21. Double polished specimens, 60 to 80 μm thick, were examined using polarized light, phase contrast, Nomarski interference contrast, and SEM. For the latter, specimens were polished with 0.05-μm alumina powder, and subsequently etched in a 0.5% (by weight) solution of $CrSO_4$ buffered to a pH of 3.5 using NaOH following the methodology of B. Sundström [*Odont. Revy* **19** (*Suppl. 13*), 1 (1968)]. A total of 23 species representing 16 genera and 10 conodont families have been examined to date and range in age from Late Cambrian to Silurian. All have white matter that contains cell lacunae and canaliculi similar to those in the specimens figured.
22. M. M. Smith, *Science* **251**, 301 (1991).
23. Although older (late Arenig or early Llanvirn) vertebrate material has been described from Australia by A. Ritchie and J. Gilbert-Tomlinson [*Alcheringa* **1**, 351 (1977)], no original hard tissues are preserved and their histology is consequently unknown. Vertebrates are here considered synonymous with craniates, following the definition of R. P. S. Jefferies [*The Ancestry of Vertebrates* (British Museum, Natural History, London, 1988)].
24. M. M. Smith, *Hist. Biol.* **3**, 97 (1989).
25. T. Ørvig, *Zool. Scr.* **18**, 427 (1989).
26. S. Bengtson, *Lethaia* **9**, 185 (1976).
27. T. Ørvig, in *Current Problems in Lower Vertebrate Phylogeny*, T. Ørvig, Ed. (Almquist & Wiksell, Stockholm, 1968) pp. 374–397; W.-E. Reif, *Evol. Biol.* **15**, 287 (1982).
28. P. Janvier, *J. Vert. Paleontol.* 1, 121 (1981).
29. L. B. Halstead, in *Problems of Phylogenetic Reconstruction*, K. A. Joysey and A. E. Friday, Eds. (Academic Press, London, 1982), pp. 159–196.
30. We would like to express our thanks to G. R. Coope and R. J. Aldridge for their valuable comments on variants of the manuscript, and to the latter for also supplying Estonian conodont material. T. Whitfield and G. A. Parker provided technical assistance and the use of facilities at the University of Newcastle upon Tyne and the University of Durham is acknowledged. The illustrated specimens prefixed BU are deposited in the Lapworth Museum, School of Earth Sciences, University of Birmingham, and that with the prefix MGUH is held at the Geological Museum, Copenhagen, Denmark.

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Natural Versus Anthropogenic Factors Affecting Low-Level Cloud Albedo over the North Atlantic

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Cloud albedo plays a key role in regulating Earth's climate. Cloud albedo depends on column-integrated liquid water content and the density of cloud condensation nuclei, which consists primarily of submicrometer-sized aerosol sulfate particles. A comparison of two independent satellite data sets suggests that, although anthropogenic sulfate emissions may enhance cloud albedo immediately adjacent to the east coast of the United States, over the central North Atlantic Ocean the variability in albedo can be largely accounted for by natural marine and atmospheric processes that probably have remained relatively constant since the beginning of the industrial revolution.

The albedo of clouds is an important but poorly understood factor influencing Earth's radiation budget (*1*) that depends nonlinearly on column-integrated liquid water content and the concentration of cloud condensation nuclei (CCN) (*2*). There is evidence that over land cloud albedo increases as cloud temperature increases (*3*). Hence, over the ocean, low-level cloud albedo might be expected to be high where sea surface temperature (SST) is also high. CCN are composed largely of submicrometer-sized aerosol sulfate particles, which have both natural and anthropogenic sources. Over the oceans, phytoplankton production of dimethyl sulfide (DMS), which outgases and is oxidized to form aerosol sulfate, has been suggested to be a major source of CCN (*2, 4*). In the Northern Hemisphere, however, the emissions of anthropogenic, continentally derived sulfate are approximately five times the emissions from natural marine sources (*5*).

In examining satellite images over the North Atlantic Ocean, we noted that the albedo of marine stratus clouds showed systematic trends over large distances (Figs. 1 and 2). In particular, in a latitude band corresponding to the highest anthropogenic sulfate fluxes from the North American continent, albedo generally decreased from the western to eastern regions of the Atlantic basin (Fig. 2B). This gradient suggests that emissions of anthropogenic continental sulfate may affect the albedo of oceanic clouds thousands of kilometers from the coast. We examined the relative importance of anthropogenic and natural factors on the albedo of marine stratus clouds by comparing the seasonal, basin-scale distributions among upper ocean phytoplankton biomass (using chlorophyll as a proxy), SST, and low-level cloud albedo for the North Atlantic Ocean.

We elucidated the contribution of phytoplankton sources of CCN to the albedo of marine stratus clouds by comparing gridded, monthly averaged, low-level cloud albedos derived from the Earth Radiation Budget Experiment (ERBE) satellite data (*1*) with composited, surface ocean chlorophyll concentrations derived from the Coastal Zone Color Scanner (CZCS). The ERBE data, obtained from the National Oceanic and Atmospheric Administration NOAA-9 scanner measurements, were selected for the North Atlantic Ocean and analyzed for four representative midseason months: April, July, and October 1985 and January 1986. The NOAA-9 satellite is in a sun-synchronous orbit and crosses the equator at 1430 local time. The data were screened so as to include only totally overcast pixels, and a longwave filter (*6*) was then used to isolate warm and thus low-altitude clouds (primarily marine stratus). Because the satellite was in a sun-synchronous orbit, the effect of variations in solar zenith angle on albedo at a fixed latitude was largely eliminated in any given month. Albedos were calculated across seven zonal latitude bands, between 28° and 60°N (Fig. 1, left). Within each band, all pixels (approximately 50 km in diameter at nadir) for a given month were averaged for each 1° of longitude. In all, 28 submaps (corresponding to seven latitude bands and 4 months) of albedo were constructed, from the western edge of the North Atlantic basin to 20°W. At lower latitudes, in warmer months, the paucity of stratus clouds did not permit further analyses.

To obtain representative surface phytoplankton distributions, we used the entire CZCS data set for the North Atlantic Ocean. The sensor, which flew aboard Nimbus-7 between November 1978 and May 1986, acquired global observations of ocean color. Upper ocean chlorophyll concentrations were calculated from water-leaving radiances with atmospheric corrected algorithms (*7*). The spatial coverage of CZCS data for any given month was not sufficient to allow a direct monthly comparison with the albedos calculated from the ERBE data; the temporal overlap between CZCS and ERBE satellites occurred when the CZCS data transmissions were most sparse. However, the interannual variations in chlorophyll within any region

Table 1. The regional distribution of continental sulfur dioxide and sulfate sources for seven latitude bands compiled from the NAPAP data base (*9*) (units are tons per year).

Latitude band	SO_2	SO_4^{2-}	$SO_2 + SO_4^{2-}$
57°–60°N	199,655	56	199,711
52°–57°N	816,286	46,147	862,433
47°–52°N	1,428,974	33,716	1,462,690
43°–47°N	2,899,895	83,822	2,983,717
38°–43°N	12,490,324	223,553	12,713,877
33°–38°N	5,793,258	140,648	5,933,906
28°–33°N	3,118,539	53,781	3,172,320

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are significantly lower than the seasonal variations. We therefore temporally and spatially averaged all CZCS data for each month, creating average monthly global maps of the distribution of chlorophyll in the North Atlantic. For each of the 4 months of albedo data, we calculated the average chlorophyll concentration in each of the corresponding latitudinal zones for each 1° of longitude (Fig. 1, right). This analysis resulted in transocean maps of upper ocean chlorophyll, where each chlorophyll value corresponds to one albedo value for a given month within a given grid.

The analysis of variations in albedo of low clouds revealed transocean gradients that varied seasonally and with latitude (8). In 8 of the 22 analyzable cases, cloud albedo showed moderate to strong transoceanic gradients. In the remaining 14 cases, lower cloud albedo showed no systematic transoceanic trends. In the northernmost latitude band, from 57° to 60°N, albedo generally increased from west to east, reaching a maximum at the Atlantic basin at 20°W, off the south coast of Iceland (Fig. 2A). In this region low-level cloud albedo and upper ocean chlorophyll track each other remarkably, and SST is positively associated with albedo (Fig. 2A). In contrast, between 38° and 43°N, a latitude corresponding to the highest anthropogenic sulfate emissions on the North American continent (Table 1), albedo generally decreased from west to east over the ocean, especially in April and October (Fig. 2B). In this latitude band, cloud albedo was most enhanced adjacent to the east coast of the United States (Figs. 1 and 2B). Could this transoceanic trend in albedo be due to anthropogenic sulfate emissions on the North American continent?

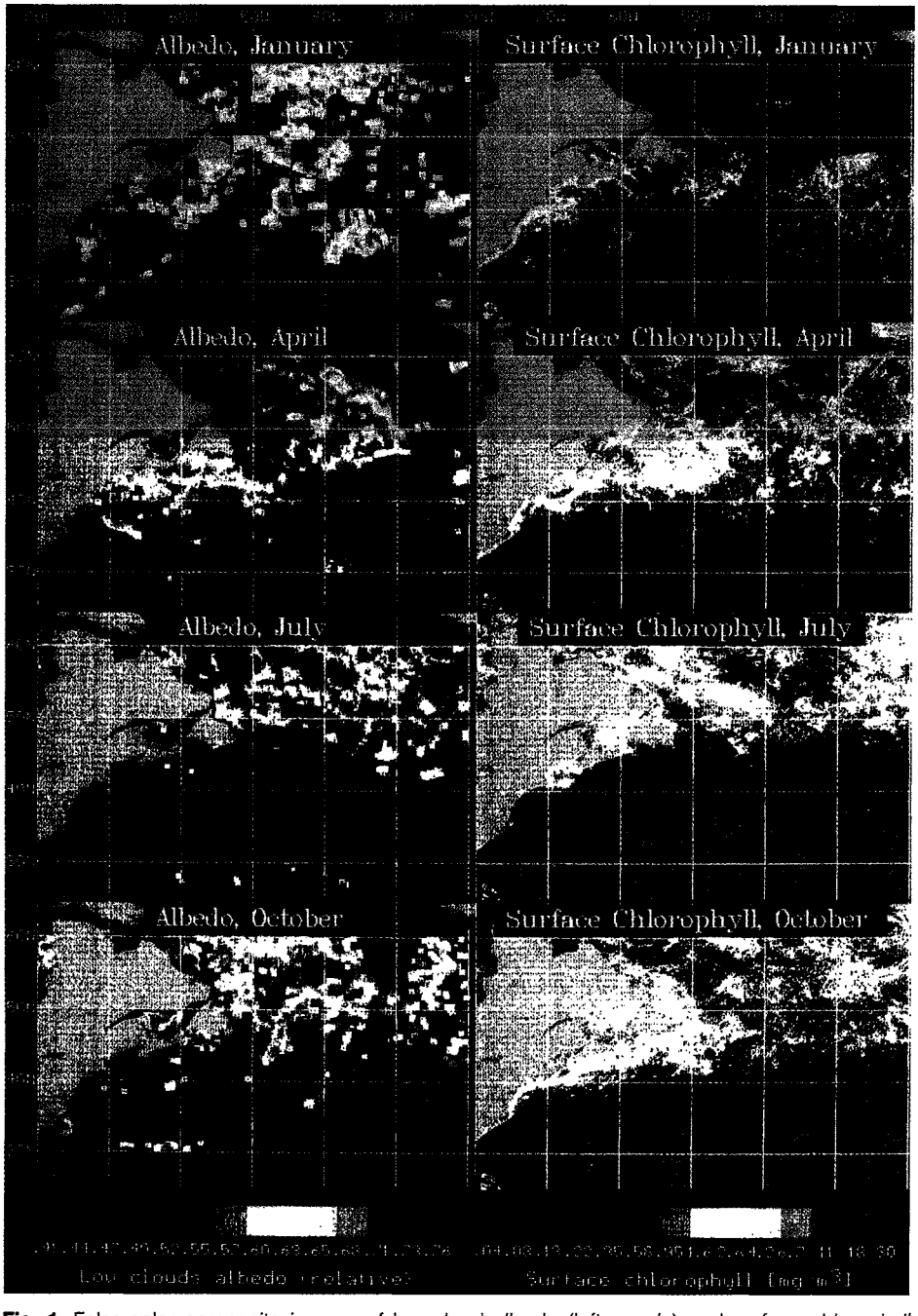

Fig. 1. False-color composite images of low cloud albedo (left panels) and surface chlorophyll concentrations (right panels). The albedo data, retrieved from ERBE, were averaged for April, July, and October 1985 and January 1986. The chlorophyll data, obtained from global monthly composites of CZCS archived data, were averaged pixel by pixel (20 by 20 km) for each month, thereby generating four average monthly color maps. The interannual variations were less than 20% of the seasonal variation. These albedo and chlorophyll data were analyzed on seven subsets of latitude, resolved in each 1° of longitude.

The relative importance of anthropogenic and natural factors that influence marine stratus cloud albedo can be inferred from an examination of the seasonal relation among SST, chlorophyll, and albedo between 38° and 43°N (Fig. 2B). In this latitude band, high SST is accompanied by low albedo and vice versa in all three cases, and the anthropogenic sulfate source is high and relatively invariant throughout the year (9). Superimposed on the anthropogenic source term, however, is a seasonally varying phytoplankton source term (Fig. 1). In January, except in the region immediately adjacent to the east coast of North America, phytoplankton chlorophyll is relatively low throughout the North Atlantic. Cloud albedo is also highest immediately adjacent to the coast; east of 65°W, however, there is little trend (Fig. 2B). In April and October, both albedo and chlorophyll decrease from 65° to 20°W. Mean lower atmospheric winds are westerly in January between 38° and 43°N (10).

If anthropogenic aerosol sulfate were responsible for the transoceanic gradient in albedo observed east of 65°W in April and October in this latitude band, we would expect to find a similar transoceanic gradient in January, when the anthropogenic source term is high relative to the phytoplankton source term. We do not. Furthermore, analyses of ERBE data for January 1987 revealed similar results, suggesting that interannual variability cannot account for the seasonal differences in the transocean albedo variations. These results suggest that east of 65°W transoceanic gradients in marine stratus cloud albedo are affected much more by natural marine processes (SST and phytoplankton abundance) than by anthropogenic CCN sources.

The fact that in certain regions high chlorophyll is associated with high albedo may be somewhat surprising as a number of studies have indicated that the relation between the values of oceanic DMS and phytoplankton chlorophyll is weak (11). DMS is produced by

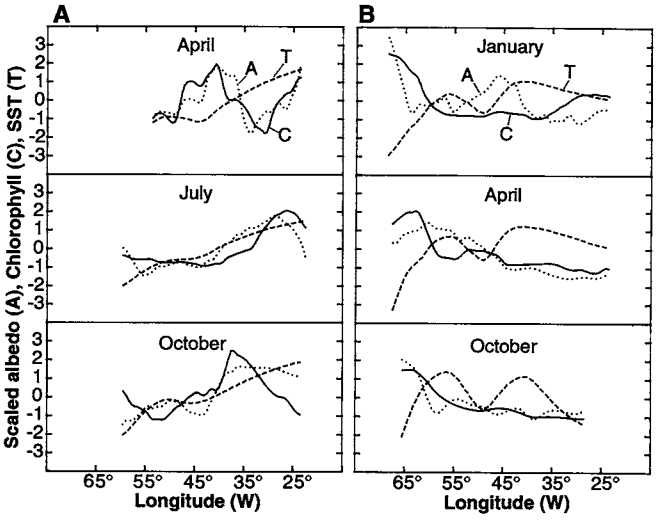

Fig. 2. Representative spatial and seasonal distributions of averaged (*8*), scaled cloud albedo (A, dotted lines), SST (T, dashed lines), and phytoplankton chlorophyll (C, solid lines). Each variable was scaled by $(x_i - x)/\sigma$, where x_i is the observed value, x is the mean, and σ is the standard deviation. Data from two latitude bands are presented, (**A**) from 57° to 60°N and (**B**) from 38° to 43°N. In these figures, the chlorophyll values were shifted 400 km downwind (*8*).

some groups of phytoplankton, such as chromophytes and coccolithophorids, more than other groups, such as diatoms or cyanobacteria (*12*). The increase in both albedo and chlorophyll between 52° and 60°W in April (Fig. 2A) corresponds to coccolithophore blooms off the coast of Iceland in the summer and to high DMS concentrations in the upper ocean (*13*). At lower latitudes, however, there are insufficient data on the temporal and spatial distributions of coccolithophores or other major DMS producers. It is possible that the relation between DMS and chlorophyll on the large spatial scales examined here may be more robust than on the small scales normally examined by surface vessels (*14*).

Analysis of the relation between SST and albedo indicated that in some regions higher albedo was associated with high SST; however, in 40% of the regions high albedo was associated with low SST. Although a multivariate model could be developed for each region with SST and chlorophyll used to predict albedo (*15*), our results suggest that the relation among the albedo of marine stratus clouds, cloud temperature, and SST is complex and cannot be generalized for the basin throughout the year.

We conclude that, near the continental margin, both natural and anthropogenic processes can contribute to the enhanced albedo of marine stratus clouds; we cannot quantitatively apportion the relative importance of these two factors from the available data. Over the central North Atlantic Ocean basin, however, much of the variability in albedo appears to be related solely to natural factors. Although over the last 100 years anthropogenic sulfate emissions have increased exponentially, natural marine emissions of DMS probably have remained relatively constant (*16*). The anthropogenic emissions appear to have affected noncloud reflectivity (*17*); however, the effect of human activities on cloud albedo appears to be minimal in the remote marine environment.

REFERENCES AND NOTES

1. V. Ramanathan *et al.*, *Science* **243**, 57 (1989); E. F. Harrison *et al.*, *J. Geophys. Res.* **95**, 18687 (1990).
2. R. J. Charlson, *et al.*, *Nature* **326**, 655 (1987).
3. E. M. Feigelson, *Beitr. Phys. Atmos.* **51**, 203 (1978); A. K. Bates and Harshvardhan, *J. Geophys. Res.* **92**, 8483 (1987).
4. G. P. Ayers, *et al.*, *Nature* **349**, 404 (1991).
5. T. S. Bates, B. K. Lamb, A. Geunther, J. Dignon, R. E. Stoiber, *J. Atmos. Chem.*, in press.
6. We distinguished low-level clouds from high-level clouds using the filter [*F*(clear) − *F*(overcast)]/*F*(clear) < 0.125, where *F*(clear) is the monthly mean clear-sky longwave flux at a scanning point and *F*(overcast) is the instantaneous overcast longwave flux at a scanning point (*F* values are in watts per square meter). Sea ice cover was determined on the basis of climatological data.
7. H. R. Gordon, J. W. Brown, R. H. Evans, *Appl. Opt.* **27**, 862 (1988); C. R. McClain, G. C. Feldman, W. E. Esaias, in *Global Change Atlas*, C. Parkinson, J. Foster, R. Gurney, Eds. (Cambridge Univ. Press, Cambridge, in press).
8. Spatial autocorrelation analysis revealed that albedo was autocorrelated with a length scale of 3° of longitude whereas chlorophyll was autocorrelated with a length scale of 5° of longitude. We spatially averaged the albedo data to conform to the chlorophyll length scale. For further comparison, chlorophyll data were shifted 400 km downwind (to the east), conforming to the optimal cross-correlation between the two variables.
9. "The 1985 NAPAP (National Acid Precipitation Assessment Program) emissions inventory (Version 2): Development of the annual data on modeler's tapes" (Publ. EPA-600/7-89-012a, Environmental Protection Agency, Washington, DC, 1989).
10. Y.-J. Han and S.-W. Lee, *Mon. Weather Rev.* **111**, 1554 (1983).
11. C. Leck, *et al.*, *J. Geophys. Res.* **95**, 3353 (1990); T. S. Bates, *et al.*, *Nature* **329**, 319 (1987); P. M. Holligan, *et al.*, *Cont. Shelf. Res.* **7**, 273 (1987).
12. M. D. Keller, W. K. Bellow, R. R. L. Guillard, in *Biogenic Sulfur in the Environment*, E. S. Saltzman and W. J. Cooper, Eds. (American Chemical Society, Washington, DC, 1989), pp. 167–182; M. O. Andreae, W. R. Barnard, J. M. Ammons, *Ecol. Bull. (Stockholm)* **35**, 167 (1983).
13. P. M. Holligan and W. M. Balch, in *Particle Analysis in Oceanography*, S. Demers, Ed. (Springer-Verlag, New York, 1991), pp. 301–324.
14. D. L. Savole and J. M. Prospero, *Nature* **339**, 685 (1989); A. M. Thompson, W. E. Esaias, R. L. Iverson, *J. Geophys. Res.* **95**, 20551 (1990).
15. Product moment correlation analysis indicated that, of the 22 analyzable cases, albedo and chlorophyll were significantly ($P \leq 0.10$) positively correlated in 11 and significantly negatively correlated in 1. Albedo and SST were significantly positively correlated in 9 and significantly negatively correlated in 5. A two-parameter linear model using SST and chlorophyll accounted for more than 50% of the variance in albedo in 14 cases.
16. R. J. Charlson *et al.*, *Science* **255**, 423 (1992).
17. R. J. Charlson, J. Langer, H. Rodhe, C. B. Levoy, S. G. Warren, *Tellus Ser. AB* **43**, 152 (1991).

18. This research was supported by the U.S. Department of Energy, the National Aeronautics and Space Administration, and the Electric Power Research Institute. We thank S. Schwartz, P. Minnett, P. Michael, A. Morel, P. Holligan, and R. Charlson for discussions, and G. Feldman for providing the global CZCS data set.

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Functional Specialization of Olfactory Glomeruli in a Moth

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The specific function of the glomerular structures present in the antennal lobes or olfactory bulbs of organisms ranging from insects to humans has been obscure because of limitations in neuronal marking methods. By tracing individual neurons in the moth *Agrotis segetum*, it was determined that physiologically distinct types of pheromone receptor neurons project axons to different regions of the macroglomerular complex (MGC). Each glomerulus making up the MGC has a specific functional identity, initially processing information about one specific pheromone component. This indicates that, at least through the first stage of synapses, olfactory information moves through labeled lines.

Olfactory glomerulus function has been studied by a variety of methods, including activity mapping by deoxyglucose injections (*1, 2*) or tracing by antero- or retrograde filling of afferent neurons (*3–6*). These studies have involved large numbers of sensory cells and have thus shown activation of large areas in the olfactory bulbs or lobes, or filling of large numbers of neurons of unknown specificity. We have here recorded electrophysiologically from single, pheromone-specific receptor cells on