



Late-Neoproterozoic Deep-Ocean Oxygenation and the Rise of Animal Life

Don E. Canfield, *et al.*
Science **315**, 92 (2007);
DOI: 10.1126/science.1135013

The following resources related to this article are available online at www.sciencemag.org (this information is current as of August 26, 2008):

Updated information and services, including high-resolution figures, can be found in the online version of this article at:

<http://www.sciencemag.org/cgi/content/full/315/5808/92>

Supporting Online Material can be found at:

<http://www.sciencemag.org/cgi/content/full/1135013/DC1>

A list of selected additional articles on the Science Web sites **related to this article** can be found at:

<http://www.sciencemag.org/cgi/content/full/315/5808/92#related-content>

This article **cites 31 articles**, 9 of which can be accessed for free:

<http://www.sciencemag.org/cgi/content/full/315/5808/92#otherarticles>

This article has been **cited by** 34 article(s) on the ISI Web of Science.

This article has been **cited by** 9 articles hosted by HighWire Press; see:

<http://www.sciencemag.org/cgi/content/full/315/5808/92#otherarticles>

This article appears in the following **subject collections**:

Paleontology

<http://www.sciencemag.org/cgi/collection/paleo>

Information about obtaining **reprints** of this article or about obtaining **permission to reproduce this article** in whole or in part can be found at:

<http://www.sciencemag.org/about/permissions.dtl>

Late-Neoproterozoic Deep-Ocean Oxygenation and the Rise of Animal Life

Don E. Canfield,^{1*} Simon W. Poulton,² Guy M. Narbonne³

Because animals require oxygen, an increase in late-Neoproterozoic oxygen concentrations has been suggested as a stimulus for their evolution. The iron content of deep-sea sediments shows that the deep ocean was anoxic and ferruginous before and during the Gaskiers glaciation 580 million years ago and that it became oxic afterward. The first known members of the Ediacara biota arose shortly after the Gaskiers glaciation, suggesting a causal link between their evolution and this oxygenation event. A prolonged stable oxic environment may have permitted the emergence of bilateral motile animals some 25 million years later.

Large, architecturally complex life forms first appeared about 575 million years ago (Ma) (1, 2). These life forms are epitomized by the Ediacara biota, a globally distributed assemblage of fossil impressions of centimeter- to meter-scale soft-bodied organisms and colonies. The Ediacara biota developed after the Gaskiers glaciation at 580 Ma and abruptly disappeared coincident with the Cambrian explosion of skeletal animals about 35 million years later (3, 4). The Ediacara biota most likely included a mixture of stem-group animals and potentially other extant kingdoms of eukaryotes, along with fossils that may represent “failed experiments” in evolution (3). Fossilized animal embryos (5) dated at 560 to 580 Ma (6) further support the view that animals were an important part of Ediacaran life. Animals have an absolute requirement for oxygen, and it has been widely hypothesized that a late-Neoproterozoic rise in oxygen created an environment permissive for animal evolution (7–10). Direct evidence for late-Neoproterozoic ocean oxygenation, however, has been lacking. We used several geochemical tracers to show that the deep ocean became oxidized shortly before the first appearance of the Ediacara biota.

In the Avalon Peninsula, Newfoundland, 6 km of late-Neoproterozoic sedimentary rocks represent at least 15 million years of late-Neoproterozoic time (Fig. 1). The sediment sequence begins about 800 m below the glacial deposits and cap carbonate of the Gaskiers Formation dated at 580 Ma (2). The Gaskiers glaciation was the last of the major Neoproterozoic glaciations (4, 11) and is represented on four continents (12), although it was probably not as widespread as the previous

Sturtian and Marinoan “snowball” glaciations (11, 12). Ediacara-type fossils are present through most of the post-Gaskiers succession. The first Ediacaran fossils, represented by a low-diversity assemblage of *Ivesheadia* (“pizza disks”), *Thectardis*, and species of *Charnia* (1, 3, 4, 13) (Fig. 2, A and B), were found in the upper Drook Formation within 5 million years of the glacial terminus. These are the earliest large and architecturally complex eukaryote fossils known anywhere in the world. By 565 Ma, the high-density and high-diversity Ediacaran assemblages of Mistaken Point existed (Fig. 2C) (3, 13, 14), and numerous occurrences of Ediacaran disks continue through the Fermeuse Formation (Fig. 2D).

The Ediacaran animals of the Avalon Peninsula lived on the sea floor in deep-water environments well below the photic zone (3, 13, 15). The Mall Bay through Briscal Formations (Fig. 1) accumulated as axial basin floor deposits in water depths exceeding several hundred meters, and possibly extending 1 km or more (3, 16). The Mistaken Point and Trepassy Formations repre-

sent a deep-water slope environment (14, 15). Beginning with the Fermeuse Formation, the sequence gives way to mudstones likely deposited as delta front deposits (3, 17). The Neoproterozoic sediments of Newfoundland were deposited at the northern margins of ancient Gondwana, with no evidence for basin restriction, suggesting open access to the global ocean (18, 19).

We used iron extraction techniques to explore ocean redox conditions. In this approach, operationally defined iron extraction protocols (20) are used to partition iron into its highly reactive components and its unreactive phases. Highly reactive iron includes iron oxide, carbonate, and sulfide minerals; this represents the iron that is geochemically and biologically active during early sediment diagenesis (21). By contrast, “unreactive” iron is geochemically inert on early diagenetic time scales. Previous studies have shown that in a broad suite of marine sediments deposited from an oxygen-containing water column, the ratio of highly reactive iron to total iron (FeHR/FeT) is consistently below 0.38, with a modern average (\pm SD) of 0.26 ± 0.08 (22, 23) and a Phanerozoic average (past 542 million years and excluding the modern) of 0.15 ± 0.06 (23). By contrast, sediments deposited from anoxic water columns may obtain additional reactive iron from iron mineral formation in the water column; in these environments, FeHR/FeT may exceed 0.38.

This is true both if the anoxic water column is sulfidic, such as the modern Black Sea (22) and ancient sulfidic marine water bodies (23, 24), and if it contained dissolved iron, as was the case early in Earth’s history (25). We also used the concentrations of organic carbon and pyrite sulfur, as well as the isotopic composition of sulfur, to aid our characterization of the depositional environment (26) (table S1).

There is a marked difference in the proportion of highly reactive iron in sediments depos-

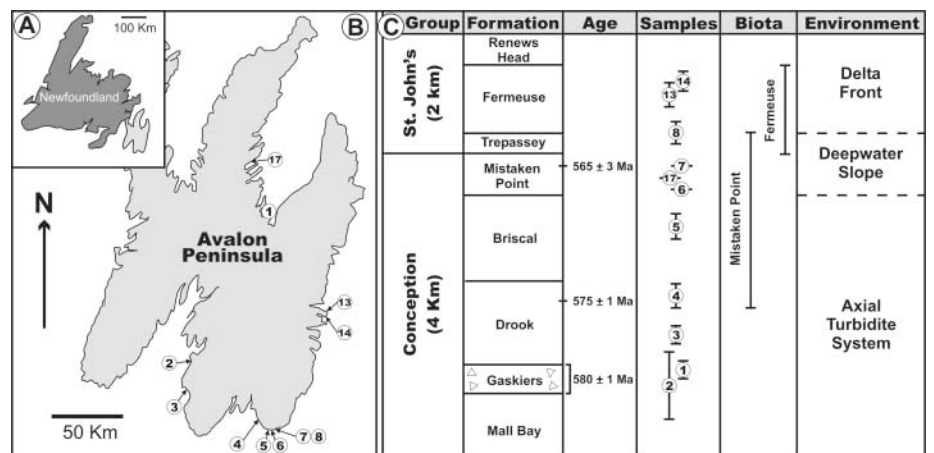


Fig. 1. Location (A and B) and stratigraphic setting (C) of geochemical samples. Location numbers are the same as in (19) (sites 1, 2, and 4 to 17) and (39) (sites 1 to 8, 13, and 14), which contain details on the precise location, access, lithostratigraphy, sedimentology, and fossil taxa for each locality. The supporting online material includes stratigraphic positioning of the samples (26). U/Pb dates are from (2, 40).

¹Nordic Center for Earth Evolution (NordCEE) and Institute of Biology, University of Southern Denmark, Campusvej 55, 5230 Odense M, Denmark. ²School of Civil Engineering and Geosciences, Newcastle University, Newcastle upon Tyne, NE1 7RU, UK. ³Department of Geological Sciences and Geological Engineering, Queen’s University, Kingston, Ontario K7L 3N6, Canada.

*To whom correspondence should be addressed. E-mail: dec@biology.sdu.dk

ited before and after the Gaskiers glaciation (Fig. 3A). In numerous instances, the Gaskiers diamictite shows FeHR/FeT ratios exceeding 0.38, indicative of anoxic deposition. This is also the case, to a lesser extent, in the upper Mall Bay Formation. In other cases, the FeHR/FeT ratio of Gaskiers and Mall Bay samples is less than 0.38 but more than both the modern and Phanerozoic average ratios (Fig. 3A). In these cases, the extraction results are somewhat equivocal, but given the numerous instances in which FeHR/FeT exceeds 0.38 and the high overall ratios of FeHR/FeT, the results suggest that the water column was anoxic during deposition of the Gaskiers diamictite and probably also the upper Mall Bay (27). There is little sulfide sulfur in these rocks, and most of the reactive iron is bound as iron oxide and iron carbonate (26). Therefore, a sulfidic water column can be ruled out (25), indicating that the water column was most likely ferruginous, containing elevated concentrations of dissolved ferrous iron (Fe^{2+}). Therefore, the deep-ocean chemistry accompanying the Gaskiers glaciation (and possibly also the Mall Bay) appears similar to the water chemistry associated with the earlier “snowball Earth” glaciations, in which banded iron formations accompanied the deposition of Sturtian-aged diamictites (about 700 Ma) (11) and Fe-enriched carbonates were deposited immediately after the Marinoan glaciation (about 630 Ma) (28), both of which are indicative of ferruginous oceanic conditions.

In sediment accumulated immediately after the Gaskiers glaciation and during a period of time representing more than 15 million years, most FeHR/FeT ratios are much lower than in

the underlying rocks and fall between the Phanerozoic and modern average for oxic sediment deposition; nearly all are less than 0.38 (Fig. 3A). These data provide evidence for a long period of stable deep-water oxic marine conditions. Overall, our data point to a pre-Drook anoxic iron-containing ocean giving way to oxic marine conditions after the Gaskiers glaciation.

For the Mall Bay through the Trepassey Formations, organic carbon concentrations are, in general, extremely low and are completely consistent with deposition in oligotrophic deep-water basinal or outer slope marine settings (29). Whereas higher organic carbon concentrations might be expected under anoxic conditions (30), our rather low concentrations in the Mall Bay and Gaskiers Formations are similar to those found (0.1 to 0.3 weight % C) in the Sturtian-aged (about 730 Ma) Rapitan Iron Formation, which also deposited from anoxic Fe-containing waters (31). The somewhat higher concentrations observed in the Fermeuse Formation are consistent with an environment closer to shore of higher sediment deposition rate such as a delta front would offer.

The isotopic composition of sulfur is quite variable but demonstrates patterns consistent with the above scenario for deep-ocean oxygenation, providing further insights into the nature of ocean chemistry. The isotopic composition of sulfide in pre-Gaskiers sediments is consistently greater than zero, indicating relatively small fractionations from seawater sulfate of around 18 ± 10 per mil (Fig. 3C) [the isotopic composition of seawater sulfate from 590 to 560 Ma is well constrained at between 22 and 28 per mil (32)]. This, combined with generally

low concentrations of organic carbon and sulfide, is consistent with low rates of sulfate reduction under sulfate-limiting concentrations. Previous modeling (33) suggests that such low fractionations should occur with submillimolar sulfate concentrations. Higher fractionations in the Gaskiers, and particularly in the Drook Formation, demonstrate a change in the sulfur cycle. Indeed, the higher post-Mall Bay fractionations are consistent with an increase in sulfate concentration, which allows the expression of higher fractionations when compared with those produced with low sulfate levels. This pattern of increased fractionations also occurs with sediments deposited in association with and immediately after the Sturtian and Marinoan glaciations (34) and is thus a general feature of Neoproterozoic glacial and postglacial deposits.

To explain these increased fractionations, we suggest that glacial melting increased the nutrient load to the ocean. This stimulated primary production and carbon burial and thus increased atmospheric oxygen levels. Increased oxygen enhanced the oxidative weathering of sulfide to sulfate on the continents, thus increasing the flux of sulfate to the ocean and marine sulfate concentrations. The presence of anoxygenic photosynthetic biomarkers in post-Sturtian and post-Marinoan deposits argues against substantial ocean oxygenation after the earlier Neoproterozoic glaciations (35, 36), but the post-Gaskiers event was sufficient to result in oxygenation of the deep ocean. A return to much lower fractionations in post-Mistaken Point sediments could reflect a return to lower marine sulfate concentrations or, perhaps more likely, a reduction in isotope fractionation as might be expected with higher rates of sediment deposition and increased rates of sulfate reduction in a delta-front environment (33).

Our evidence for deep-water oxygenation in the post-Gaskiers ocean may place some constraints on the minimum level of atmospheric oxygen at this time. We reason as follows: Organic matter produced in the surface ocean consumes oxygen during degradation as it falls through the water column. In the modern ocean, oxygen concentrations reach a minimum at depths of 500 to 1500 m (37). The magnitude of the oxygen deficit is about 40 to 100 μM in the North Atlantic and 100 to 300 μM in the North Pacific (37). If we assume that the ocean structure was similar to its structure today and that the Drook and Briscal Formations were deposited in water depths of 500 to 1500 m, then oxygen deficits would have ranged somewhere between 40 and 300 μM . If we take 40 μM as the most conservative estimate, then at least this much O_2 was dissolved in the waters supplying the deep ocean. Probably a bit more oxygen was required, given that the Ediacaran biota would have likely needed 10 to 20 μM for their respiration (38), which we add to our minimum estimate of the oxygen content of the water supplying the deep ocean. At present,

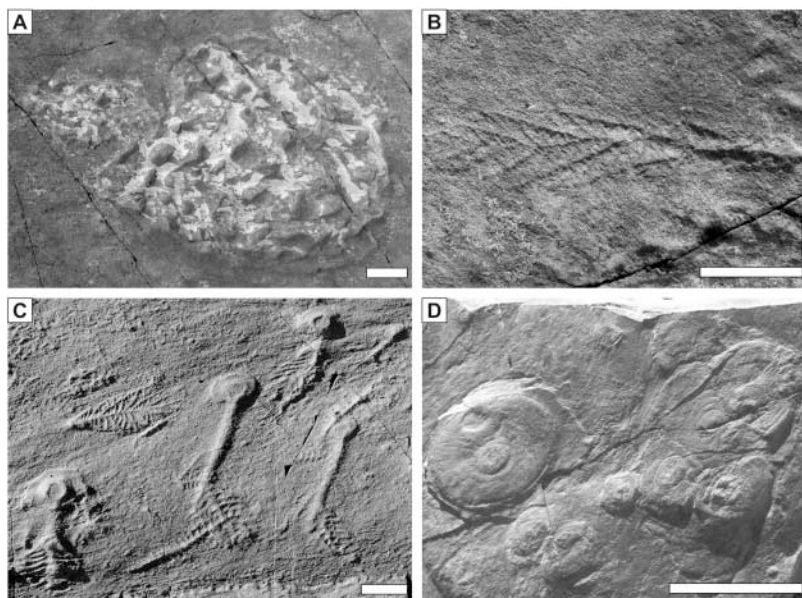


Fig. 2. Ediacaran fossils from Newfoundland. Scale bars represent 5 cm. (A and B) Low-diversity assemblage of fossils from the Drook Formation (575 Ma) at locality 4. (A) Two specimens of the discoid fossil *Ivesheadia*. (B) *Charnia* frond. (C) High-diversity Mistaken Point assemblage (565 Ma), exhibiting large fronds (*Charniodiscus*) along with frondose, bushlike, and spindle-shaped rangeomorph fossils at locality 7. (D) Fermeuse assemblage (about 560 Ma) of *Aspidella* disks at locality 13.

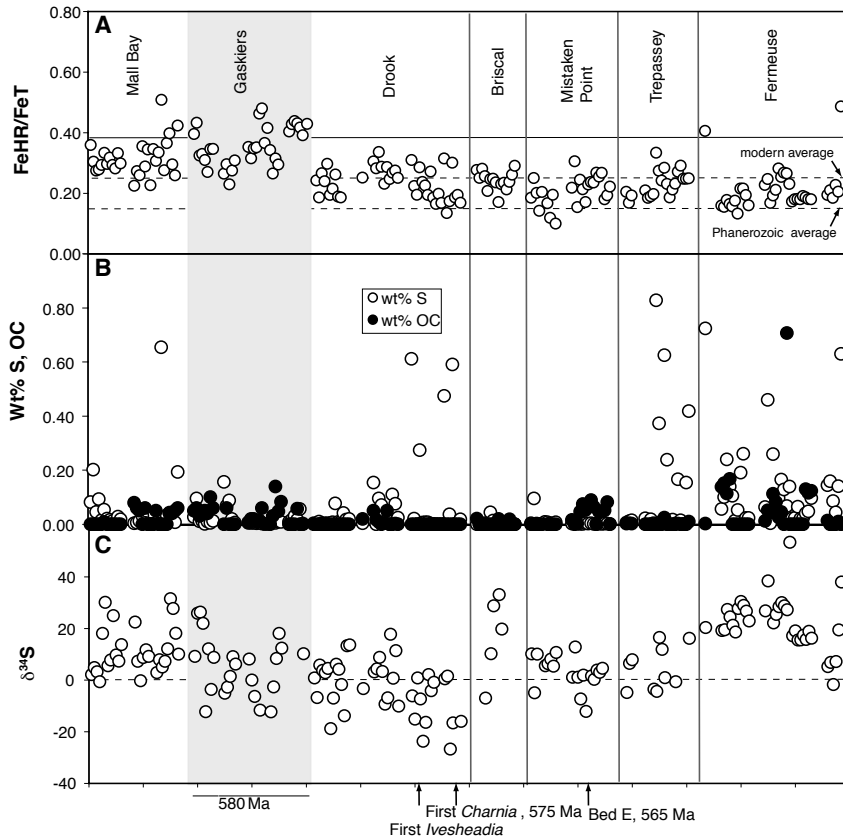


Fig. 3. The chemistry of late-Neoproterozoic sediments from the Avalon Peninsula, Newfoundland. **(A)** FeHR/FeT ratios. Solid line represents the 0.38 ratio. Dashed lines represent the ratios for average modern and average Phanerozoic sediments deposited in an oxic water column. **(B)** Concentrations of reduced sulfur (pyrite) and organic carbon (OC) by weight (wt) %. **(C)** Isotopic composition of pyrite sulfur. A dashed line at 0 per mil is shown for reference. Also indicated are key dates (as in Fig. 1) and the stratigraphic level of prominent fossil locations.

deep water is formed at high latitudes with an air-saturated O₂ concentration of 325 μM. If we require a minimum of 50 μM O₂ in this water, then we need to saturate with atmosphere containing greater than 15% of present day oxygen levels. Thus, 15% of present day oxygen levels is a minimum estimate for post-Gaskiers atmospheric O₂.

In the Avalon region, this oxygenation was stable and persisted for at least 15 million years. In our preferred scenario, this oxygenation was widespread, marking the first time that oxygen concentrations reached levels permissive for the metabolism of large multicellular heterotrophic eukaryotes. If so, evolution into this new permissive ecology could have been quite rapid (7), resulting in the emergence of the Ediacara biota within 5 million years (1, 2), and recognizable motile animals within another 20 million years (3, 4). In another scenario, the Ediacaran biota populating Avalonia evolved earlier, perhaps before the Gaskiers glaciation, and migrated to Avalon after oxygenation of the local environment. The available data support the first scenario, but further exploration of pre-Gaskiers ocean chemistry and

biology will help to elucidate the possibility of the second.

References and Notes

- G. M. Narbonne, J. G. Gehling, *Geology* **31**, 27 (2003).
- S. A. Bowring, P. Myrow, E. Landing, J. Ramenzani, *Astrobiology* **2**, 112 (2002).
- G. M. Narbonne, *Annu. Rev. Earth Planet. Sci.* **33**, 421 (2005).
- A. H. Knoll, M. R. Walter, G. M. Narbonne, N. Christie-Blick, *Lethaia* **39**, 13 (2006).
- S. Xiao, Y. Zhang, A. H. Knoll, *Nature* **391**, 553 (1998).
- D. Condon, M. Zhu, S. Bowring, W. Wang, J. Yang, *Science* **308**, 95 (2005).
- A. H. Knoll, *Life on a Young Planet: The First Three Billion Years of Evolution on Earth* (Princeton Univ. Press, Princeton, NJ, 2003).
- L. V. Berkner, L. C. Marshall, *J. Atmos. Sci.* **22**, 225 (1965).
- A. H. Knoll, *Science* **256**, 622 (1992).
- C. R. Marshall, *Annu. Rev. Earth Planet. Sci.* **34**, 355 (2006).
- P. F. Hoffman, D. P. Schrag, *Terra Nova* **14**, 129 (2002).
- G. P. Halverson, in *Neoproterozoic Geobiology and Paleobiology, Topic in Geobiology*, S. Xiao, A. J. Kaufman, Eds. (Kluwer, New York, 2005), vol. 27, pp. 231–271.

- M. E. Clapham, G. M. Narbonne, J. G. Gehling, *Paleobiology* **29**, 527 (2003).
- S. B. Misra, *Geol. Soc. Am. Bull.* **82**, 979 (1971).
- D. A. Wood, R. W. Dalrymple, G. M. Narbonne, J. G. Gehling, M. E. Clapham, *Can. J. Earth Sci.* **40**, 1375 (2003).
- S. Gardiner, R. N. Hiscott, *Can. J. Earth Sci.* **25**, 1579 (1988).
- H. Williams, A. F. King, *Geol. Surv. Can. Mem.* **389** (1979).
- C. R. Scotese, PALEOMAP Project (Arlington, TX, 2001), vol. 51.
- G. M. Narbonne, R. W. Dalrymple, M. La Flamme, J. Gehling, W. D. Boyce, *Life After Snowball: The Mistaken Point Biota and the Cambrian of Newfoundland, NAPC Field Trip Guide* (North American Paleontological Convention, Halifax, Canada, 2005).
- S. W. Poulton, D. E. Canfield, *Chem. Geol.* **214**, 209 (2005).
- D. E. Canfield, *Geochim. Cosmochim. Acta* **53**, 619 (1989).
- R. Raiswell, D. E. Canfield, *Am. J. Sci.* **298**, 219 (1998).
- S. W. Poulton, R. Raiswell, *Am. J. Sci.* **302**, 774 (2002).
- Y. Shen, D. E. Canfield, A. H. Knoll, *Am. J. Sci.* **302**, 81 (2002).
- S. W. Poulton, P. Fralich, D. E. Canfield, *Nature* **431**, 173 (2004).
- Materials and methods are available as supporting material on Science Online.
- Although FeHR/FeT ratios exceeding 0.38 are strongly indicative of sediment deposition in an anoxic water column, anoxic deposition can also yield lower ratios if the flux of clastic material is sufficient to overwhelm the water-column flux of iron. This happens, for example, in turbidite intervals in the Black Sea (22). Also, localized situations of preferential continentally derived iron oxide deposition or sediment iron remobilization can yield FeHR/FeT ratios of greater than 0.38, as is sometimes the case in inner shore environments (23). However, we are aware of no instances whereby oxic deposition in fully marine settings has resulted in FeHR/FeT ratios of greater than 0.38, and this is the case for both continental margin sediments and deep-sea sediments such as red clays (23). As further evidence of enhanced iron deposition in pre-Drook sediments, we highlight that many intervals of the Gaskiers diamictite weather blood-red in the field, in stark contrast to the greenish gray color of the Drook.
- M. T. Hurtgen, G. P. Halverson, M. A. Arthur, P. F. Hoffmann, *Earth Planet. Sci. Lett.* **245**, 551 (2006).
- E. T. Premuzic, C. M. Benkovitz, J. S. Gaffney, J. J. Walsh, *Org. Geochem.* **4**, 63 (1982).
- D. E. Canfield, *Chem. Geol.* **114**, 315 (1994).
- C. Klein, N. J. Beukes, *Econ. Geol.* **88**, 542 (1993).
- D. A. Fike, J. P. Grotzinger, L. M. Pratt, R. E. Summons, *Nature* **444**, 744 (2006).
- K. S. Habicht, M. Gade, B. Thamdrup, P. Berg, D. E. Canfield, *Science* **298**, 2372 (2002).
- P. Gorjan, J. J. Vevers, M. R. Walter, *Precambrian Res.* **100**, 151 (2000).
- A. N. Olcott, A. L. Sessions, F. A. Corsetti, A. J. Kaufman, T. Flavio de Oliveira, *Science* **310**, 471 (2005).
- A. N. Olcott, C. Li, A. L. Sessions, F. A. Corsetti, P. Peng, *Geochim. Cosmochim. Acta* **70**, A456 (2006).
- W. S. Broecker, T.-H. Peng, *Tracers in the Sea* (Lamont-Doherty Geological Observatory, Palisades, NY, 1982).
- B. Runnegar, *Global Planet. Change* **5**, 97 (1991).
- G. M. Narbonne, R. W. Dalrymple, J. G. Gehling, *Neoproterozoic Fossils and Environments of the Avalon Peninsula, Newfoundland*. (Geological Association of Canada, Guidebook B5, St. John's, Canada, 2001).
- A. P. Benus, in *Trace Fossils, Small Shelly Fossils and the Precambrian-Cambrian Boundary*, E. Landing, G. M. Narbonne, P. Myrow, Eds. (New York State Museum and Geological Survey Bulletin, Albany, NY, 1988), vol. 463, pp. 8–9.

41. Our work was funded by the Danish National Research Foundation (Danmarks Grundforskningsfond), a Natural Environment Engineering Research Council Research Fellowship (S.W.P.), the Natural Sciences and Engineering Research Council of Canada, and a Queen's Research Chair. We thank the Parks and Natural Areas, and Government of Newfoundland and

Labrador for scientific permits; the Portugal Cove South Interpretation Centre for help and support; and M. Laflamme and L. Salling for help.

Supporting Online Material
www.sciencemag.org/cgi/content/full/1135013/DC1
Materials and Methods

Table S1
References

12 September 2006; accepted 27 October 2006
Published online 7 December 2006;
10.1126/science.1135013
Include this information when citing this paper.

Climate Change Affects Marine Fishes Through the Oxygen Limitation of Thermal Tolerance

Hans O. Pörtner* and Rainer Knust

A cause-and-effect understanding of climate influences on ecosystems requires evaluation of thermal limits of member species and of their ability to cope with changing temperatures. Laboratory data available for marine fish and invertebrates from various climatic regions led to the hypothesis that, as a unifying principle, a mismatch between the demand for oxygen and the capacity of oxygen supply to tissues is the first mechanism to restrict whole-animal tolerance to thermal extremes. We show in the eelpout, *Zoarces viviparus*, a bioindicator fish species for environmental monitoring from North and Baltic Seas (Helcom), that thermally limited oxygen delivery closely matches environmental temperatures beyond which growth performance and abundance decrease. Decrements in aerobic performance in warming seas will thus be the first process to cause extinction or relocation to cooler waters.

Climate change is projected to affect individual organisms, the size and structure of their populations, the species composition of communities, and the structure and functioning of ecosystems. Effects include poleward or high-altitude shifts in the distribution of ectothermic animals (1). A comprehensive mechanistic understanding has so far been lacking (2) but is needed for prediction of climate change effects. Physiological studies can address the mechanisms and reasons for the thermal sensitivity of organisms and their life stages.

In aquatic animals, a decrease in the capacity to perform aerobically (a drop in aerobic scope) characterizes the onset of thermal limitation at both ends of the thermal envelope [pejus thresholds T_p , fig. S1 (3–6)]. The reduction in aerobic scope is caused by limited capacity of circulatory and ventilatory systems to match oxygen demand. Such a constraint affects all higher functions (muscular activity, behavior, growth, and reproduction) and might thereby shape the long-term fate of species. Aerobic scope becomes minimal beyond low or high critical temperatures (T_c). Survival is then passive and time-limited, supported by anaerobic metabolism and protection of proteins and membranes by heat shock proteins and antioxidative defense. Thermal tolerance is hierarchical, with narrowing windows from molecular to cellular to systemic levels (6).

Temperate species are able to acclimatize and shift the thermal window through changes in mitochondrial densities as well as other molecular to systemic adjustments of functional capacities (3, 6–10) (fig. S1). Limits to acclimatization are set by trade-offs at various structural and functional levels that constrain the width of the thermal window, for example, through the trend to minimize energy turnover in relation to climate variability (9, 10).

We investigated thermal limitation of the common eelpout, *Zoarces viviparus*, in its southernmost distribution area, the German Wadden Sea (part of the southern North Sea) during summer and thereby tested the ecological relevance of the concept of oxygen- and capacity-limited thermal tolerance (fig. S1). During the past 40 years, water temperatures in the German Bight increased by 1.13°C (at Helgoland Roads). Cold winters with sea surface temperatures (SSTs) around -1°C had occurred about once every 10 years up to 1944 but were experienced only once since 1960 (11). Models predict further SST increments for the next 90 to 100 years, by about 1.6° to 3.0°C in the northern and even by 3.0° to 3.9°C in the shallower southern North Sea (12), accompanied by rising sea levels (13 to 68 cm by 2050) and an increasing frequency of storm events (13).

Comparison of existing data sets indicates that field observations can be explained by the eelpout's physiological responses to warming (Fig. 1). The relative abundance of the non-migratory eelpout decreases upon warming (5-year running means, data from 1954 to 1989, Fig. 1A) (14, 15), reflecting a higher mortality

in hot summers. Reduced field abundance coincides with reduced growth of laboratory-maintained, temperature-acclimated individuals (Fig. 1B). Individual growth is a key parameter shaping population growth and depends on aerobic scope. Lopsided growth curves result from the exponential rise in net aerobic scope upon warming, which is counterbalanced by the concomitant exponential rise in baseline metabolic costs (Fig. 1). Both abundance and growth begin to fall beyond upper pejus temperatures (T_p) (Fig. 1, C to E), reflecting the species-specific limits of acclimation capacity.

Pejus temperatures were derived from limitations in circulatory capacity (Fig. 1C), which occur before ventilatory limitations in eelpout (*Z. viviparus* and *Pachycara brachycephalum*) and Atlantic cod (*Gadus morhua*) (4, 16–18). The loss of aerobic scope can also be derived from the shift of critical oxygen tensions, P_c , or concentrations, $[O_2]_c$. P_c or $[O_2]_c$ indicate oxygen limitation to the passive organism in hypoxia and the onset of anaerobic metabolism. Upon warming, $[O_2]_c$ reaches air saturation at T_c , where anaerobic metabolism begins in animals exposed to fully aerated waters (Fig. 1D). Aerobic scope thus begins to fall when $[O_2]_c$ starts to rise beyond T_p (Fig. 1E). Warming exacerbates oxygen limitations not only by the forced rise in oxygen demand, but also by reducing oxygen solubility (Fig. 1E).

The analysis of ecological responses in relation to 5-year running means of summer maxima, albeit improving the signal-to-noise ratio, may not precisely quantify temperatures and mechanisms effective in the field. Analysis of individual summers in long-term data series (19) should provide more detailed insight into cause-and-effect relationships (Figs. 2 and 3). The limited data set indicates that extreme temperatures of previous summers cause reduced abundance. Sampling took place in July, so the effects of the hottest season only become visible in the next year. Thermal limitation of aerobic scope may also translate into the next year by reducing the degree of successful fertilization and reproduction.

Thermal sensitivity is likely to be enhanced at large body sizes. In contrast to eelpout from the Baltic or from colder regions like the Russian White Sea, eelpout of the Wadden Sea only reach a maximum body length of about 23 cm at a maximum age of 3 to 4 years (20). A preliminary analysis of seasonal changes in size frequency distribution (fig. S2) shows that older specimens (larger than 20 cm) have low overall abundance and thus high mortality rates. High

Alfred Wegener Institute for Polar and Marine Research, Animal Ecophysiology, Postfach 12 01 61, 27515 Bremerhaven, Germany.

*To whom correspondence should be addressed. E-mail: hpoertner@awi-bremerhaven.de