energy when flying in formation, this arrangement may also favour communication and coordination within the group — for example, by helping birds to stay in visual contact[4,10] and enabling flight-pass and velocity information to be conveyed between them[6]. This may explain why several other naturally occurring configurations of bird flocks are aerodynamically neutral or even disadvantageous relative to solitary flight[8,11].

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Deep-sea ecology

Developmental arrest in vent worm embryos

Temperature is a key factor in controlling the distribution of marine organisms and is particularly important at hydrothermal vents, where steep thermal gradients are present over a scale of centimetres[1]. The thermophilic worm *Alvinella pompejana*, which is found at the vents of the East Pacific Rise (2,500-m depth), has an unusually broad thermotolerance (20–80 °C) as an adult[2,3], but we show here that the temperature range required by the developing embryo is very different from that tolerated by adults. Our results indicate that early embryos may disperse through cold abyssal water in a state of developmental arrest, completing their development only when they encounter water that is warm enough for their growth and survival.

We obtained early embryos of *A. pompejana* by *in vitro* fertilization, and reared them at temperatures ranging from 2 °C to 20 °C under atmospheric and deep-sea pressures. We monitored mortality (diagnosed by the breakdown of the plasma membrane or by production of irregular cytoplasmic blebs) and zygotic cleavage during early development.

Embryos kept at 20 °C and one atmosphere of pressure all died within 24 h (Fig. 1a), although many completed the first cleavage. At 14 °C and 10 °C, 70–90% of zygotes cleaved, with rates varying as a function of temperature. At 2 °C, oocytes and embryos remained intact, without cleaving, for 72 h (Fig. 1a) and for at least a further 8 days, when we stopped the experiment.

As low hydrostatic pressure inhibits cleavage in other deep-sea invertebrates[4], some irregular cleavages in our one-atmosphere incubations were not unexpected. When we repeated the incubation experiments at *in situ* pressures (250 atmospheres),

we obtained qualitatively similar results (Fig. 1b), with fewer abnormalities.

To investigate whether cold-water developmental arrest is reversible, we maintained zygotes at 2 °C for 72 h, exposed them to a 10 °C heat pulse for 45 min, and incubated them at 2 °C for a further 24 h. Although embryos maintained at 2 °C never underwent cleavage, those exposed to a short heat pulse resumed development, and cleavage continued even after the embryos were

moved back into cold water (Fig. 1c).

The large difference in temperature tolerance between adults (20–80 °C) and embryos (2–20 °C) precludes the possibility of embryonic development inside adult worm tubes. Optimal temperatures for development (10–15 °C) are found close to the bases of hydrothermal-vent chimneys. As eggs are negatively buoyant upon release, some embryos probably develop on or near the sea floor, just below the adult habitat. However, it is likely that at least some embryos are dispersed by currents and carried to new sites through cold (2 °C) abyssal sea water, as occurs in other vent species[5,6]. Our results show that embryos of *A. pompejana* survive but do not develop at this temperature.

It has been suggested that dispersing larvae of hydrothermal-vent bivalves[7] and polychaetes[8] may delay their development until they encounter warm water. Our results provide empirical evidence for such reversible developmental arrest in a vent species; a similar phenomenon has been reported in larvae of the bathyal echinoid *Linopneustes longispinus*[9]. Although we do not know how long the embryos of *A. pompejana* remain viable at low temperatures, this temperature-sensitive mechanism for controlling development may result in
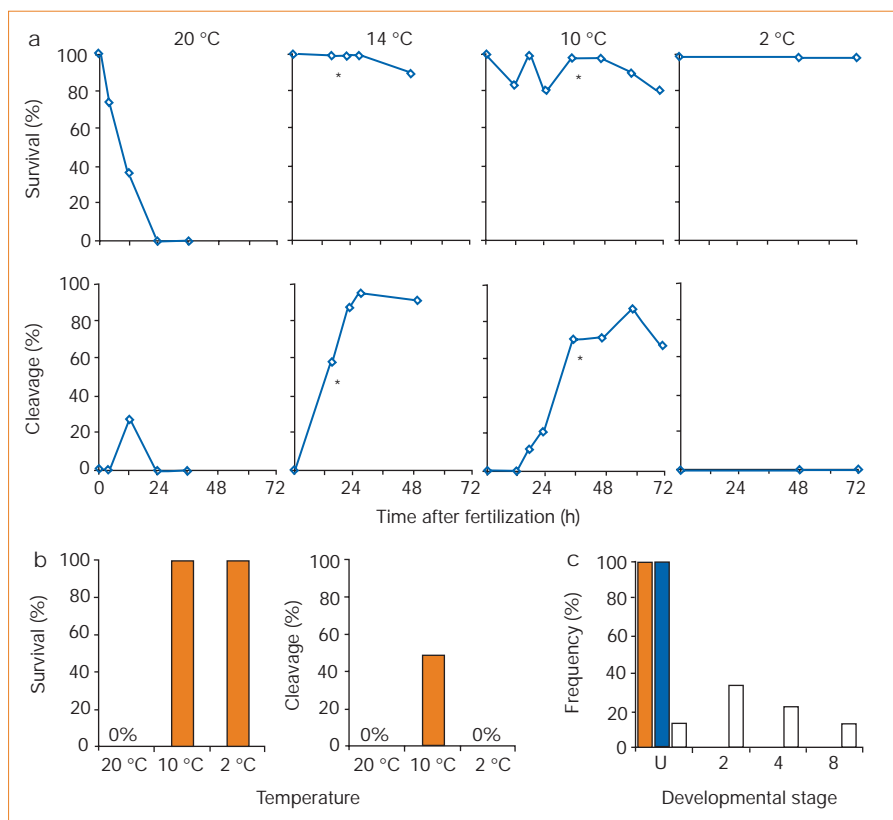
Figure 1 Effects of temperature on early embryos of *Alvinella pompejana*. **a,** Percentage of embryos surviving (top) and cleaving (bottom) when incubated at one atmosphere of pressure and at temperatures of 2–20 °C. At least 20 embryos were scored per sample, except for 2 samples (asterisks), which contained fewer embryos. **b,** Survival and cleavage at the indicated temperatures after 48 h at a pressure of 250 atmospheres. **c,** Distribution of cleavage stages in embryos incubated at 2 °C for 24 h (orange bar) and 8 days (blue bar) and in 72-h embryos exposed to a 45-min heat pulse at 10 °C (white bars), then transferred back to 2 °C for a further 24 h. Developmental stages are two- to eight-cell stages. U, uncleaved.

very long dispersal distances.

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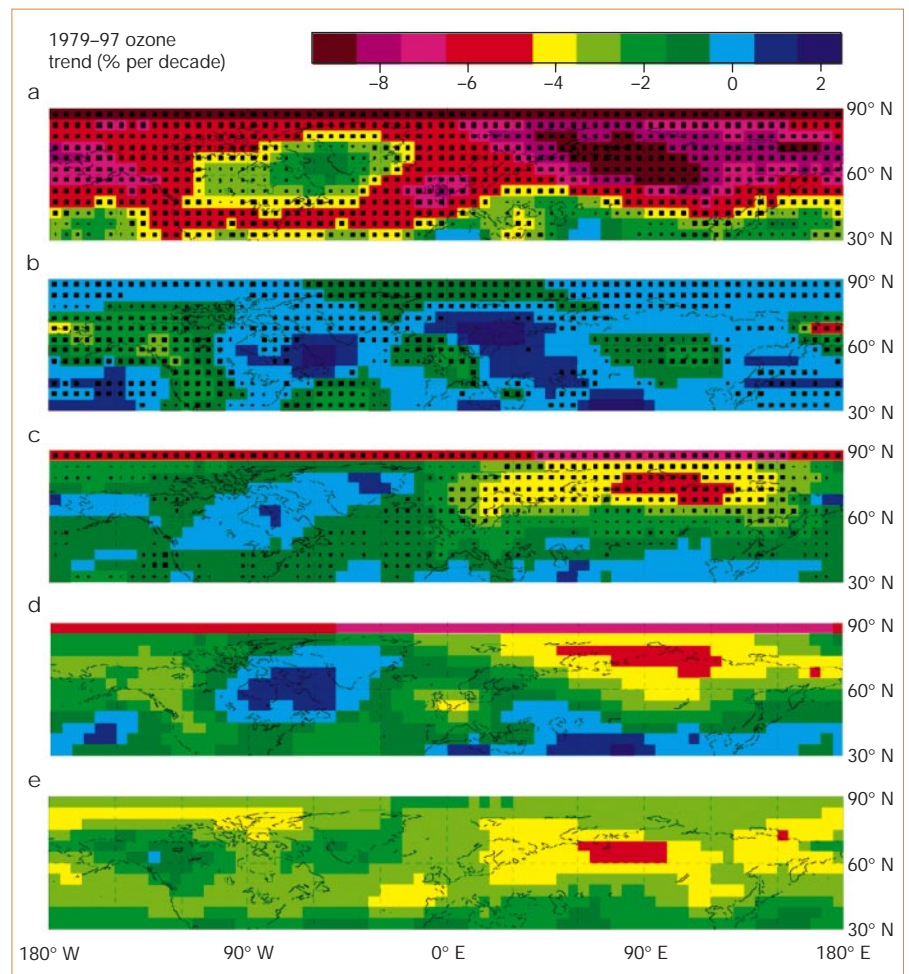   P. A.) 225–231 (Olsen & Olsen, Fredensborg, Denmark, 1989).

Geophysics

Longitudinal variation in springtime ozone trends

Satellite measurements indicate that mid-latitude ozone depletion in the Northern Hemisphere spring during 1979–97 was worst over Europe and Russia[1]. Here we show that these longitudinal differences in ozone trends are due to a combination of decadal variations in the circulation[2,3] and transport of ozone-depleted air from the polar vortex. Any increase in ozone depletion in the polar vortex as a result of future cooling of the stratosphere would therefore be particularly bad over Europe and Russia.

Massive ozone depletion inside the Arctic vortex has occurred frequently during the past decade. As the total ozone mapping spectrometer satellite data we use here have gaps from December 1994 to July 1996 and in May 1994 (ref. 4), the principal part of the vortex depletion during 1979–97 is included by using the 1993 and 1997 depletions (depletions originating from the vortex in 1997 are taken from ref. 5). They were calculated by tracking the ozone-depleted air with reverse domain-filling trajectory calculations covering the altitude region of ozone depletion.

We calculated diabatic descent using a radiation scheme[6]; ozone-depletion mixing ratios were regridded every seventh day to introduce almost realistic average mixing[5]. The 1993 calculations were carried out in the same way, and the vortex depletion was taken from ref. 7, using a correction for diffusive transport into the vortex taken from 1997 calculations[8]. The column-integrated depletion amounts to 79 Dobson units, which is comparable to earlier values[9].

We applied a multiple linear-regression model[1] to the column ozone, assuming a linear trend and including the quasi-biennial oscillation (with appropriate lag[10]) and solar cycle as independent variables. The trend is shown in Fig. 1a: black dots indicate where trends are significant. To calculate the effect of circulation changes and vortex depletions on the ozone trends, we used the geopotential height at a pressure of 25,000 pascals (geometric height, about 10 km) supplied by the European Centre for Medium-Range Weather Forecasts, as well as the transported depletion in 1993 and 1997 (zero in other years), instead of the linear ozone trend in the regression model.

Figure 1b shows the trend in ozone levels that may be explained by the trend in the 25,000-pascal geopotential height. The height trend accounts for the fact that the downward ozone trend is small south of Greenland and large over the United Kingdom, but it does not explain the large trends over Scandinavia and Russia, for example.

Figure 1c shows the effect of vortex depletions on ozone trends and helps to explain the large downward ozone trends over Scandinavia and Russia. The positive trends shown are non-physical and not significant. By neglecting vortex depletion in years other than 1993 and 1997, the effect of vortex depletion will be underestimated. Statistics showing the April–May location of the vortex (remnants) in two other years with large vortex ozone depletions (1996 and 2000) reveal that the most probable location is over Europe and Russia, indicating that this is a robust, climatological feature (data not shown). The part of the mid-latitude (30°–60° N) trend that may be attributed to vortex depletions is 0.8% per decade, or 19% of the observed ozone trend on average. This might be compared to the 25% of the observed ozone depletion in

Figure 1 Ozone trends in the April–May periods of 1979–97. **a,** Calculated overall ozone trend. Large black dots indicate a significant trend with 95% confidence; small dots indicate 68% confidence. **b,** Ozone trend due to the trend in the height of 25,000-pascal pressure. This explains why the downward ozone trend is small south of Greenland and large over the United Kingdom. **c,** Ozone trend due to vortex depletions in 1993 and 1997. This accounts for most of the large downward ozone trend over Scandinavia and Russia. **d,** Sum of the trends shown in **b** and **c**. This explains 81% of the variance in mid-latitude ozone trends in **a**. **e,** The residual trend, caused by factors such as local ozone depletion outside the vortex, is roughly independent of longitude.