

continent's 'super-hunters' as per the overkill theory, we might ask why did they not find and kill off mammoths on St Paul? Mammoths on that earlier island complex at 13,000 yr BP would have been easily visible in a treeless landscape when St Paul was separated from the mainland by a narrow channel, in the most likely path of coastal watercraft colonists (Fig. 1b). This becomes part of a broader issue because dwarf mammoths of the California near-shore Channel Islands pose a similar situation. There is no evidence that the Channel Island dwarf mammoths were hunted at around 13,000 yr BP, and they did not become extinct at that time. Rather, these island mammoths became extinct at the time Clovis-aged people invaded the islands at around 11,000 yr BP<sup>21</sup>. Clearly, some island mammoth extinctions were the result of human colonization; however, on St Paul that does not seem to have been the case. □

**Methods**

Despite ground surveys and excavations on St Matthew Island for potential Quaternary outcrops, and excavated test pits, other researchers and myself have failed to find evidence of Quaternary fossils there. I searched the large collections from Alaska in the University of Alaska Museum, Fairbanks, US National Museum, Washington, and American Museum of Natural History, New York, for fossil bones from the Bering Sea islands. Those specimens are listed in the Supplementary Information. All specimens in this study were dated by the AMS radiocarbon-dating method at the NSF-University of Arizona AMS Facility at Tucson.

The Pribilof M<sup>3</sup> was located at the US National Museum (USNM 23455). Provenance data indicate that the tooth was excavated by R. E. Carroll in 1964 from Northeast Point, 75 cm below the surface. The M<sup>3</sup> showed a mid-range stage of wear, indicating an adult animal. Maximum width at the 12th plate was 6.5 cm, frequency of enamel plates was 9.23 per 10 cm, and the enamel thickness averaged around 1.2 mm. The roots had been abraded away almost to the ventral bases of the enamel plates, resulting in a smoothly worn contour, suggesting gentle rounding forces like wind-blown sand. The incompleteness of the St Paul specimen makes it difficult to judge body size. Island dwarfing is a general rule for large mammals<sup>2</sup>. Such dwarfing is a process of genetic change, but proboscideans are also known to possess unusual developmental size plasticity in response to conditions during their life<sup>22,23</sup>. Ongoing work on St Paul may furnish an answer to this question of dwarfing.

I double-checked the first date of 7,908 ± 100 yr BP from the NSF-Arizona Laboratory (AA26010). That split-sample (AA34501) dated at 8,015 ± 85 yr BP. The sample was further re-dated at the Oxford ORAU facility at 8,010 ± 40 yr BP (OxA-13027).

The stable isotope <sup>13</sup>C-21.5 analysis from the University of Arizona laboratory for the Pribilof M<sup>3</sup> fell into the <sup>13</sup>C mid-range of mainland M<sup>3</sup>s from that same laboratory that averaged 21.60 ± 0.70 yr (n = 83), so we can assume insignificant marine isotope contamination that might distort the dating by differential marine fractionization of the <sup>13</sup>C and <sup>14</sup>C isotopes of carbon.

Received 8 March; accepted 27 April 2004; doi:10.1038/nature02612.

1. Palombo, M. R. *The World of Elephants. Proc. 1st Internatl. Cong.* 486–491 (Comune Di Roma, Consiglio Nazionale della Ricerca, Rome, 2001).
2. Sondaar, P. Y. in *Major Patterns of Vertebrate Evolution* (eds Hecht, M. K., Goody, P. C. & Hecht, M. B.) 671–707 (Plenum, New York, 1977).
3. Agenbroad, L. D. Pygmy mammoths, *Mammuthus exilis*, from Channel Islands National Park, California (USA). *Deinsea* 9, 1–39 (2003).
4. Vartanyan, S. L., Garutt, V. E. & Sher, A. V. Holocene dwarf mammoths from Wrangel Island in the Siberian Arctic. *Nature* 362, 336–339 (1993).
5. Manley, W. F. *Postglacial Flooding of the Bering Land Bridge: A Geospatial Animation v1*. INSTAAR2002 ([http://instaar.colorado.edu/QGISL/bering\\_land\\_bridge](http://instaar.colorado.edu/QGISL/bering_land_bridge))
6. Guthrie, R. D. Rapid body size decline in Alaskan Pleistocene horses before extinction. *Nature* 426, 169–171 (2003).
7. Falconer, D. S. *An Introduction to Quantitative Genetics* (Longman, Harlow, 1989).
8. Frankham, R. Inbreeding and extinction: island populations. *Conserv. Biol.* 12, 665–675 (2000).
9. Hopkins, D. M. & Einarsson, T. Pleistocene glaciation on St. George Is. Pribilof Islands. *Science* 152, 343–345 (1966).
10. Sulerzhitsky, L. D. & Romanenko, F. A. The 'twilight' of the mammoth fauna in the Asiatic Arctic. *Ambio* 28, 251–255 (1999).
11. Crossen, K. J., Graham, R. W., Veltre, D. W. & Yesner, D. *Abstr. Ann. Geol. Soc. Am. Conf. NW Div.* 424 (Geol. Soc. Am., Seattle, Washington, 2003).
12. Scheffer, V. B. Rise and fall of a reindeer herd. *Sci. Monthly* 73, 356–362 (1951).
13. Colinvaux, P. A. Historical ecology in Beringia: the south land bridge coast at St. Paul Island. *Quat. Res.* 16, 18–36 (1981).
14. Guthrie, R. D. *Frozen Fauna of the Mammoth Steppe* (Univ. Chicago Press, Chicago, 1990).
15. Ager, T. A. Late Quaternary vegetation and climate history of the Bering Land Bridge from St. Michael Island western Alaska. *Quat. Res.* 60, 17–31 (2003).
16. Martin, P. S. in *Quaternary Extinctions* (eds Martin, P. S. & Klein, R. G.) 345–403 (Univ. Arizona Press, Tucson, 1984).
17. Guthrie, R. D. in *Quaternary Extinctions* (eds Martin, P. S. & Klein, R. G.) 259–298 (Univ. Arizona Press, Tucson, 1984).
18. Agenbroad, L. D., Johnson, J. & Morris, D. *Abstr. Am. Quat. Assoc. 17th AMQUA Biennial Meeting* (Am. Quat. Assoc., Univ. Alaska, Anchorage, 2002).
19. Fitzhugh, W. W. Global cultural change: new views of circumpolar lands and people. *Anthro. News Natl Mus. Nat. Hist.* 9, 1 (1997).

20. Gerasimov, D., Girya, E., Pitulko, V. & Tikhonov, A. *New Materials for the Interpretation of the Site Chertov Ovrug on the Wrangel Island* [in Russian] 379–383 (Mat. 2nd Dikov's conf., Magadan, SVKNII, 2002).
21. Fladmark, K. R. Routes: alternate migration corridors for early man in North America. *Am. Antiq.* 4, 55–69 (1977).
22. Laws, R. M., Parker, I. S. C. & Johnston, R. C. B. *Elephants and their Habitats: the Ecology of Elephants in North Bunyoro, Uganda* (Clarendon, Oxford, 1975).
23. Lister, A. M. Epiphyseal fusion and postcranial age determination in woolly mammoth. *Ann. Nat. Hist. Mus. Rotterdam* 6, 79–87 (1999).

Supplementary Information accompanies the paper on [www.nature.com/nature](http://www.nature.com/nature).

**Acknowledgements** I thank O. Geist and R. Carroll who collected these island fossils, and the curators of the UAM, USNM and ANMH. M. L. Guthrie edited the manuscript. A. Lister and A. J. Stuart provided reviews, and they also corroborated the mammoth date using their NERC Grant. My dating projects have been funded by the NSF.

**Competing interests statement** The author declares that he has no competing financial interests.

**Correspondence** and requests for materials should be addressed to R.D.G. ([ffrdg@uaf.edu](mailto:ffrdg@uaf.edu)).

.....

## Upwelling-driven nearshore hypoxia signals ecosystem and oceanographic changes in the northeast Pacific

Brian A. Grantham<sup>1\*</sup>, Francis Chan<sup>2\*</sup>, Karina J. Nielsen<sup>4\*</sup>, David S. Fox<sup>5</sup>, John A. Barth<sup>3</sup>, Adriana Huyer<sup>3</sup>, Jane Lubchenco<sup>2</sup> & Bruce A. Menge<sup>2</sup>

<sup>1</sup>Washington State Department of Ecology, Coastal and Estuarine Assessment Unit, Olympia, Washington 98504, USA

<sup>2</sup>Oregon State University, Department of Zoology and

<sup>3</sup>College of Oceanic and Atmospheric Sciences, Corvallis, Oregon 97331, USA

<sup>4</sup>Sonoma State University, Department of Biology, Rohnert Park, California 94928, USA

<sup>5</sup>Oregon Department of Fish and Wildlife, Marine Resources Program, Newport, Oregon 97365, USA

\* These authors contributed equally to this work

Seasonal development of dissolved-oxygen deficits (hypoxia) represents an acute system-level perturbation to ecological dynamics and fishery sustainability in coastal ecosystems around the globe<sup>1–3</sup>. Whereas anthropogenic nutrient loading has increased the frequency and severity of hypoxia in estuaries and semi-enclosed seas<sup>3,4</sup>, the occurrence of hypoxia in open-coast upwelling systems reflects ocean conditions that control the delivery of oxygen-poor and nutrient-rich deep water onto continental shelves<sup>1</sup>. Upwelling systems support a large proportion of the world's fisheries<sup>5</sup>, therefore understanding the links between changes in ocean climate, upwelling-driven hypoxia and ecological perturbations is critical. Here we report on the unprecedented development of severe inner-shelf (<70 m) hypoxia and resultant mass die-offs of fish and invertebrates within the California Current System. In 2002, cross-shelf transects revealed the development of abnormally low dissolved-oxygen levels as a response to anomalously strong flow of subarctic water into the California Current System. Our findings highlight the sensitivity of inner-shelf ecosystems to variation in ocean conditions, and the potential impacts of climate change on marine communities.

Large-scale fluctuations in ocean climate, such as the El Niño/Southern Oscillation and the Pacific Decadal Oscillation, dominate inter-annual and inter-decadal variability in ocean biology<sup>6</sup>. Iden-

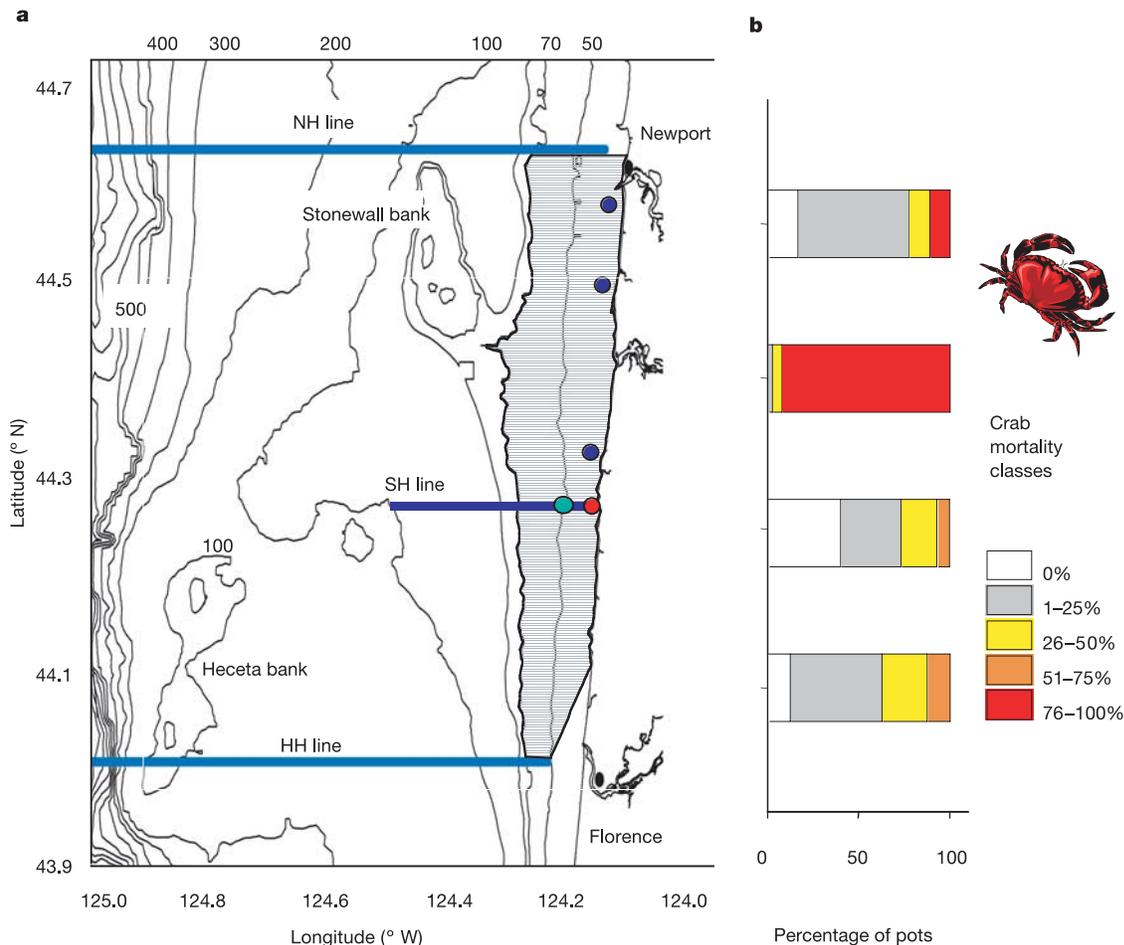
tifying the direct and indirect pathways through which basin-scale changes in ocean conditions act on coastal systems is a central challenge in forecasting the sensitivity and resilience of upwelling ecosystems to climate change. Whereas increases in thermocline depth and upwelling forcing are predicted responses of eastern boundary current systems to climatic warming<sup>7,8</sup>, the net impacts of regional transport and biogeochemical modifications on the structure and dynamics of coastal ecosystems remain poorly resolved. Assessments of contemporary extremes in ocean conditions offer one direct approach for resolving such uncertainties in ecological sensitivity and response. In summer 2002, anomalous changes in the physical and biogeochemical properties of the California Current System<sup>9,10</sup> provided an unprecedented opportunity to assess the impacts of large-scale changes in ocean conditions on nearshore upwelling ecosystem dynamics.

Severe inner-shelf hypoxia was detected during coastal oceanographic cruises along the 44.65 N to 44.00 N portion of the California Current System (Figs 1a and 2). Between July and September 2002, bottom dissolved-oxygen concentrations of 0.21–1.57 ml l<sup>-1</sup> were found to extend from the shelf break to nearshore stations (2–5 km offshore) along all hydrographic lines (Fig. 2 and Supplementary Fig. 1). Dissolved-oxygen concentrations of <1.43 ml l<sup>-1</sup> are generally considered hypoxic<sup>11</sup>. Inner-shelf cruises within this region along the Strawberry Hill (SH) line recorded bottom dissolved-oxygen concentrations of <1.0 ml l<sup>-1</sup>

within 700 m of the surf zone, confirming the development of hypoxia as a shelf-wide phenomenon. At the observed height of hypoxia, dissolved-oxygen-deficient bottom waters occupied up to 40 m of the water column (Supplementary Fig. 2a). Transect data from combined cruises indicate that hypoxic conditions covered at least 820 km<sup>2</sup> of shelf area inshore of the 70-m isobath (Fig. 1a and Supplementary Fig. 1).

The inner-shelf region of the Oregon coast encompasses habitats for several fish populations of important management concern<sup>12</sup>. The effects of hypoxia on benthic fish and invertebrate communities were marked. During remotely operated vehicle (ROV) video surveys, only dead fish and dead or moribund invertebrates were found on patch reefs adjacent to the SH line (Fig. 3). In contrast, rockfish densities in previous years averaged 12.8 per 100 m<sup>2</sup> (Fig. 3) and invertebrate die-offs were not observed in previous surveys. Commercial fishery data revealed crab (*Cancer magister*) mortality to be >75% in crab pots (Fig. 1b) compared with the normal 0%. The Oregon Department of Fish and Wildlife (ODFW) received concurrent reports of large numbers of dead fish and invertebrates washing ashore within the affected region, consistent with our own field observations. Scuba divers reported unusually large aggregations of fish in shallow (<25 m) waters<sup>13</sup>. These unusual observations are consistent with organisms suffocating or seeking oxygen refugia in shallow but atypical habitats.

The development of severe hypoxia in the shallowest reaches of



**Figure 1** Location of the 2002 hypoxic zone and hydrographic transects off Oregon. **a**, Annual ROV patch reef surveys (green circle). Additional hydrographic stations (blue circles) and the acoustic Doppler current profiler (ADCP) location (red) are indicated. The

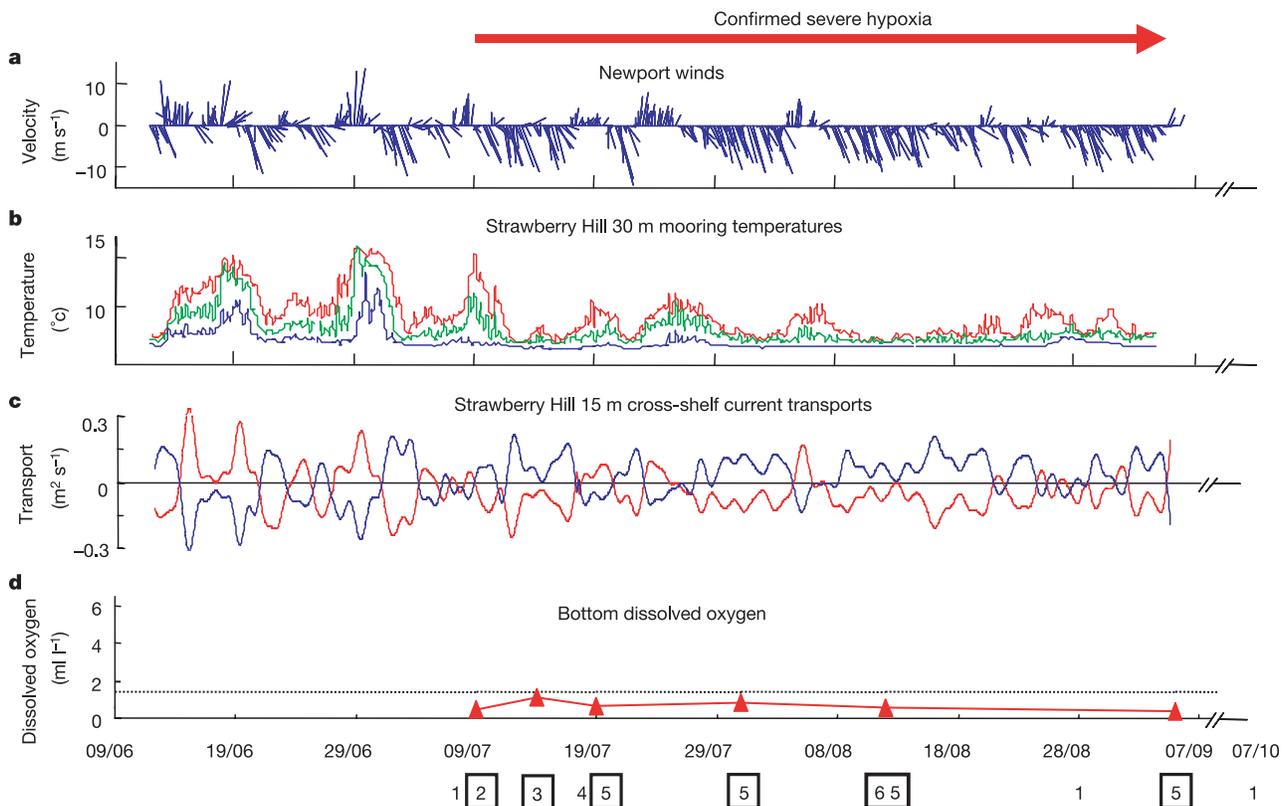
minimum estimated spatial extent of the severe hypoxic zone over the inner shelf (~820 km<sup>2</sup>) is shown (grey). **b**, Proportional mortality of crabs (sampled 16, 17 July 2002) among 80 crab pots deployed within four regions of the hypoxia zone.

the open coast (inshore of the 30-m isobath) is surprising given the potential for air–sea  $O_2$  equilibration during periods of strong turbulent mixing. Significant wave heights reached over 3 m during the hypoxic period. Strong winds favouring upwelling were nevertheless ineffective in eroding stratification on the inner shelf (Fig. 2a, b). Cross-shelf transects revealed the presence of dissolved-oxygen-depleted water offshore on all hydrographic lines (Supplementary Fig. 1). Upwelling forcing thus resulted in the net shoreward transport of cold, saline, dissolved-oxygen-depleted deep water onto the inner shelf (Fig. 2b, c). All bottom dissolved-oxygen values recorded for stations along the 40–55-m isobaths fell below  $1.43 \text{ ml l}^{-1}$ , suggesting that hypoxia was persistent for at least the 60-day period bracketed by shipborne observations (Fig. 2d). Although upwelling of the dissolved-oxygen-deficient bottom water can create hypoxic conditions over the outer shelf, the development of severe hypoxia inshore of the 70-m isobath is atypical and hypoxia-induced marine life die-offs have not previously been recorded for the Oregon shelf. The anomalous nature of the 2002 hypoxic event is strongly evident when compared with recent and historical records (see Methods). Shelf stations along the Newport Hydrographic line exhibited bottom dissolved-oxygen values that were sharply depressed relative to upwelling season means (Fig. 4a, b).

Summertime upwelling induces the transport of deep-sea water that is low in dissolved oxygen onto continental shelves, and results in the intersection of nutrient-rich halocline water with the sea

surface<sup>14</sup>. Consequently, the presence of bottom water that is anomalously low in dissolved oxygen across the shelf can reflect decreases in the oxygen content of upwelled source water before its arrival on the shelf, and/or increases in shelf export production in 2002. An extensive oxygen minimum zone (OMZ), where dissolved oxygen falls below  $0.5 \text{ ml l}^{-1}$ , exists along the continental margins of the northeast Pacific Ocean<sup>15</sup>. Off the coast of Oregon the OMZ is usually located off the shelf at depths of 700–900 m (refs 15, 16). The source of water (with salinity of 33.9) that is upwelled into the bottom boundary layer of the inner shelf lies between ~100–200 m (Supplementary Fig. 2), well above the observed upper boundary of the OMZ. Water that has upwelled from these depths typically has dissolved-oxygen concentrations of  $1.8\text{--}3.6 \text{ ml l}^{-1}$  (ref. 16); however, in 2002, dissolved oxygen in source water along the 33.9 isohaline at the shelf break fell to near or below hypoxic levels ( $1.27\text{--}1.67 \text{ ml l}^{-1}$ ) (Fig. 4c).

Although dissolved oxygen had already reached hypoxic levels at the shelf break, respiration can further exacerbate dissolved-oxygen deficits as bottom boundary water transits shoreward over the shelf, particularly if surface organic carbon sources are sizeable. During summer upwelling a coastal jet of the southward-flowing California Current follows the shelf break offshore around Heceta and Stonewall banks<sup>14,17</sup>, with weak mean flows inshore of the two banks over the shelf<sup>18</sup>. Chlorophyll *a* concentrations in this region are consistently higher than those in surrounding areas and are fuelled by outcropping of nutrient-rich water (salinity, 32.8–33.8) from the



**Figure 2** Timeline of observations, both continuous (a–c) and discrete (1–6). Numbers 1–6 below the x axis are positioned along the timeline at the times when the corresponding surveys/station measurements were conducted. Boxed numbers relate to the red triangles in d that are directly above. 1, ODFW survey; 2, GLOBEC NH line; 3, GLOBEC HH line; 4, crab pot retrieval; 5, PISCO SH line; 6, GLOBEC SH line. a, Wind velocities. Negative values represent upwelling-favourable winds. b, Temperatures at

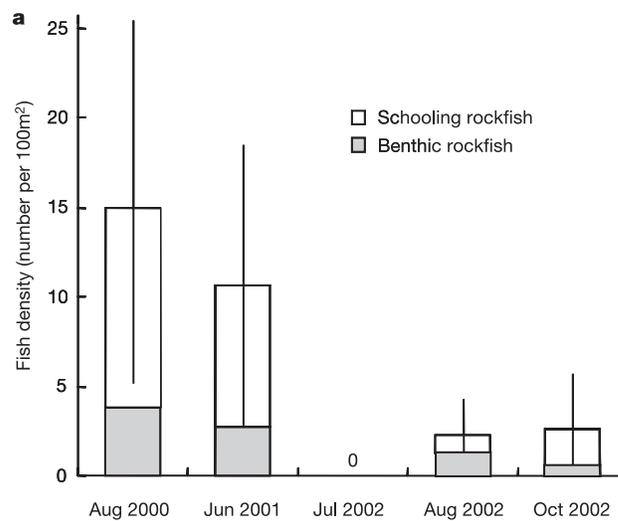
depths of 4 m (red), 14 m (green) and 29 m (blue). c, ADCP-derived cross-shelf transport estimates for surface wind-driven (red) and bottom boundary (blue) layers. Positive values represent onshore flows. d, Bottom dissolved-oxygen concentration (dotted line marks hypoxia threshold) measured at the indicated inner-shelf (40–55 m) stations along the NH, SH and HH lines.

## letters to nature

halocline (Supplementary Fig. 3). In 2002, halocline source water was 1 °C colder and nitrate concentrations were elevated by 11.6  $\mu\text{M}$  (or 64%) over past years<sup>9,10</sup>. As a result, standing stocks of phytoplankton across the bank were two to three times higher than those observed in the four preceding years<sup>19</sup> and surface dissolved oxygen was strongly elevated relative to long-term means (Fig. 4a, b). Inner-shelf chlorophyll *a* concentrations were also high throughout the study (Supplementary Table 1), with maximum concentrations of 219  $\mu\text{g l}^{-1}$  occurring during a massive *Thalassiosira* bloom in mid-August (Supplementary Fig. 2). Dissolved-oxygen concentrations along the 33.9 isohaline decreased from the shelf break to the inner shelf (Supplementary Fig. 1), suggesting that a further depletion of oxygen occurred over the shelf as a result of respiration of fluxed carbon.

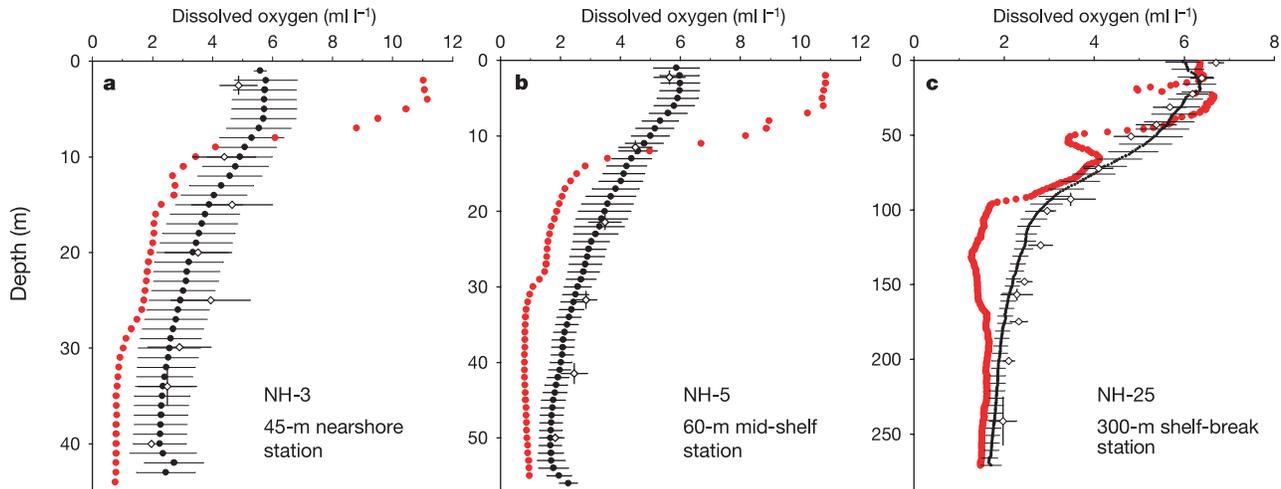
Hypoxia is well documented for other major eastern boundary currents, where its frequency and intensity have been linked to

inter-annual changes in ocean climate<sup>11,20,21</sup>. It now seems that large-scale anomalies in northeast Pacific conditions have given rise to the novel emergence of severe inner-shelf hypoxia in Oregon. In July 2002, the permanent halocline that is present off the coasts of Oregon and Vancouver Island was 1 °C colder, and surface salinities were lower, than in previous years<sup>10</sup>. Data on sea-surface height<sup>22</sup>, drifter tracks<sup>23</sup> and mid-shelf currents<sup>24</sup> suggest an anomalous invasion of nutrient-rich, subarctic water into the California Current System as being the causative agent behind these changes<sup>10</sup>. The observed deviations in the circulation of the California Current System further reflect large-scale wind stress anomalies present over the northeast Pacific in 2002 (ref. 25). Because upwelling transports waters that can be both dissolved-oxygen deficient and nutrient rich onto productive continental-shelf and seamount systems, hypoxia may represent a general and critical link between climatic variability, shifts in ocean circulation and marine ecological change. The



**Figure 3** Impact of hypoxia on rockfish communities. **a**, Densities of schooling and benthic rockfish (*Sebastes* spp.) near the SH line from annual ROV surveys in 2000–02. Both schooling and benthic rockfish densities differed significantly between years (analysis of variance:  $F = 7.75$ , degrees of freedom (d.f.) = 2, 10,  $P = 0.009$ ;  $F = 4.71$ , d.f. = 2, 10,  $P = 0.036$ , respectively). Schooling rockfish were lower in October 2002 than in 2000 or 2001 (Scheffe test:  $P = 0.013$  and  $P = 0.041$ , respectively). Benthic rockfish densities were lower in October 2002 than in 2000

(Scheffe test:  $P = 0.042$ ), but did not differ from 2001 (Scheffe test:  $P = 0.161$ ). Error bars indicate 95% confidence intervals. Rockfish species observed included: black (*Sebastes melanops*), canary (*S. pinniger*), copper (*S. caurinus*), quillback (*S. maliger*), yelloweye (*S. ruberrimus*) and yellowtail (*S. flavidus*) rockfish as well as unidentified juveniles and lingcod (*Ophiodon elongatus*). Lingcod, yelloweye and canary rockfish are classified as 'over-fished' by the National Marine Fisheries Service. **b, c**, ROV survey images of rockfish, August 2000 (**b**) and mortality, July 2002 (**c**).



**Figure 4** Dissolved-oxygen profiles. **a–c**, July 2002 (red circles), recent (black circles) and historical (open diamonds) summertime (July to September) mean ( $\pm 95\%$  confidence intervals) dissolved-oxygen profiles for the nearshore (**a**), mid-shelf (**b**) and

shelf-break (**c**) stations. Recent values span 1998–2001. Historical values cover: **a**, 1967–69, 1972; **b**, 1960–69, 1972; **c**, 1960–69, 1972. NH-3, NH-5 and NH-25 refer to stations along the Newport Hydrographic line.

abrupt emergence of severe shallow-water hypoxia in the California Current System further highlights the importance of ecological thresholds in mediating ecosystem sensitivity to climatic variability, and reinforces the fundamental need for ecosystem-based management of coastal fisheries and habitats. □

**Methods**

**Remotely operated vehicle surveys**

ODFW’s Marine Resources Program began conducting annual surveys of rockfish and rocky reef habitat along the Oregon coast in 2000. The ROV travels ~1 m above the sea floor and records information on fish and habitat to an average maximum distance of 4.5 m out from the vehicle, using a video camera and laser-based measurement system. In July 2002, six strip transects covering a total area of ~250 m<sup>2</sup> were surveyed. Data reports and detailed methods are available online<sup>26</sup>.

**Hydrographic transects**

Since July 1997, the GLOBEC LTOP program has conducted three to five surveys annually along the Newport Hydrographic (NH) and Heceta Head (HH) lines (44.65 N and 44.0 N, respectively). Dissolved oxygen has been measured since August 1998. A GLOBEC SeaSoar<sup>27</sup> survey of the Heceta/Stonewall bank region was conducted from 9–11 July 2002 (Supplementary Fig. 1). The SeaSoar is a towed, undulating platform equipped with a SeaBird SBE9/11 plus conductivity–temperature–depth (CTD) profiler and a WETLabs WETStar fluorometer. On 11 August 2002, temperature, conductivity, depth, dissolved oxygen and chlorophyll *a* fluorescence were sampled at five stations (40–100 m in depth) along the SH line using a SeaBird SBE9/11 plus CTD and a SBE43 dissolved-oxygen sensor, and a Seapoint fluorometer. LTOP and SeaSoar data reports, including methods, are available online<sup>16,27</sup>. Additional historical-dissolved-oxygen data for NH line stations were obtained from the World Ocean Database (<http://www.nodc.noaa.gov>).

Temperature, conductivity and chlorophyll *a* fluorescence were sampled along the SH line and additional nearshore stations on 19 and 31 July, 12 August and 5 September 2002 using a SeaBird SBE25 CTD with a WETLabs WETStar fluorometer. Chlorophyll *a* and dissolved-oxygen concentrations were obtained from Niskin bottle samples. Dissolved oxygen was analysed immediately with a YSI 556 polarographic oxygen meter that was calibrated in subsequent cruises against Winkler titration-based measurements. Chlorophyll *a* samples were filtered on board the research vessel, packed on ice and returned to the laboratory for analysis on a Turner TD-700 fluorometer.

**Moorings-based measurements**

Inner-shelf moorings were deployed at 15- and 30-m depths along the SH line. The 15-m mooring was equipped with a SeaBird SBE 16 conductivity and temperature module. Both moorings were outfitted with the misters (Onset StowAway XTI) that spanned the water column. Estimates of the cross-shelf surface and bottom transports were found using a bottom-mounted ADCP (RD Instruments 600 kHz Workhorse Sentinel) at 15 m along the SH line. Measurements were rotated into their principal axis (4° true), and depth-averaged mean cross-shelf velocities were first subtracted from each velocity profile. The resulting zero-mean profiles were extrapolated vertically to the surface and the bottom, giving a profile that covers the entire water column. The surface (bottom) transport is then defined and computed as the integral of this zero-mean velocity profile from the surface (bottom) down (up) to the first zero crossing. Hourly average transport values were low-pass filtered with a 40-h cutoff to remove tidal variations.

**Crab mortality data**

A commercial fisherman recorded the GPS (global positioning system) coordinates and mortality rates of dungeness crabs (*C. magister*) retrieved from 80 crab pots set inshore of the Heceta/Stonewall bank area. The traps were set at depths of 8–50 m, allowed to soak for 7–10 days and retrieved on 16–17 July 2002. The average number of crabs per pot for each region (Fig. 1) was 21 ( $\pm 3$  s.d.).

Received 12 March; accepted 27 April 2004; doi:10.1038/nature02605.

1. Naqvi, S. W. A. *et al.* Increased marine production of N<sub>2</sub>O due to intensifying anoxia on the Indian continental shelf. *Nature* **408**, 346–349 (2000).
2. Diaz, R. J. Overview of hypoxia around the world. *J. Environ. Qual.* **30**, 275–281 (2001).
3. Rabalais, N. N. & Turner, R. E. in *Coastal Hypoxia: Consequences for Living Resources and Ecosystems* (eds Rabalais, N. N. & Turner, R. E.) 1–36 (American Geophysical Union, Washington DC, 2001).
4. National Research Council. *Coastal Waters: Understanding and Reducing the Effects of Nutrient Pollution* (National Academy Press, Washington DC, 2000).
5. Pauly, D. & Christensen, V. Primary production required to sustain global fisheries. *Nature* **374**, 255–257 (1995).
6. Chavez, F. P., Ryan, J., Lluch-Cota, S. E. & Niquen, M. From anchovies to sardines and back: Multidecadal change in the Pacific Ocean. *Science* **299**, 217–221 (2003).
7. Bakun, A. Global climate change and intensification of coastal ocean upwelling. *Science* **247**, 198–201 (1990).
8. Roemmich, D. & McGowan, J. Climatic warming and the decline of zooplankton in the California Current. *Science* **267**, 1324–1326 (1995).
9. Wheeler, P. A., Huyer, A. & Fleischbein, J. Cold halocline, increased nutrients and higher productivity off Oregon in 2002. *Geophys. Res. Lett.* [online] **30**, 8021 (2003) (doi:10.1029/2003GL017395).
10. Freeland, H. J., Gatién, G., Huyer, A. & Smith, R. L. Cold halocline in the northern California current: an invasion of subarctic water. *Geophys. Res. Lett.* [online] **30**, 1141 (2003) (doi:10.1029/2002GL016663).
11. Diaz, R. J. & Rosenberg, R. Marine benthic hypoxia: a review of its ecological effects and the behavioural responses of benthic macrofauna. *Oceanogr. Mar. Biol. Ann. Rev.* **33**, 245–303 (1995).
12. National Marine Fisheries Service. *Our Living Oceans* (NOAA Technical Memo NMFS-F/SPO-41, US Department of Commerce, Washington DC, 1999).
13. Dillman, T. *Abundance of Fish on Area Reefs Delights, Puzzles Divers* (Newport News-Times, Newport, Oregon, 2002).
14. Huyer, A. Coastal upwelling in the California current system. *Prog. Oceanogr.* **112**, 259–284 (1983).
15. Kamykowski, D. & Zentara, S. J. Hypoxia in the world ocean as recorded in the historical data set. *Deep-Sea Res.* **37**, 1861–1874 (1990).
16. Fleischbein, J. Northeast Pacific long term observation program. *US GLOBEC* (<http://ltop.coas.oregonstate.edu/~ctd/>) (2003).
17. Huyer, A., Smith, R. L. & Pillsbury, R. D. Observations in a coastal upwelling region during a period of variable winds (Oregon coast, July 1972). *Tethys* **6**, 391–404 (1974).
18. Oke, P. R. *et al.* A modelling study of the three-dimensional continental shelf circulation off Oregon. Part I: Model-data comparisons. *J. Phys. Oceanogr.* **32**, 1360–1382 (2002).
19. Thomas, A. C., Strub, T., Brickley, P. & James, C. Anomalous satellite-measured chlorophyll concentrations in the northern California Current in 2001–2002. *Geophys. Res. Lett.* [online] **30**, 8022 (2003) (doi:10.1029/2003GL017409).
20. Bailey, G. W., Beyers, C. J. B. & Lipschitz, S. R. Seasonal variation of oxygen deficiency in waters off southern south west Africa in 1975 and 1976 and its relation to the catchability and distribution of the cape rock lobster *Jasus lalandii*. *S. Afr. J. Mar. Sci.* **3**, 197–214 (1985).
21. Morales, C. E., Hormazabal, S. E. & Blanco, J. L. Interannual variability in the mesoscale distribution of the depth of the upper boundary of the oxygen minimum layer off northern Chile (18–24S): Implications for the pelagic system and biogeochemical cycling. *J. Mar. Res.* **57**, 909–932 (1999).
22. Strub, P. T. & James, C. Altimeter estimates of anomalous transports into the northern California Current during 2000–2002. *Geophys. Res. Lett.* [online] **30**, 8025 (2003) (doi:10.1029/2003GL017513).
23. Barth, J. A. Anomalous southward advection during 2002 in the northern California Current:

- evidence from Lagrangian surface drifters. *Geophys. Res. Lett.* [online] **30**, 8024 (2003) (doi:10.1029/2003GL017511).
24. Kosro, P. M. Enhanced southward flow over the Oregon shelf in 2002: a conduit for subarctic water. *Geophys. Res. Lett.* [online] **30**, 8023 (2003) (doi:10.1029/2003GL017436).
25. Murphree, T., Bograd, S. J., Schwing, F. B. & Ford, B. Large-scale atmosphere–ocean anomalies in the northeast Pacific during 2002. *Geophys. Res. Lett.* [online] **30**, 8026 (2003) (doi:10.1029/2003GL017303).
26. Fox, D. S., Amend, M., Merems, A. & Appy, M. Near-shore rocky reef assessment. *Oregon Dept. Fish Wildl. Mar. Prog.* ([http://hmsc.oregonstate.edu/odfw/habitat/reports/2000kelp\\_reef\\_report.pdf](http://hmsc.oregonstate.edu/odfw/habitat/reports/2000kelp_reef_report.pdf)) (2000).
27. O'Malley, R. SeaSoar observations during the Coastal Ocean Advances in Shelf Transport (COAST) mesoscale surveys I and II. (<http://damp.coas.oregonstate.edu/coast/seasoar>) (2003).

Supplementary Information accompanies the paper on [www.nature.com/nature](http://www.nature.com/nature).

**Acknowledgements** We thank A. Kirincich for ADCP analyses, S. Oda and A. Walters for assistance and A. Pazar for crab fishery data. The Partnership for Interdisciplinary Studies of Coastal Oceans, funded by the David and Lucile Packard Foundation, and the US GLOBEC program, jointly funded by NSF and NOAA, both contributed to this work. J.A.B. acknowledges additional funding from NSF. ODFW ROV survey work was funded in part by the Oregon Department of Land Conservation and Development through NOAA.

**Competing interests statement** The authors declare that they have no competing financial interests.

**Correspondence** and requests for materials should be addressed to F.C. ([chanft@science.oregonstate.edu](mailto:chanft@science.oregonstate.edu)).

## Enhanced partner preference in a promiscuous species by manipulating the expression of a single gene

Miranda M. Lim<sup>1</sup>, Zuoxin Wang<sup>2</sup>, Daniel E. Olazábal<sup>1</sup>, Xianghui Ren<sup>3</sup>, Ernest F. Terwilliger<sup>3</sup> & Larry J. Young<sup>1</sup>

<sup>1</sup>Center for Behavioral Neuroscience and Department of Psychiatry and Behavioral Sciences, Emory University, Atlanta, Georgia 30322, USA

<sup>2</sup>Department of Psychology and Neuroscience Program, Florida State University, Tallahassee, Florida 32306, USA

<sup>3</sup>Harvard Institutes of Medicine and Beth Israel Deaconess Medical Center, Boston, Massachusetts 02115, USA

The molecular mechanisms underlying the evolution of complex behaviour are poorly understood. The mammalian genus *Microtus* provides an excellent model for investigating the evolution of social behaviour. Prairie voles (*Microtus ochrogaster*) exhibit a monogamous social structure in nature, whereas closely related meadow voles (*Microtus pennsylvanicus*) are solitary and polygamous<sup>1</sup>. In male prairie voles, both vasopressin and dopamine act in the ventral forebrain to regulate selective affiliation between adult mates, known as pair bond formation, as assessed by partner preference in the laboratory<sup>2–4</sup>. The vasopressin V1a receptor (V1aR) is expressed at higher levels in the ventral forebrain of monogamous than in promiscuous vole species<sup>5</sup>, whereas dopamine receptor distribution is relatively conserved between species. Here we substantially increase partner preference formation in the socially promiscuous meadow vole by using viral vector V1aR gene transfer into the ventral forebrain. We show that a change in the expression of a single gene in the larger context of pre-existing genetic and neural circuits can profoundly alter social behaviour, providing a potential molecular mechanism for the rapid evolution of complex social behaviour.

Fewer than 5% of mammalian species have a monogamous social structure, which typically includes pair bond formation between

adult mates and the biparental care of offspring<sup>6</sup>. Central administration of vasopressin facilitates each of these monogamous-typical behaviours in male prairie voles through V1aRs in the brain<sup>7–9</sup>. The distribution of V1aRs in the brain varies considerably between monogamous and promiscuous vole species<sup>5</sup> (Fig. 1).

Species-specific patterns of V1aR expression have provided insight into the neural mechanisms underlying pair bond formation. In particular, the ventral pallidum, located within the ventral forebrain and the mesolimbic dopamine reward pathway, highly expresses V1aRs in monogamous prairie and pine voles (*Microtus pinetorum*), but not in promiscuous meadow or montane voles (*Microtus montanus*)<sup>5,10</sup>. Site-specific infusion of a selective V1aR antagonist into the ventral pallidum blocks pair bond formation in prairie voles<sup>4</sup>. Ventral forebrain V1aR expression is also higher in both the monogamous *Peromyscus* California mouse and the monogamous marmoset monkey than in promiscuous *Peromyscus* or primate species<sup>11–14</sup>. Thus, V1aRs in the ventral forebrain are crucial for pair bond formation, and this V1aR pattern seems to be correlated with monogamous social organization across diverse taxa.

Although genetic analysis of V1aR shows more than 99% conservation of gene sequence between vole species, monogamous prairie and pine voles have an expansion of repetitive microsatellite DNA in the 5' regulatory region of the gene, whereas promiscuous montane and meadow voles do not<sup>9</sup>. Furthermore, species-specific V1aR expression patterns seem to be determined by proximate regulatory sequences of the gene, because mice transgenic for the prairie vole V1aR coding sequence and its flanking regions display prairie-like patterns of V1aR binding in the brain<sup>9</sup>. Because microsatellite DNA is highly unstable, it is possible that instability in the V1aR regulatory region could result in altered V1aR expression in different brain regions, leading to differences in social behaviour. We proposed that increased V1aRs in the ventral pallidum, in particular, could shift some individuals within a species to form pair bonds and ultimately result in the stable selection of monogamous social organization. To test this hypothesis directly, we used viral vector-mediated gene transfer to overexpress V1aR in the ventral pallidum in the socially promiscuous meadow vole, in essence recreating a singular evolutionary event in the laboratory.

The study consisted of three groups of meadow voles. The experimental group (V1aR-vp) overexpressed V1aR bilaterally in the ventral pallidum ( $n = 11$ ). The first control group (Ctrl-vp) received ventral pallidal infusions of a vector expressing the *lacZ* gene ( $n = 11$ ). The second control group (Ctrl-other) consisted of animals whose viral injections were inadvertently placed outside the ventral pallidum ( $n = 9$ ); these animals were regressed, *ex post facto*, in the analysis after the completion of behavioural testing. V1aR autoradiography revealed a significant elevation of V1aR binding in the ventral pallidum of the V1aR-vp animals to about threefold that in the two control groups (Fig. 2). This is comparable to the degree of V1aR binding observed in the prairie vole (Fig. 1e).

All animals were paired with a behaviourally receptive female for 24 h, and subsequently placed in a partner preference test in which the animal could access both the partner and a novel female of comparable stimulus value. During the 3-h test, the time spent in side-by-side contact ('huddling') with each female was recorded.

The V1aR-vp group spent significantly more time huddling with the partner than the stranger ( $P < 0.01$ , Student's *t*-test), whereas the Ctrl-vp and Ctrl-other groups did not ( $P > 0.05$ , Student's *t*-test) (Fig. 3a). In addition, all the animals in the V1aR-vp group spent more time huddling with the partner than the stranger (11 of 11), whereas control animals were uniformly distributed across a wide range and did not prefer the partner significantly more than expected by random chance (12 of 20;  $P > 0.05$ ,  $\chi^2$  test) (Fig. 3b). V1aR-vp animals also spent significantly more time in total side-by-side contact with the partner than the control animals ( $P < 0.01$ ,