in areas of life-support breathing apparatus and thermal protection. Scientific polar ice diving has developed into a research tool for intensive sampling and experimental programs by marine ecologists describing under-ice ecosystem structure, and provided insights into how benthic communities respond to disturbance. Direct scuba observations have established the remarkable continuity that exists in species distribution and abundances. The ability to scuba dive in a stable, marine benthic community in polar habitats provides researchers with a unique opportunity to understand the structuring forces at a population level and selective adaptations at an organismal level. Research by Moran and Woods using cutting-edge methods in underwater environmental measurement developed and tested a sophisticated model for metabolic regulation in embryos developing on the sea floor. Work by Marsh in understanding energy utilization during development in an Antarctic sea urchin highlighted a novel mechanism of metabolic energy conservation associated with protein metabolism. A current research focus is on environmental imprinting via epigenetic modifications to genomic DNA, which could have a large impact on cellular physiological activities. This could possibly function as a mechanism for regulating large-scale shifts in cellular energy utilization, perhaps serving as the key mechanism by which organisms have adapted to polar life in the cold and dark. McClintock and coworkers' discovery regarding feeding deterrents in an Antarctic sponge has fueled an extraordinary understanding of chemically mediated defense in polar benthic communities.

INTRODUCTION

Polar marine ecosystems are vastly understudied. In general, they possess unique features related to extremes of temperature, photoperiod, and the frequent occurrence of a sea ice layer at the ocean–atmosphere boundary. It is this latter feature of sea ice dynamics that makes these habitats particularly challenging for studying benthic macroorganisms (both animals and plants). Surface ice conditions confound the collection of living specimens and constrain logistics for in situ experimental manipulations. Consequently, scientific research activities in polar coastal margins focusing on benthic organisms require well-organized and -trained scuba diving teams for direct observations, collections, and experiments. Scientific research on polar marine organisms poses many challenges. In areas where sea ice coverage is significant in terms of either a solid layer or high ice floe densities, great skill and caution must be exercised by dive teams engaged in scuba diving activities. Scientific ice diving in polar regions has yielded a wealth of information that could not have been obtained by any other sampling methods. The ability of a diver to make direct under-ice observations and the delicate skill with which critical samples can be collected or experimental arrays handled have yielded critical new knowledge of the richly diverse and ecologically complex polar habitats. In short, polar ice diving

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has developed as a mature branch of scientific diving that is irreplaceable in terms of the discoveries that have been made and will continue to be made.

DIVING

Techniques and strategies for diving in polar ice environments have received considerable expert attention in recent years (Lang and Sayer, 2007; Lang, 2009). Local dive-site conditions can be variable and require unique solutions to mitigate risk. However, there are some aspects to polar ice diving that all scientific divers face, which we briefly summarize below to provide an overview of the challenges that are involved with scientific ice diving in polar coastal zones. Readers should consult Lang and Sayer (2007) and Krupnik et al. (2009) for more details specific to ice diving research activities.

The biggest challenge to ice diving can be limited options for water entry and exit. In floe environments, dynamic interactions of winds and currents can establish significant risks for the ability of a diver under water to navigate back to a safe exit point. In conditions with a solid sea ice surface, divers operate as if in an underwater cavern with restricted access. Diving is not conducted under conditions where there is any doubt about the ability to return to the exit location. Once all the risk factors have been identified and mitigated, then underwater work can commence. A second significant challenge is thermal protection for the diver while under water. Drysuits are standard equipment now and there are a variety of commercial designs using heavy-duty, tear-resistant outer-layer materials to make the suits durable under harsh field conditions. Drysuits need to be fitted to the diver's body, with sufficient extra space to allow for several layers of insulating undergarments. A third challenge for working in water under ice is buoyancy control. Maintaining a larger air volume in the drysuit to accommodate the insulating undergarments results in more potential for large air pockets to move around within the suit and cause sudden shifts in balance points and trim levels. More air necessitates more lead weight, and so a larger total mass of the diver plus equipment requires greater attention to suit-volume regulation for maintaining neutral buoyancy. A fourth challenge is ensuring that the diver has the appropriate equipment for a safe dive. This mostly means that divers must have first- and second-stage regulators that are designed for use in sea water at -2°C without developing internal ice crystals that could result in a free-flow event. A great deal of scrutiny must be exerted to ensure that any regulator used under the ice is not prone to free-flow events.

SCIENCE

Some of the most important work involving early ecological descriptions of under-ice benthic communities in McMurdo Sound were made by wetsuit divers in the mid-sixties and resulted in seminal papers by Paul Dayton and John Pearse (Pearse, 1966, 1967; Dayton et al., 1969, 1974). Dayton and Pearse were pioneers in making detailed underwater observations and experiments, and continued productive Antarctic research careers with their students by utilizing scuba as the first tool for observation and collection (Dayton and Oliver, 1977; Oliver, 1984; McClintock and Pearse, 1986, 1987; Pearse et al., 1991; Pearse and Lockhart, 2004). Scientific ice diving became the primary mechanism for intensive sampling and experimental programs by marine ecologists describing under-ice ecosystem structure (Slattery and Oliver, 1986; Brey et al., 1995; Slattery and McClintock, 1995; Blight et al., 2010). The ability to perform direct experimentation under the ice has provided many insights into how benthic communities respond to disturbance (Lenihan et al., 2003; Conlan et al., 2004; Kim et al., 2007; Conlan et al., 2010; Kim et al., 2010) and the delicate balance that exists between abiotic selection pressures and population survival (growth, reproduction, and recruitment) in marine communities subjected to continuous harsh environmental conditions.

We now have a much better understanding of the longevity of polar benthic communities and how shifts in trophic organization may proceed over much more gradual time scales than in other marine ecosystems (Brey et al., 1995; McClintock and Pearse, 1986, 1987). Direct scuba observations and research diving activities for the last 40 years have established the remarkable continuity that exists over this time frame in species distribution and abundances. This level of system equilibrium is only possible because of the seasonally and annually stable ecosystem structure. The only other comparable marine ecosystems are the abyssal plains of the deep oceans, where direct observations are only possible via deep submergence vehicles. The ability to scuba dive and directly observe, collect, and manipulate a stable marine benthic community in polar habitats provides researchers with a unique opportunity to understand the structuring forces at a population level and selective adaptations at an organismal level. The majority of the biosphere on this planet, 75% by volume, consists of a single habitat type: cold (~2°C), dark sea water. One of the few places where this habitat type is accessible by scuba is along the coastal margins of Antarctica.

Ongoing research by the coauthors of this paper continues a tradition of strong scientific diving programs in coastal Antarctic habitats. The observation, collection, and experimentation that is afforded from a first-person perspective by actively engaging in under-ice research constantly fuels new discoveries and new questions (McClintock et al., 2010b). As the field of biology has been moving more and more toward molecular-level understandings based on increasingly sophisticated technologies, scientific diving remains an important tool for collecting organisms necessary for physiological, biochemical, and molecular genetic research.

Work by Amy Moran, in collaboration with Art Woods, has used cutting-edge methods in underwater environmental measurement to develop and test a sophisticated model for metabolic regulation in embryos developing on the sea floor (Woods and Moran, 2008a, 2008b; Woods et al., 2009; Moran and

Woods, 2010). In general, the availability of oxygen in seawater and the rate of oxygen consumption by an organism is a critical balance (supply versus demand) that is unique in polar environments. One facet where this is particularly important is for the egg capsules of nudibranchs (Mollusca). Here, the deposition of numerous embryos into a single capsule is under a tight selective constraint of ensuring that sufficient oxygen is available in the center of the capsule so that all embryos can survive through development. The research of Woods and Moran has made many interesting discoveries of embryo size, egg-capsule size, capsule density, and capsule geometry that are associated with adaptations for survival of nudibranch embryos in polar habitats. Questions of oxygen transport, growth regulation, metabolic energy utilization, and developmental period remain key questions for understanding the life-history adaptations of many polar marine invertebrate species. Pursuing this work will require additional in situ work under the ice.

Work by Adam Marsh has focused on understanding energy utilization during development in an Antarctic sea urchin (Marsh and Manahan, 1999; Marsh et al., 1999; Marsh and Manahan, 2000; Marsh et al., 2001). Metabolic efficiency is an overriding feature of many species in polar ecosystems where primary production is severely limited to only a small portion of each year. Many invertebrate larval forms have feeding structures and rely on the capture of exogenous food for their nutrition. However, in polar ecosystems, there is very little food available in the water column throughout most of the austral spring and summer developmental periods. Work in the Manahan laboratory has demonstrated a fascinating and novel mechanism of metabolic energy conservation associated with protein metabolism: the net cost of protein accumulation (net of synthesis and degradation) is much less in the embryos of the Antarctic sea urchin than in any other known marine organism (Marsh et al., 2001).

Recent work by Marsh is delving into genomic-level responses to temperature stress (Fielman and Marsh, 2005; Ulrich and Marsh, 2009) and the potential for salinity stress to become an important selection force in the future (Cowart et al., 2009). We are now focusing on environmental imprinting via epigenetic modifications to genomic DNA, which could have a large impact on cellular physiological activities. This would function as a major mechanism for regulating large-scale shifts in cellular energy utilization, perhaps serving as the key mechanism by which organisms have adapted to polar life in the cold and dark. Despite the molecular focus of ongoing studies, diving operations under the ice for collections and observations remain an important component of this field work.

Work by Jim McClintock has been prolific, particularly in collaboration with marine natural products chemist Bill Baker and phycologist Charles Amsler. A simple discovery regarding feeding deterrents in an Antarctic sponge has fueled an extraordinary understanding of chemically mediated defense in polar benthic communities (McClintock and Vernon, 1990; McClintock and Gauthier, 1992; Peters et al., 2009, 2010; Aumack et al., 2010). The revolutionary discovery here was McClintock's shattering of a paradigm that asserted that chemical defense in polar environments was not important because of the lack of predation pressures in comparison to tropical coral reefs (where chemical defense was well documented; Slattery and McClintock, 1995). This work completely shifted our perspective of the role of predation in shaping polar benthic communities. Subsequent work on identifying chemical deterrents that exist in polar organisms (both plants and animals) has led to a better understanding of the precarious balance in oligotrophic systems that exists among predators and their sessile prey or herbage. Knowing about these biochemical-level interactions that exist among species has led to a much broader understanding of processes that shape polar benthic community structure, particularly in terms of the interactions between consumers and producers (Amsler et al., 2009a, 2009b; McClintock et al., 2010a).

SUMMARY

There is no substitute for direct observation. Much of what we know today about polar benthic communities was derived from questions that scientific divers asked based on their own observations. In truth, we know much less about benthic coastal habitats below polar sea ice than other marine systems (perhaps with the exception of the deep sea). Even after 50 years of scuba exploration there remains a host of research questions to ponder. The limited access to the environment imposed by sea ice coverage substantially reduces the observation time often taken for granted when exploring a rocky intertidal pool or snorkeling on a coral reef. Scientific diving by principal investigators is an essential component of establishing a working knowledge of what "normal" looks like under the ice in Antarctica, and a key focus of future polar diving is to provide basic information that will help to identify and evaluate the impact of environmental change on these unique habitats.

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REFERENCES

Amsler, C. D., M. O. Amsler, J. B. McClintock, and B. J. Baker. 2009a. Filamentous algal endophytes in macrophytic Antarctic algae: Prevalence in hosts and palatability to mesoherbivores. *Phycologia,* 48:324–334. http://dx.doi.org/10.2216/08-79.1.

Amsler, C. D., K. Iken, J. B. McClintock, and B. J. Baker. 2009b. Defenses of polar macroalgae against herbivores and biofoulers. *Botanica Marina*, 52:535–545. http://dx.doi.org/10.1515/BOT.2009.070.

Aumack, C. F., C. D. Amsler, J. B. McClintock, and B. J. Baker. 2010. Chemically mediated resistance to mesoherbivory in finely branched macroalgae along the western Antarctic peninsula. *European Journal of Phycology*, 45:19–26. http://dx.doi.org/10.1080/09670260903171668.

Blight, L. K., D. G. Ainley, S. F. Ackley, G. Ballard, T. Ballerini, R. L. Brownell, Jr., C.-H. C. Cheng, M. Chiantore, D. Costa, M. C. Coulter, P. K. Dayton, A. L. Devries, R. Dunbar, S. Earle, J. T. Eastman, S. D. Emslie, C. W. Evans, R. A. Garrott, S. Kim, G. Kooyman, A. Lescroel, M. Lizotte, M. Massaro, S. Olmastroni, P. J. Ponganis, J. Russell, D. B. Siniff, W. O. Smith, Jr., B. S. Stewart, L. Stirling, J. Willis, P. Wilson, and E. J. Woehler. 2010. Fishing for data in the Ross Sea. *Science,* 330:1316. http://dx.doi.org/10.1126/science.330.6009.1316.

Brey, T., J. Pearse, L. Basch, J. McClintock, and M. Slattery. 1995. Growth and production of *Sterechinus neumayeri* (Echinoidea: Echinodermata) in McMurdo Sound, Antarctica. *Marine Biology*, 124:279–292. http://dx.doi.org/10.1007/BF00347132.

Conlan, K. E., S. L. Kim, H. Lenihan, and J. Oliver. 2004. Benthic changes during 10 years of organic enrichment by McMurdo Station, Antarctica. *Marine Pollution Bulletin,* 49:43–60. http://dx.doi.org/10.1016/j.marpolbul.2004.01.007.

Conlan, K. E., S. L. Kim, A. R. Thurber, and E. Hendrycks. 2010. Benthic changes at McMurdo Station, Antarctica following local sewage treatment and regional iceberg-mediated productivity decline. *Marine Pollution Bulletin,* 60:419–432. http://dx.doi.org/10.1016/j.marpolbul.2009.10.009.

Cowart, D. A., P. N. Ulrich, D. C. Miller, and A. G. Marsh. 2009. Salinity sensitivity of early embryos of the Antarctic sea urchin, *Sterechinus neumayeri*. *Polar Biology,* 32:435–441.

Dayton, P. K., and J. Oliver. 1977. Antarctic soft-bottom benthos in oligotrophic and eutrophic environments. *Science,* 197:55–58. http://dx.doi.org/10.1126/science.197.4298.55.

Dayton, P. K., G. A. Robilliard, and A. L. Devries. 1969. Anchor ice formation in McMurdo Sound, Antarctica and its biological effects. *Science*, 163:273–274. http://dx.doi.org/10.1126/science.163.3864.273.

Dayton, P. K., G. A. Robilliard, R. Paine, and L. Dayton. 1974. Biological accommodation in benthic community at McMurdo Sound, Antarctica. *Ecological Monographs*, 44:105–128. http://dx.doi.org/10.2307/1942321.

Fielman, K., and A. G. Marsh. 2005. Genome complexity and repetitive DNA in metazoans from extreme marine environments. *Gene*, 362:98–108. http://dx.doi.org/10.1016/j.gene.2005.06.035.

Kim, S. L., K. K. Hammerstom, K. E. Conlan, and A. R. Thurber. 2010. Polar ecosystem dynamics: Recovery of communities from organic enrichment in McMurdo Sound, Antarctica. *Integrative Comparative Biology*, 50:1031–1040. http://dx.doi.org/10.1093/icb/icq058.

Kim, S. L., A. Thurber, K. K. Hammerstrom, and K. E. Conlan. 2007. Seastar response to organic enrichment in an oligotrophic polar habitat. *Journal of Experimental Marine Biology and Ecology,* 346:66–75. http://dx.doi.org/10.1016/j.jembe.2007.03.004.

Krupnik, I., M. A. Lang, and S. E. Miller, eds. 2009. *Smithsonian at the poles: Contributions to International Polar Year science*. Washington D.C.: Smithsonian Institution Scholarly Press.

Lang, M. A. 2009. Parameters of extreme environment diving. In *The future of diving: 100 years of Haldane and beyond*, ed. M. A. Lang and A. O. Brubakk, pp. 153–159. Washington, D.C.: Smithsonian Institution Scholarly Press.

Lang, M. A., and M. D. J. Sayer, eds. 2007. *Proceedings of the International Polar Diving Workshop, Svalbard, March 15–21, 2007*. Washington, D.C.: Smithsonian Institution.

Lenihan, H., C. Peterson, S. L. Kim, K. E. Conlan, R. Fairey, C. McDonald, J. Grabowski, and J. Oliver. 2003. Variation in marine benthic community composition allows discrimination of multiple stressors. *Marine Ecology Progress Series*, 261:63–73. http://dx.doi.org/10.3354/meps261063.

Marsh, A. G., P. Leong, and D. Manahan. 1999. Energy metabolism during embryonic development and larval growth of an Antarctic sea urchin. *Journal of Experimental Biology*, 202:2041–2050.

Marsh, A. G., and D. Manahan. 1999. A method for accurate measurements of the respiration rates of marine invertebrate embryos and larvae. *Marine Ecology Progress Series*, 184:1–10. http://dx.doi.org/10.3354/meps184001.

———. 2000. Metabolic differences between "demersal" and "pelagic" development of the Antarctic sea urchin *Sterechinus neumayeri*. *Marine Biology*, 137:215–221. http://dx.doi.org/10.1007/s002270000364.

Marsh, A. G., R. Maxson, and D. Manahan. 2001. High macromolecular synthesis with low metabolic cost in Antarctic sea urchin embryos. *Science*, 291:1950–1952. http://dx.doi.org/10.1126/science.1056341.

McClintock, J. B., C. D. Amsler, and B. J. Baker. 2010a. Overview of the chemical ecology of benthic marine invertebrates along the western Antarctic peninsula. *Integrative and Comparative Biology,* 50:967–980. http://dx.doi.org/10.1093/icb/icq035.

McClintock, J. B., C. D. Amsler, A. L. Moran, H. A. Woods, and B. J. Baker. 2010b. Introduction to the symposium: Advances in Antarctic marine biology. *Integrative and Comparative Biology,* 50:948–949. http://dx.doi.org/10.1093/icb/icq005.

McClintock, J. B., and J. Gauthier. 1992. Antimicrobial activities of Antarctic sponges. *Antarctic Science,* 4:179–183. http://dx.doi.org/10.1017/S0954102092000270.

McClintock, J. B., and J. S. Pearse. 1986. Organic and energetic content of eggs and juveniles of Antarctic echinoids and asteroids with lecithotrophic development. *Comparative Biochemistry and Physiology, A. Physiology,* 85:341–345. http://dx.doi.org/10.1016/0300-9629(86)90259-8.

———. 1987. Biochemical composition of Antarctic echinoderms. *Comparative Biochemistry and Physiology, B. Biochemistry and Molecular Biology,* 86:683–687. http://dx.doi.org/10.1016/0305-0491(87)90211-2.

McClintock, J. B., and J. Vernon. 1990. Chemical defense in the eggs and embryos of Antarctic sea stars (Echinodermata). *Marine Biology,* 105:491–495. http://dx.doi.org/10.1007/BF01316320.

Moran, A. L., and H. A. Woods. 2010. Limits to diffusive O_2 transport: Flow, form, and function in nudibranch egg masses from temperate and polar regions. *PLoS One*, 5:1–8. http://dx.doi.org/10.1371/journal.pone.0012113.

Oliver, J. 1984. Selection for asexual reproduction in an Antarctic polychaete worm. *Marine Ecology Progress Series*, 19:33–38. http://dx.doi.org/10.3354/meps019033.

Pearse, J. S. 1966. Antarctic asteroid *Odontaster validus*: Constancy of reproductive periodicities. *Science,* 152:1763–1764. http://dx.doi.org/10.1126/science.152.3730.1763.

———. 1967. Coelomic water volume control in Antarctic sea-star *Odontaster validus*. *Nature,* 216:1118–1119. http://dx.doi.org/10.1038/2161118a0.

Pearse, J. S., and S. Lockhart. 2004. Reproduction in cold water: Paradigm changes in the 20th century and a role for cidaroid sea urchins. *Deep Sea Research Part II: Topical Studies in Oceanography,* 51:1533–1549. http://dx.doi.org/10.1016/j.dsr2.2004.06.023.

Pearse, J. S., J. B. McClintock, and I. Bosch. 1991. Reproduction of Antarctic benthic marine invertebrates: Tempos, modes, and timing. *American Zoologist*, 31:65–80.

Peters, K. J., C. D. Amsler, J. B. McClintock, and B. J. Baker. 2010. Potential chemical defenses of Antarctic sponges against sympatric microorganisms. *Polar Biology*, 33:649–658. http://dx.doi.org/10.1007/s00300-009-0741-z.

Peters, K. J., C. D. Amsler, J. B. McClintock, R. W. M. van Soest, and B. J. Baker. 2009. Palatability and chemical defenses of sponges from the western Antarctic Peninsula. *Marine Ecology Progress Series*, 385:77–85. http://dx.doi.org/10.3354/meps08026.

Slattery, M., and J. B. McClintock. 1995. Population structure and feeding deterrence in three shallow-water Antarctic soft corals. *Marine Biology*, 122:461–470. http://dx.doi.org/10.1007/BF00350880.

Slattery, P., and J. Oliver. 1986. Scavenging and other feeding-habits of lysianassid amphipods (*Orchomene* spp.) from McMurdo Sound, Antarctica. *Polar Biology*, 6:171–177. http://dx.doi.org/10.1007/BF00274880.

Ulrich, P. N., and A. G. Marsh. 2009. Thermal sensitivity of mitochondrial respiration efficiency and protein phosphorylation in the clam *Mercenaria mercenaria*. *Marine Biotechnology*, 11:608–618. http://dx.doi.org/10.1007/s10126-009-9177-2.

Woods, H. A., and A. L. Moran. 2008a. Oxygen profiles in egg masses predicted from a diffusion-reaction model. *Journal of Experimental Biology*, 211:790–797. http://dx.doi.org/10.1242/jeb.014613.

———. 2008b. Temperature–oxygen interactions in Antarctic nudibranch egg masses. *Journal of Experimental Biology,* 211:798–804. http://dx.doi.org/10.1242/jeb.014621.

Woods, H. A., A. L. Moran, C. P. Arango, L. Mullen, and C. Shields. 2009. Oxygen hypothesis of polar gigantism not supported by performance of Antarctic pycnogonids in hypoxia. *Proceedings of the Royal Society, B: Biological Sciences*, 276(1659):1069–1075. http://dx.doi.org/10.1098/rspb.2008.1489.