Nations, Geneva, 2000).
3. Gonzalez, E. *et al. Proc. Natl Acad. Sci. USA* **96,** 12004–12009 (1999).
4. Wilkinson, D., Abdool Karim, S. S., Williams, B. & Gouws, E. *J. Acqu. Imm. Def. Syndr.* **23,** 405–409 (2000).
5. Gregson, S., Donnelly, C. A., Parker, C. G. & Anderson, R. M. *AIDS* **10,** 1689–1697 (1996).
6. Stephens, J. C. *et al. Am. J. Hum. Genet.* **62,** 1507–1515 (1998).
7. Charlesworth, B. *Evolution in Age-Structured Populations* (Cambridge Univ. Press, Cambridge, 1980).
8. Census (International Programs Center, Population Division, United States Census Bureau, 2000).

Climate change

Increasing shrub abundance in the Arctic

The warming of the Alaskan Arctic during the past 150 years[1] has accelerated over the last three decades[2] and is expected to increase vegetation productivity in tundra if shrubs become more abundant[3,4]; indeed, this transition may already be under way according to local plot studies[5] and remote sensing[6]. Here we present evidence for a widespread increase in shrub abundance over more than 320 km^2 of Arctic landscape during the past 50 years, based on a comparison of historic and modern aerial photographs. This expansion will alter the partitioning of energy in summer[7] and the trapping and distribution of snow in winter[8], as well as increasing the amount of carbon stored in a region that is believed to be a net source of carbon dioxide[9].

During oil exploration of the United States Naval Petroleum Reserve no. 4 in northern Alaska in 1948–50, low-altitude oblique photographs of exceptional clarity were taken at thousands of locations between the Brooks Range and the Arctic coast[10]. In July of 1999 and 2000, we took photographs at 66 of the same locations spanning an area 400 km (east to west) by 150 km. We analysed pairs of new and old photographs for changes in the three principal deciduous shrubs, dwarf birch (*Betula nana*), willow (*Salix* sp.) and green alder (*Alnus crispa*), and for changes in treeline white spruce (*Picea glauca*) along the southern edge of the study area.

In 36 of the 66 repeat photo-pairs, we found distinctive and, in some cases, dramatic increases in the height and diameter of individual shrubs, in-filling of areas that had only had a scattering of shrubs in 1948–50, and expansion of shrubs into previously shrub-free areas (Figs 1, 2). At treeline sites, there was a marked increase in the extent and density of the spruce forest (Fig. 2). In some cases, shrub-dominated vegetation that covered about 10% of the landscape in 1948–50 had doubled by 2000. In the 30 photo-pairs in which the amount of deciduous shrubs had not increased, there was no detectable reduction in shrub abundance either.

The increase in shrub abundance appears to have been mainly the result of the growth and expansion of alder, perhaps partly because dark-coloured alder are the most conspicuous shrubs (Fig. 1). However, in several photographs ($n = 4$), birch and willow were also seen to have increased in abundance. All three species belong to the same functional group and respond to experimental warming and fertilization in a positive manner[5]. This indicates that the abundance of the smaller dispersed birch and willow found throughout tussock tundra may also be increasing, and so our detection of change could be conservative. These smaller shrubs comprise most of the shrub biomass in the study area.

Our study area is in a location where human and natural disturbances (leading to successional changes) are minimal, so we attribute much of the increase in the abundance of shrubs to the recent change in climate. During the Early Holocene, warming in the Alaskan Arctic was accompanied by one or more large-scale shrub invasions[11], and today shrub abundance increases along latitudinal temperature gradients[12]. These findings, combined with our observations, show that the vegetation of the region is able to respond to changes in climate, perhaps rapidly. The extensive peat deposits[13] are evidence that the region has been an important sink for global carbon in the geological past. The increased primary production inferred from our photographic analysis could be a significant contributor to changes in the high-latitude carbon budget, as well as contributing to important changes in the exchange of surface energy.

Matthew Sturm*, Charles Racine†, Kenneth Tape‡
**US Army Cold Regions Research & Engineering Laboratory–Alaska, PO Box 35170, Fort Wainwright, Alaska 99703, USA*
e-mail: msturm@crrel.usace.army.mil
†US Army Cold Regions Research & Engineering Laboratory, 72 Lyme Road, Hanover, New Hampshire 03755, USA
‡Geophysical Institute, University of Alaska–Fairbanks, PO Box 757320, Fairbanks, Alaska 99775, USA

1. Overpeck, J. *et al. Science* **278,** 1251–1256 (1997).
2. Serreze, M. C. *et al. Climatic Change* **46,** 159–207 (2000).
3. Epstein, H. E., Walker, M. D., Chapin, F. S. & Starfield, A. M. *Ecol. Applic.* **10,** 824–841(2000).

Figure 1 The Ayiyak River (N68° 53′, W152° 31′), showing an increase in the density of shrub patches, the growth of individual shrubs and an expansion of shrubs into areas that were previously shrub-free. A and B denote the same locations in the old and new photographs.

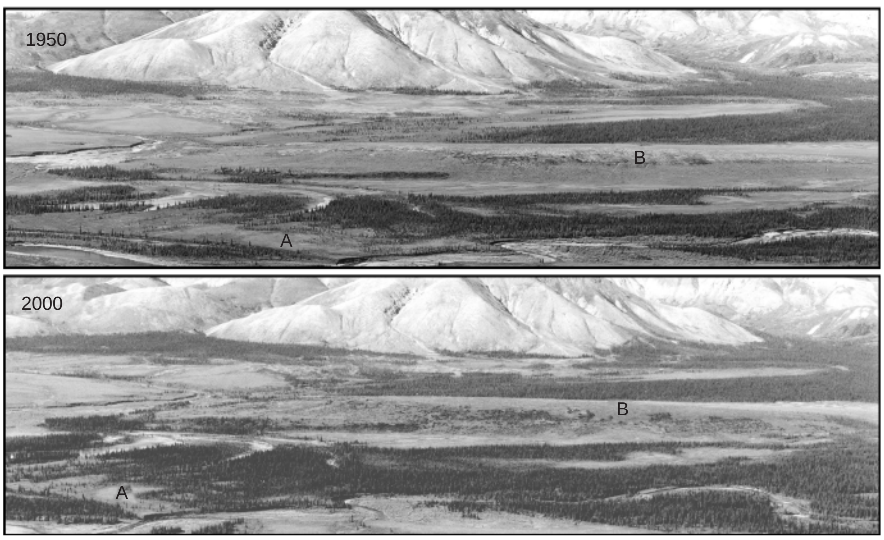

Figure 2 The Kugururok River (N68° 06′, W161° 31′), showing in-filling of spruce stands (A) and increased abundance of shrubs in the middle ground (B); A and B denote the same locations in the old and new photographs.

4. McGuire, A. D. *et al. Glob. Change Biol.* **6,** 141–150 (2000).
5. Chapin, F. S. *et al. Ecology* **73,** 694–711 (1995).
6. Myneni, R. B. *et al. Nature* **386,** 698–702 (1997).
7. Chapin, F. S. *et al. J. Climate* **13,** 2002–2010 (2000).
8. Sturm, M. *et al. J. Climate* **14,** 336–344 (2001).
9. Oechel, W. C. *et al. Nature* **406,** 978–981 (2000).
10. Reed, J. C. *US Geol. Surv. Prof. Pap.* **302** (1958).
11. Anderson, P. M. & Brubaker, L. B. in *Global Climates Since the Last Glacial Maximum* (ed. Wright, H. E. Jr) 386–400 (Univ. Minnesota Press, Minneapolis, 1993).
12. Bliss, L. C. & Matveyeva, N. V. in *Circumpolar Arctic Vegetation* (eds Chapin, F. S. *et al.*) 59–89 (Academic, San Diego, 1992).
13. Billings, W. D. *Quat. Sci. Rev.* **6,** 155–177 (1987).

Sensory adaptation

Tunable colour vision in a mantis shrimp

Systems of colour vision are normally identical in all members of a species, but a single design may not be adequate for species living in a diverse range of light environments. Here we show that in the mantis shrimp *Haptosquilla trispinosa*, which occupies a range of depths in the ocean, long-wavelength colour receptors are individually tuned to the local light environment. The spectral sensitivity of specific classes of photoreceptor is adjusted by filters that vary between individuals.

Colour vision in mantis shrimps involves up to 16 types of visual pigment[1–3]. Spectral sensitivity is further tuned in an unusual way: transparent, coloured filters are placed in front of four classes of receptors[3–5]. Most mantis shrimp species occupy a narrow depth range, and the spectral properties of the filters vary with their characteristic depth. Species in shallow water with bright, broad-spectrum illumination have filters that tune some photoreceptors to very long wavelengths, with sensitivity peaking at wavelengths greater than 600 nm. As sea water selectively attenuates long-wavelength light[6], these receptors would be ineffective at depths exceeding 10 m. In deeper-living species, corresponding filters transmit shorter wavelengths, providing a better match to the prevailing light conditions[3,7]. Animals that live in either environment may thereby perceive colour throughout almost the entire spectral range of available light.

H. trispinosa, however, lives at depths ranging from barely subtidal to 30 m or more, and long-wavelength photoreceptor classes that are useful near the surface would not function in deep water. To meet this challenge, different individuals within the species could express different sets of visual pigments, or filters could vary between individuals. At Lizard Island, Australia, we collected adults of *H. trispinosa* at depths of 1 m and 15 m and characterized the visual pigments and filters in their retinae using microspectrophotometry[1,5]. Deep and shallow populations had identical visual pigments (data not shown), but the filters that tune the long-wavelength receptor types (Fig. 1a, arrows) were significantly shifted towards shorter wavelengths in deeper-living animals. Thus, their underlying receptors could discriminate hues within the bluer spectrum present in deep water. We calculate that, despite a 96% reduction in illumination at wavelengths longer than 575 nm, the tuning of long-wavelength receptors of animals living at 15 m allows them to capture incident photons at 75% of the rate observed for surface dwellers.

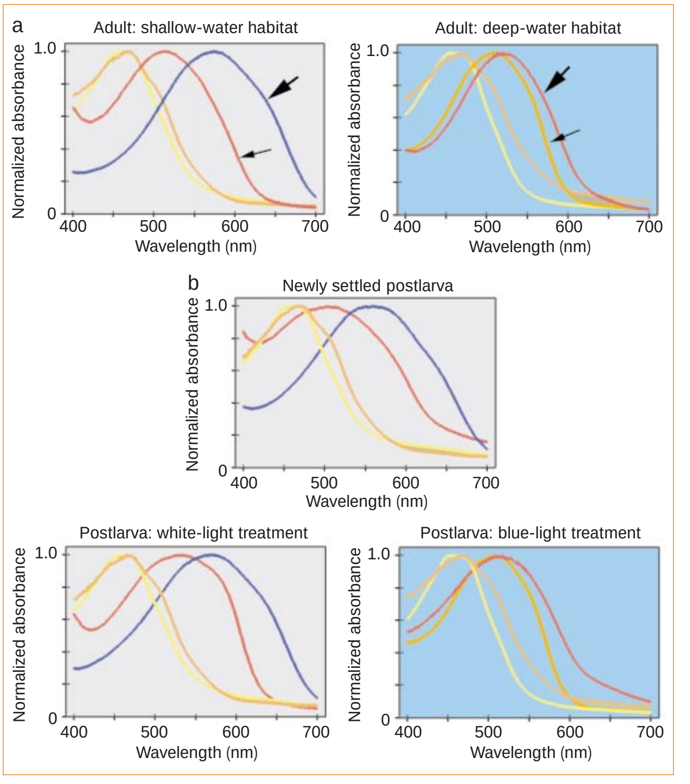

Figure 1 Normalized, average absorption spectra ($n = 2$–9) of all filter classes in *H. trispinosa* retinae. The colour of each line represents how the filter class appears to the human eye. The spectral maxima of visual pigments in the receptors that underlie each filter class are (described using filter colours in the upper-left panel): yellow, 508 nm; orange, 537 nm; red, 539 nm; blue, 558 nm. **a,** Filters in adults from shallow water (1 m) and deep water (15 m). The two longer-wavelength classes, which appear red (thin arrows) and blue (thick arrows) in retinae of shallow-water individuals, absorb shorter wavelengths in deeper-living adults. **b,** Filters of newly settled postlarvae and of juveniles after 3 months in white or blue light.

We investigated whether the occurrence of different filter sets can be influenced by conditions during development. Newly metamorphosed postlarvae of *H. trispinosa* live in shallow water and have filters like those of shallow-water adults (Fig. 1b). We reared postlarvae under laboratory lighting, either in blue light lacking wavelengths longer than 550 nm or under broad-spectrum white fluorescent light. After 3 months, individuals reared in white light retained the filter classes of shallow-living adults, whereas the filters of the blue-light group were characteristic of deep-water populations (Fig. 1b).

To our knowledge, this is the first demonstration in any species of a tunable colour-vision system that responds directly to the light environment. The response involves precise changes in a unique system of spectral filters. Although some fish, amphibians and crustaceans vary their spectral sensitivity by changing their visual-pigment chromophores, this is controlled by environmental temperature or photoperiod[8,9]. Sensitivity also changes ontogenetically in some fish[10], perhaps by hormonal control. In mantis shrimps, tuning could be regulated by the overall level of illumination, which decreases with depth, or could be controlled by the spectral quality of incident light.

Colour vision in *H. trispinosa* is influenced to a surprising extent by developmental conditions. Individuals living at different depths have different colour perception and may rely on different biological signals to compensate for this. In any case, these mantis shrimps express an impressive degree of phenotypic plasticity in tailoring their visual systems to their habitats. We suspect that intraspecific variation in visual function may be widespread among species that occupy variable light environments.

Thomas W. Cronin*, Roy L. Caldwell†, Justin Marshall‡
**Department of Biological Sciences, University of Maryland Baltimore County, Baltimore, Maryland 21250, USA*
e-mail: cronin@umbc.edu
†Department of Integrative Biology, University of California, Berkeley, California 94720, USA
‡Vision, Touch and Hearing Research Centre, University of Queensland, Brisbane 4072, Australia

1. Cronin, T. W. & Marshall, N. J. *Nature* **339,** 137–140 (1989).
2. Marshall, J. & Oberwinkler, J. *Nature* **401,** 873–874 (1999).
3. Cronin, T. W., Marshall, N. J. & Caldwell, R. L. *Phil. Trans. R. Soc. Lond. B* **355,** 1263–1267 (2000).
4. Marshall, N. J. *Nature* **333,** 557–560 (1988).
5. Cronin, T. W., Marshall, N. J., Caldwell, R. L. & Shashar, N. *Vision Res.* **34,** 2639–2656 (1994).
6. McFarland, W. N. & Munz, F. W. *Vision Res.* **15,** 1063–1070 (1975).
7. Cronin, T. W., Marshall, N. J. & Caldwell, R. L. *Vision Res.* **34,**