

# Increased productivity in the subantarctic ocean during Heinrich events

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Massive iceberg discharges from the Northern Hemisphere ice sheets, 'Heinrich events', coincided with the coldest periods of the last ice age<sup>1</sup>. There is widespread evidence for Heinrich events and their profound impact on the climate and circulation of the North Atlantic Ocean, but their influence beyond that region remains uncertain<sup>1</sup>. Here we use a combination of molecular fingerprints of algal productivity and radioisotope tracers of sedimentation to document eight periods of increased productivity in the subpolar Southern Ocean during the past 70,000 years that occurred within 1,000–2,000 years of a Northern Hemisphere Heinrich event. We discuss possible causes for such a link, including increased supply of iron from upwelling and increased stratification during the growing season, which imply an alteration of the global ocean circulation during Heinrich events. The mechanisms linking North Atlantic iceberg discharges with subantarctic productivity remain unclear at this point. We suggest that understanding how the Southern Ocean was altered during these extreme climate perturbations is critical to understanding the role of the ocean in climate change.

Ice-age cycles are paced by periodic changes in Earth's orbital geometry that modulate the amount of solar radiation reaching Northern Hemisphere ice sheets<sup>2</sup>. For reasons that remain unclear, the climate system is susceptible to sudden shifts during glacial intervals, when continental ice sheets are large, sea level and atmospheric greenhouse gas concentrations are low, and sea ice in both hemispheres is extensive. Instability arising from ice-sheet dynamics, stochastic resonance in the climate system or some yet-to-be-identified forcing mechanism caused massive surges of icebergs from Northern Hemisphere ice sheets to the North Atlantic every ~5–10 kyr during glacial intervals of the Pleistocene epoch that coincided with the harshest conditions of the glacial period in Europe<sup>1</sup>. Large debris fields spanning the North Atlantic sea floor are the remnants of so-called Heinrich events. Gravel in marine sediments thousands of kilometres from land must have been delivered by icebergs whose debris-laden undersides once scoured the continents.

Eight such episodes (Heinrich events and the Younger Dryas event) occurred between 10 and 70 kyr ago<sup>1,3,4</sup>. Each resulted in freshening and cooling of surface waters of the North Atlantic<sup>3,1</sup>. Synchronous changes in the chemistry or biology of sediment cores from the southwest equatorial Atlantic<sup>5</sup>, the southeast subtropical Atlantic<sup>6</sup> and the Arabian Sea, and in a stalagmite from southeastern China, argue for a widespread impact of Heinrich events on climate<sup>1</sup>.

Although some data<sup>1,7</sup> and models<sup>8,9</sup> suggest that flooding the North Atlantic with icebergs arrested production of North Atlantic Deep Water, thus causing a decrease in the poleward flux of heat to Europe, other data<sup>10</sup> and models<sup>11</sup> suggest otherwise. That current models and data do not agree on the nature, sign or magnitude of change in North Atlantic thermohaline circulation caused by the most extreme climate events of the past 100,000 years

illustrates the need for further study of the coupling between ocean circulation and abrupt climate change.

The Southern Ocean plays a central role in the global thermohaline circulation. Most deep-water production occurs there, as does about half of the return (upwelling) flux of deep water to the surface<sup>12</sup>. Although prominent warm episodes in Antarctica coincided with six of the eight Heinrich events (including the Younger Dryas)<sup>13</sup>, almost nothing is known about this southern branch of the global thermohaline circulation during Heinrich events. Here we present the first evidence of major perturbations in the Southern Ocean during Heinrich events, by demonstrating that algal productivity soared in subantarctic waters of the southwest Pacific and southeast Atlantic oceans at those times.

Algal productivity in the southwest Pacific east of New Zealand was inferred from the sedimentary concentration of alkenones, C<sub>37</sub> methyl ketones unique to coccolithophorid algae, and brassicasterol (24-methylcholesta-5,22E-dien-3 $\beta$ -ol), a marker for diatoms<sup>14</sup>. Alkenones were measured every 2 cm in the upper 10.39 m, and brassicasterol and *n*-octacosanol were measured every 2–4 cm between 4.74 and 10.01 m, of core MD97-2120, retrieved from the Chatham rise, east of the South Island of New Zealand, at 45° 32.06' S, 174° 55.85' E, in 1,210 m of water. The site underlies subantarctic water and has probably remained south of the Subtropical Convergence as a result of bathymetric control provided by the Chatham rise of the position of the Subtropical Front<sup>15</sup>. A chronology for the core was developed by Pahnke *et al.*<sup>16</sup> from ten radiocarbon dates between 0 and 36 kyr ago, the <sup>14</sup>C-dated Kawakawa tephra layer at 26.2 kyr ago, and by graphical correlation of a benthic foraminiferal oxygen isotope record in core MD97-2120 with a reference record tied to the Greenland GISP2 ice-core chronology. Age control points are shown at the top of Fig. 1.

Alkenone and brassicasterol concentrations exhibit distinct concentration maxima coinciding with each Heinrich event (or the Younger Dryas) within the uncertainty of the age model (Fig. 1a). Uncertainty in the age of the biomarker maxima—especially the most prominent events 65–35 kyr ago that are too old to be dated by radiocarbon—together with the uncertainties in the actual ages of the Heinrich events, makes it impossible to determine whether the biomarker maxima lead, lag or are coincident with Heinrich events. Nevertheless, even with dating uncertainties of several thousand years before 35 kyr ago, the number and timing of subantarctic biomarker maxima are remarkably similar to the pattern of Heinrich events. Furthermore, there are about half as many biomarker peaks as there are interstadial (Dansgaard-Oeschger) events in Greenland ice during the studied interval, making a causal relationship with D–O events unlikely. We thus interpret the similar patterns of biomarker maxima and Heinrich events to indicate a mechanistic relationship between them.

Increased concentrations of algal biomarkers in subantarctic sediments near the time of Heinrich events were not limited to the Chatham rise. Alkenone concentration maxima occurred with near synchrony half way around the globe in sediments of the Cape basin, southeast Atlantic Ocean (core TN057-21-PC2, from 41° 08' S, 7° 49' E and 4,981 m water depth), during the period 65–35 kyr ago, when Heinrich events H4–H6 occurred (Fig. 1d). The similar number, timing and magnitude of lipid biomarker concentration changes at the two sites 65–35 kyr ago (Fig. 1a,d) suggests that the events may have had a common cause.

Understanding what caused the biomarker maxima will provide important clues about conditions in the Southern Ocean during Heinrich events. Three factors influence algal biomarker concentrations in sediments: (1) their production rate in overlying surface water, (2) their preservation rate in the water column and sediments, and (3) their dilution by other sedimentary components.

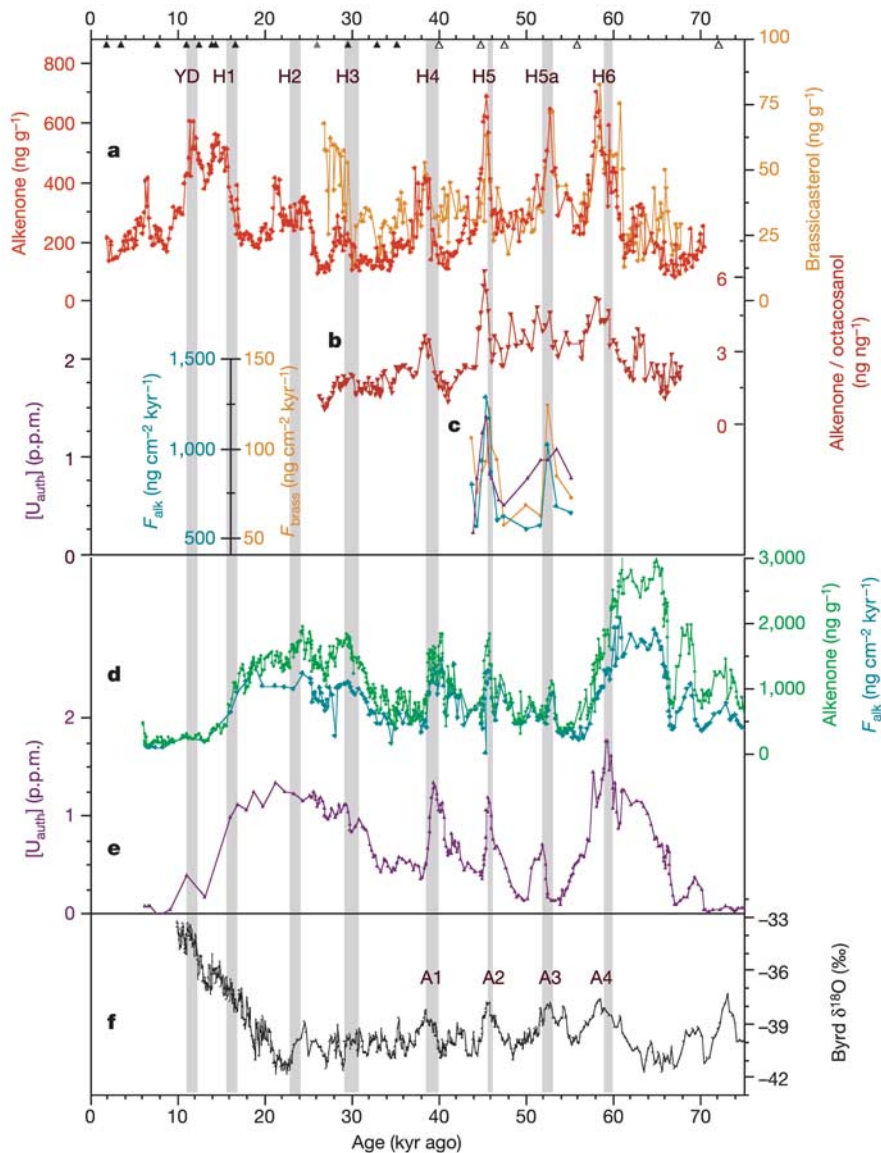
The influence of changing preservation rates was evaluated first by measuring the concentration of the terrestrial plant biomarker, *n*-octacosanol (C<sub>28</sub>-*n*-alcohol), and comparing its variation in

MD97-2120 sediment to that of alkenones (Fig. 1b). A maximum in the ratio of the marine algal lipid to the terrestrial plant lipid occurred in association with each alkenone maximum 65–27 kyr ago, implying that diagenetic reactions, which are expected to influence the two lipids similarly, were not the primary cause of the alkenone concentration maxima.

A second argument against changing preservation rates being the main driver of alkenone concentration changes comes from the hydrography at the two sites where water depth, sediment accumulation rate and bottom-water chemistry differ substantially.

At depths of 1,210 m, the Pacific site lies within oxygen-rich Antarctic Intermediate Water. At depths of 4,981 m, the Atlantic site lies within oxygen-depleted Circumpolar Deep Water. It is difficult to imagine a mechanism for improving alkenone preservation at both sites simultaneously by changing ocean circulation and related changes in the concentration of dissolved oxygen in waters overlying the core sites.

The influence of dilution by other sedimentary components on algal lipid concentrations was evaluated by computing  $^{230}\text{Th}$ -normalized biomarker fluxes<sup>17,18</sup>. A maximum of  $^{230}\text{Th}$ -normalized



**Figure 1** Subantarctic productivity changes during Heinrich events. **a**, Alkenone (red) and brassicasterol (orange) concentrations in Chatham rise core MD97-2120. Covariation of these biomarkers for coccolithophorids and diatoms, respectively, indicates that algal productivity increased during Heinrich events. **b**, Ratio of alkenones to *n*-octacosanol in core MD97-2120. An excess of algal lipids (alkenones) relative to terrestrial plant lipids (*n*-octacosanol) in H3–H6 implies that lipid preservation was not the primary cause of the algal biomarker concentration increases. **c**,  $^{230}\text{Th}$ -normalized flux of alkenones ( $F_{\text{alk}}$ ; blue) and brassicasterol ( $F_{\text{brass}}$ ; orange), and the concentration of  $U_{\text{auth}}$  (purple) in Chatham rise core MD97-2120. **d**, Alkenone concentration (green) and  $^{230}\text{Th}$ -normalized alkenone flux (blue) in Cape basin (southeast Atlantic) core TN057-21-PC2 (refs 17, 18). **e**, The concentration of authigenic uranium in Cape basin core TN057-21-PC2 (refs 17, 18). **f**,  $\delta^{18}\text{O}$  variations, a proxy for air temperature, in the Byrd, Antarctica, ice core<sup>13</sup>. Prominent Antarctic temperature maxima A1–A4 (ref. 13) coincide with subantarctic

productivity maxima and H4–H6. Age control points for MD97-2120 are shown at the top of panel **a**. Black triangles correspond to  $^{14}\text{C}$  dates on the planktonic foraminifera *Globigerina bulloides*, the grey triangle to the Kawakawa tephra, and open triangles to oxygen isotopic tie points to core MD95-2042 in the North Atlantic<sup>16</sup>. Age control for TN057-21-PC2 was provided by graphical comparison of magnetic intensity variations in the sediment with cosmogenic isotope production changes in Greenland ice<sup>30</sup>. Calendar ages of the Heinrich events and the Younger Dryas (YD) are indicated by vertical grey bars, the thickness of which span their duration and age range from recent studies<sup>3,4</sup>. Concentrations of alkenones, *n*-octacosanol and brassicasterol were determined by gas chromatography with flame-ionization detection and co-injected standards, following identification by gas chromatography-mass spectrometry<sup>18</sup>. Concentrations of U and Th isotopes were measured by isotope dilution inductively coupled plasma mass spectrometry<sup>18</sup>.

alkenone flux occurred at every maximum of alkenone concentration in sediments of the Cape basin (Fig. 1d) and at the two alkenone maxima in which we measured U and Th in sediments of the Chatham rise (Fig. 1c). Thus dilution by other sedimentary components did not cause the algal lipid concentration changes we observe. For this reason, and those discussed below, the most likely cause of increased alkenone concentrations in sediments of the Chatham rise and the Cape basin during Heinrich events was increased algal productivity.

Covariation of brassicasterol concentrations with alkenone concentrations in Chatham rise sediment 65–35 kyr ago (Fig. 1a) implies that increases in algal productivity were not limited to coccolithophorids, but probably included diatoms as well. Brassicasterol is often used as a molecular indicator for the presence of diatoms, although it is also produced by some prymnesiophytes<sup>14</sup>. High <sup>230</sup>Th-normalized fluxes of brassicasterol 46 and 52 kyr ago (Fig. 1c) supports the notion of higher algal productivity in subantarctic waters at those times.

Additional support for higher algal production comes from the concentration of authigenic uranium ( $U_{\text{auth}}$ ) in Cape basin (Fig. 1e) and Chatham rise (Fig. 1c) sediment, which increased in concert with alkenone concentrations during at least six of eight Heinrich events (Younger Dryas and H3–H6) in the Cape basin and the two Heinrich events (H5 and H5a) analysed at the Chatham rise. Both organic flux and bottom-water oxygen concentration influence  $U_{\text{auth}}$  concentrations in sediments of the Southern Ocean<sup>19</sup>. Although the two parameters are not independent—that is, remineralization of organic matter uses oxygen—previous studies have attributed increased  $U_{\text{auth}}$  in Southern Ocean sediments to increased organic flux<sup>19</sup>. Furthermore, as noted for algal lipid preservation, reduced ventilation and resultant depletion of bottom-water oxygen in response to altered ocean circulation would not be expected to occur concurrently in mid-depths (1,210 m) of the southwest Pacific and abyssal depths (4,981 m) of the southeast Atlantic.  $U_{\text{auth}}$  did not increase appreciably during H1 or H2 in the Cape basin record, perhaps because  $U_{\text{auth}}$  was limited by uranium diffusion from sea water when export production was high during marine isotope stage 2 (MIS2).

Lastly, we note that the <sup>230</sup>Th-normalized mass flux of sediment to the Chatham rise was nearly constant ( $2.2 \pm 0.4 \text{ g cm}^{-2} \text{ kyr}^{-1}$ ,  $n = 13$ ) 43–57 kyr ago, implying that changes in sediment delivery to the site were not associated with the biomarker changes. By eliminating other possible causes, we conclude that an increase in the export flux of organic matter from subantarctic surface waters south of the Chatham rise and in the Cape basin occurred near the time of Heinrich events in the Northern Hemisphere.

Evaluating the factors that may have caused increased biological productivity puts constraints on conditions in the Southern Ocean during Heinrich events. Iron limits algal productivity in the Southern Ocean<sup>20</sup>. Iron-addition experiments and molecular markers for iron stress in phytoplankton south of the Chatham rise confirm that Fe limits algal growth equatorward to the Subtropical Front<sup>21</sup>. If coccolithophorid and diatom productivity increased simultaneously, as implied by the alkenone and brassicasterol data (Fig. 1a), and the export flux of organic matter increased, as implied by the authigenic uranium activity and the algal lipid fluxes (Fig. 1a–c), increased iron availability may have been the cause.

Unlike most of the ocean, in the Southern Ocean iron comes primarily from upwelling of deep water rather than from direct input of continental dust<sup>22,23</sup>. Whether this was the case during glacial times is unknown, but dust proxies in Antarctic ice cores indicate diminished dust deposition during the productivity events<sup>24</sup>. If dust-borne iron fluxes to the Southern Ocean did not increase during Heinrich events, the most likely source of additional iron to subantarctic surface water was an increased upwelling flux of iron-enriched deep water.

Phytoplankton growth in the Southern Ocean is also limited by

light, at least at certain times and in certain places<sup>25,26</sup>. Factors leading to increased exposure to light by phytoplankton, such as increased stratification of surface waters<sup>27</sup>, may also have contributed to increased productivity during Heinrich events. A compelling association exists between warm episodes A1–A4 in Antarctica<sup>13</sup> and the most prominent four productivity maxima (at 58.5, 53, 46, and 38.5 kyr ago) (Fig. 1f). Greater stratification of Southern Ocean surface water may have occurred at these times, either by radiative heating, decreased wind stress (owing to the thermal wind relationship and supported by wind proxies in Antarctic ice<sup>24</sup>), or by increased freshwater supply associated with melting of the Antarctic Ice Sheet<sup>28</sup>.

The largest increases in subantarctic productivity occurred 35–65 kyr ago during H4–H6 (Fig. 1a–e) and coincided with the most prominent CO<sub>2</sub> (ref. 29) and Antarctic temperature<sup>13</sup> (Fig. 1f) maxima of the last glacial period. Why did productivity, CO<sub>2</sub> and temperature rise only modestly, if at all, during the Younger Dryas and H1–H3? One possibility is that conditions in the North Atlantic during Heinrich events were more similar to those during the height of the Last Glacial Maximum period 12–27 kyr ago (MIS2)—that is, colder, windier, diminished North Atlantic Deep Water production—than during the preceding warmer period 27–58 kyr ago (MIS3). Heinrich events that occurred during MIS3 may have therefore caused a larger (relative) perturbation to the existing ocean and atmospheric circulation than those that occurred during MIS2.

Existing data do not permit an unequivocal distinction between upwelling and stratification as the principal factor responsible for increased subantarctic productivity associated with Heinrich events. Neither are the two factors mutually exclusive, as increased summer stratification may have coincided with times of increased upwelling. The value of these new records is that they provide the first evidence for prominent alterations of the Southern Ocean during Heinrich events. As such, they define targets for future research. For example, future studies should explore evidence for increased abundance of icebergs and reduced surface salinity to test the possibility that pulses of ice (freshwater) from Antarctica increased stratification at times of increased productivity.

Understanding how the Southern Ocean was altered during extreme climate perturbations is critical to understanding the role of ocean circulation in climate change. A glaring lack of palaeoclimate data hinders this effort. The observation of subantarctic productivity maxima that correspond closely with Heinrich events (in number and timing) and with Antarctic warm events (in relative magnitude and timing) but poorly with D–O events, gets us a step closer towards understanding the mechanisms of abrupt climate change. □

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- Hemming, S. R. Heinrich events: massive late Pleistocene detritus layers of the North Atlantic and their global climate imprint. *Rev. Geophys.* **42**, doi:10.1029/2003RG000128 (2004).
- Hays, J. D., Imbrie, J. & Shackleton, N. J. Variations in the Earth's orbit: pacemaker of the ice ages. *Science* **194**, 1121–1132 (1976).
- van Kreveld, S. *et al.* Potential links between surging ice sheets, circulation changes, and the Dansgaard–Oeschger cycles in the Irminger Sea, 60–18 kyr. *Paleoceanography* **15**, 425–442 (2000).
- Rashid, H., Hesse, R. & Piper, D. J. W. Evidence for an additional Heinrich event between H5 and H6. *Paleoceanography* **18**, 1077, doi:10.1029/2003PA000913 (2003).
- Arz, H. W., Pätzold, J. & Wefer, G. Correlated millennial-scale changes in surface hydrography and terrigenous sediment yield inferred from last-glacial marine deposits off northeastern Brazil. *Quat. Res.* **50**, 157–166 (1998).
- Little, M. G. *et al.* Trade wind forcing of upwelling, seasonality, and Heinrich events as a response to sub-Milankovitch climate variability. *Paleoceanography* **12**, 568–576 (1997).
- McManus, J. F., Francois, R., Gherardi, J.-M., Keigwin, L. D. & Brown-Leger, S. Collapse and rapid resumption of Atlantic meridional circulation linked to deglacial climate changes. *Nature* **428**, 834–837 (2004).
- Rind, D. *et al.* Effects of meltwater in the GISS coupled atmosphere–ocean model 2. A bipolar seesaw in Atlantic Deep Water production. *J. Geophys. Res.* **106**, 27355–27365 (2001).
- Rahmstorf, S. Ocean circulation and climate during the past 120,000 years. *Nature* **419**, 207–214 (2002).
- Piotrowski, A. M., Goldstein, S. L., Hemming, S. R. & Fairbanks, R. G. Intensification and variability of ocean thermohaline circulation through the last deglaciation. *Earth Planet. Sci. Lett.* **225**, 205–220 (2004).
- Nilsson, J., Brostrom, G. & Walin, G. The thermohaline circulation and vertical mixing: Does weaker



density stratification give stronger overturning? *J. Phys. Oceanogr.* **33**, 2781–2795 (2003).

12. Webb, D. J. & Sugimotohara, N. Vertical mixing in the ocean. *Nature* **409**, 37 (2001).

13. Blunier, T. & Brook, E. J. Timing of millennial-scale climate change in Antarctica and Greenland during the last glacial period. *Science* **291**, 109–112 (2001).

14. Volkman, J. K. *et al.* Microalgal biomarkers: A review of recent research developments. *Org. Geochem.* **29**, 1163–1179 (1998).

15. Weaver, P. P. E., Carter, L. & Neil, H. L. Response of surface water masses and circulation to late Quaternary climate change east of New Zealand. *Paleoceanography* **13**, 70–83 (1998).

16. Pahnke, K., Zahn, R., Elderfield, H. & Schulz, M. 340,000-year centennial-scale marine record of Southern Hemisphere climatic oscillation. *Science* **301**, 948–952 (2003).

17. Sachs, J. P., Anderson, R. F. & Lehman, S. J. Glacial surface temperatures of the southeast Atlantic Ocean. *Science* **293**, 2077–2079 (2001).

18. Sachs, J. P. & Anderson, R. F. Fidelity of alkenone paleotemperature reconstructions in southern Cape basin sediment drifts. *Paleoceanography* **18**, 1082, doi:10.1029/2002PA000862 (2003).

19. Chase, Z., Anderson, R. F. & Fleisher, M. Q. Evidence from authigenic uranium for increased productivity of the glacial Subantarctic Ocean. *Paleoceanography* **16**, 468–478 (2001).

20. Martin, J. H. Glacial–interglacial CO<sub>2</sub> change: the iron hypothesis. *Paleoceanography* **5**, 1–13 (1990).

21. Boyd, P., LaRoche, J., Gall, M., Frew, R. & McKay, R. M. L. Role of iron, light, and silicate in controlling algal biomass in subantarctic waters SE of New Zealand. *J. Geophys. Res.* **104**, 13395–13408 (1999).

22. Watson, A. J. & Lefevre, N. The sensitivity of atmospheric CO<sub>2</sub> concentrations to input of iron to the oceans. *Tellus* **51B**, 453–460 (1999).

23. Lefevre, N. & Watson, A. J. Modeling the geochemical cycle of iron in the oceans and its impact on atmospheric CO<sub>2</sub> concentrations. *Glob. Biogeochem. Cycles* **13**, 727–736 (1999).

24. Steig, E. J. *et al.* Wisconsinan and Holocene climate history from an ice core at Taylor Dome, western Ross Embayment, Antarctica. *Geogr. Ann.* **82A**, 213–235 (2000).

25. Abbott, M. R., Richman, J. G., Letellier, R. M. & Bartlett, J. S. The spring bloom in the Antarctic Polar Frontal Zone as observed from a mesoscale array of bio-optical sensors. *Deep-Sea Res.* **47**, 3285–3314 (2000).

26. Mitchell, B. G., Brody, E. A., Holm-Hansen, O., McClain, C. & Bishop, J. Light limitation of phytoplankton biomass and macronutrient utilization in the Southern Ocean. *Limnol. Oceanogr.* **36**, 1662–1677 (1991).

27. Smith, W. O. Jr & Nelson, D. M. Phytoplankton bloom produced by a receding ice edge in the Ross Sea: spatial coherence with the density field. *Science* **227**, 163–167 (1985).

28. Rohling, E. J., Marsh, R., Wells, N. C., Siddall, M. & Edwards, N. R. Similar meltwater contributions to glacial sea level changes from Antarctic and northern ice sheets. *Nature* **430**, 1016–1021 (2004).

29. Indermühle, A., Monnin, E., Stauffer, B., Stocker, T. F. & Wahlen, M. Atmospheric CO<sub>2</sub> concentration from 60 to 20 kyr BP from the Taylor Dome ice core, Antarctica. *Geophys. Res. Lett.* **27**, 735–738 (2000).

30. Stoner, J. S., Channell, J. E. T., Hillaire-Marcel, C. & Kissel, C. Geomagnetic paleointensity and environmental record from Labrador Sea core MD95–2024: global marine sediment and ice core chronostratigraphy for the last 110 kyr. *Earth Planet. Sci. Lett.* **183**, 161–177 (2000).

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## Electronic tagging and population structure of Atlantic bluefin tuna

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Electronic tags that archive or transmit stored data to satellites have advanced the mapping of habitats used by highly migratory fish in pelagic ecosystems<sup>1–6</sup>. Here we report on the electronic tagging of 772 Atlantic bluefin tuna in the western Atlantic Ocean in an effort to identify population structure. Reporting electronic

tags provided accurate location data<sup>7–9</sup> that show the extensive migrations of individual fish ( $n = 330$ ). Geoposition data delineate two populations, one using spawning grounds in the Gulf of Mexico and another from the Mediterranean Sea. Transatlantic movements of western-tagged bluefin tuna reveal site fidelity to known spawning areas in the Mediterranean Sea. Bluefin tuna that occupy western spawning grounds move to central and eastern Atlantic foraging grounds. Our results are consistent with two populations of bluefin tuna with distinct spawning areas that overlap on North Atlantic foraging grounds. Electronic tagging locations, when combined with US pelagic longline observer and logbook catch data, identify hot spots for spawning bluefin tuna in the northern slope waters of the Gulf of Mexico. Restrictions on the time and area where longlining occurs would reduce incidental catch mortalities on western spawning grounds.

Giant bluefin tuna are the largest members of the family Scombridae, attaining body sizes of more than 650 kg (refs 10, 11). They are unique among teleosts for their endothermic capacity and cardiovascular physiology<sup>12,13</sup>. These traits underlie their capacity to exploit environments ranging from subarctic feeding grounds to subtropical spawning areas. Top pelagic predators such as bluefin tuna are in precipitous decline globally because of overexploitation<sup>14</sup>. The International Commission for the Conservation of Atlantic Tunas (ICCAT) manages Atlantic bluefin tuna as distinct western and eastern stocks separated by a management boundary at the 45° W meridian<sup>10,11</sup>. The spawning stock biomass of western Atlantic bluefin tuna has decreased by 80% or more since 1970 (refs 10, 11). A 20-year rebuilding plan was enacted in the early 1980s in the western Atlantic<sup>10</sup>. The most recent assessment indicates that the western stock continues to decline<sup>11</sup>, yet mortality throughout the North Atlantic remains high. Key questions remain on the biology of this species. Establishing the location and timing of reproduction, the mean age of maturity, spawning site fidelity, the ontogeny of movement patterns and the influence of climate variability on movements will improve stock assessments and subsequent management<sup>15</sup>. Here we report the spatio-temporal distributions of Atlantic bluefin tuna determined with electronic tags, discriminate two potential spawning populations, and record spawning site fidelity to the Mediterranean Sea.

We deployed 499 implantable archival tags and 273 pop-up satellite (PAT) tags on bluefin tuna in the western Atlantic (Supplementary Information)<sup>2,3,6</sup>. To date, 86 archival-tagged bluefin tuna have been recaptured; 54 in the west Atlantic, 9 in the east Atlantic and 23 in the Mediterranean Sea. Twelve PAT-tagged fish were recaptured and 237 PAT tags transmitted data to Argos satellites after 2 to 251 days after tagging (Table 1). Individual tracks of 2 to 1,623 days have been obtained.

Our database comprises 13,372 positions obtained from 330 bluefin tuna that carried electronic tags from 1996 to 2004 (Fig. 1, Table 1). Geoposition data include the following: Doppler-based Argos endpoint positions calculated for PAT tags ( $n = 237$ )<sup>9</sup>; geolocation estimates for archival ( $n = 5,171$ ) and PAT tags ( $n = 7,536$ ), using light level and sea surface temperature (SST) to estimate longitude and latitude, respectively<sup>9</sup>; Global Positioning System deployment locations for recovered archival and reporting PAT tags ( $n = 330$ ); and recapture locations from recovered archival and PAT tags ( $n = 98$ ). The distribution of these positions across the North Atlantic Ocean indicates that the western and eastern management units are strongly linked with overlapping ranges.

The electronic tagging data reveal two populations of Atlantic bluefin tuna that overlap on North Atlantic Ocean foraging grounds and sort to independent spawning areas located primarily in the Gulf of Mexico (GOM) and Mediterranean Sea (Fig. 1). A bluefin tuna was assigned to the western Atlantic spawning unit if it visited a known western Atlantic ICCAT spawning area (GOM, Bahamas or Florida Straits) for more than 7 days in winter or spring<sup>10,11,16–18</sup> and