A silty matrix still adheres to the external left half of the specimen.

For logistic reasons it has not yet been possible to clean, reconstruct and fully study the cranium, so here we offer only a preliminary assessment. For similar reasons the pelvic fragments and incisors are not described here.

A remarkable feature of UA 31 is its great anteroposterior length (204 mm) in relation to its maximum cranial breadth (130 mm). The greatest cranial breadth is located at the level of the supra-mastoid crests and with the length gives a cranial index of 63.7. Although the skull has not yet been restored and cleaned, tentative estimates suggest an endocranial capacity of 750–800 cm^3.

The neurocranium is low compared to its maximum length, but high relative to its transverse diameter. The upper-middle facial skeleton is slightly concave and marked prognathism is evident in the subnasal region. The face is narrow and short. The palate is shallow, wide and short, with its length reaching less than one-third of the total cranial length as seen in basal view. The very heavily built, forwardly projecting supraorbital torus is arched and thickened medially and over the middle of each orbit (17 mm). The minimum frontal breadth is 84.0 mm. Substantial elevation of the forehead and absence of sagittal keeling are evident in frontal view.

The frontal squame is well curved to bregma and the vault outline becomes gradually flatter on the parietals. The temporal lines originate in the form of a raised crest at the posterolateral margin of the supraorbital torus, but disappear early on the parietals. A slightly thickened angular torus is present. There is no nuchal torus, but a modest external protuberance is detectable where opistho-cranion coincides with inion.

The specimen also shows a modest protrusion of the mastoid–supramastoid–auriculare complex lateral to the temporal squame. The mastoid process is short and broad. In coronal section, the parietal walls converge slightly inferiorly (Fig. 3); there is a high positioning of the maximum biparietal breadth (125.0 mm); the parietal thickness progressively decreases up to the midline (from 7.4 to 6.0 mm); the thickness at bregma is 6.3 mm.

The cranium from Buia shows the following combination of features, which are characteristic of the African specimens referred to *Homo erectus* and *Homo ergaster*[11,12]: long ovoid braincase with low endocranial capacity; greatest cranial breadth across the supra-mastoid crests; massive supraorbital torus; opisthocranion coincident with inion. One trait typical of *H. sapiens* is the high position of the greatest biparietal breadth with parietal walls converging slightly inferiorly. This mosaic of primitive and progressive features increases the known morphological variation reported for early–middle Pleistocene *Homo* crania and urges caution in the specific assessment of UA 31. Until we have conducted a full comparative study, we prefer to leave open its specific allocation.

Given its chronological position, in the middle of the time interval 1.4–0.6 Myr, from which no human cranial remains of comparable integrity are known from Africa[13], this unique Eritrean specimen provides a new perspective on the origins of modern humans. Its age indicates that morphology like that of *H. sapiens* had begun to differentiate in Africa at ~1 Myr, which is ~0.3 Myr earlier than previously estimated[1,2,14]. □

1. Bräuer, G., Yokoyama, Y., Falguères, C. & Mbua, E. Modern human origins backdated. *Nature* **386**, 337–338 (1997).
2. Ward R. & Stringer C. Molecular handle on the Neanderthals. *Nature* **388**, 225–226 (1997).
3. Bermúdez de Castro, J. M. *et al.* A hominid from the lower Pleistocene of Atapuerca, Spain: possible ancestor to Neanderthals and modern humans. *Science* **276**, 1392–1395 (1997).
4. Bannert, D. *et al.* Zür Geologie der Danakil Senke (Nördliches Afar Gebiet) NE Aethiopien. *Geol. Rundsch.* **59**, 409–443 (1970).
5. Brinckmann, J. & Kürsten, M. *Geological Sketchmap of the Danakil Depression* (Bundesanstalt für Bodenforshung, Hannover, 1970).
6. Barberi, F. & Varet, J. Volcanism of Afar: small-scale plate tectonics implications. *Geol. Soc. Am. Bull.* **88**, 1251–1266 (1977).
7. Merla, G. *et al. Geological Map of Ethiopia and Somalia 1:2,000,000 and Comment with a Map of Major Landforms* (Centro Stampa, Firenze, 1979).
8. Garland, C.R. *Geological Survey of Ethiopia Memoir* Vol. 1 (Berhanena Selam, Addis Ababa, 1980).
9. Kalb, J. E. *et al.* Geology and stratigraphy of Neogene deposits, Middle Awash valley, Ethiopia. *Nature* **298**, 17–25 (1982).
10. Berggren, W. A., Kent, D. V., Swisher III, C. C. & Aubry, M.-P. A revised Cenozoic geochronology and chronostratigraphy. *SEPM* (special publ.) **54**, 129–212 (1995).
11. Wood, B. *Koobi Fora Research Project* Vol. 4, *Hominid Cranial Remains* (Clarendon, Oxford, 1991).
12. Tobias, P. V. *Olduvai Gorge* Vol. 4, V-IX. *The Skull, Endocasts and Teeth of Homo habilis* (Cambridge University Press, 1991).
13. Wolpoff, M. H. *Human Evolution* (McGraw-Hill, New York, 1997)
14. Clark, J. D. *et al.* African *Homo erectus*: old radiometric ages and young Oldowan assemblages in the Middle-Awash valley, Ethiopia. *Science* **264**, 1907-1909 (1994).

Selective foraging behaviour of basking sharks on zooplankton in a small-scale front

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The basking shark *Cetorhinus maximus* is the second largest fish species, attaining lengths of up to 11 m. During summer months in temperate coastal waters circumglobally, these sharks filter-feed on surface zooplankton[1–4] near water-mass boundaries (fronts)[5,6]; however, little else is known about their biology[1]. Their foraging behaviour has not been investigated until now, although they have been described[2] as indiscriminate planktivores that are unlikely to orientate to specific plankton-rich waters. We have now tracked basking sharks responding to zooplankton gradients. We show that they are selective filter-feeders that choose the richest, most profitable plankton patches. They forage along thermal fronts and actively select areas that contain high densities of large zooplankton above a threshold density. They remain for up to 27 hours in rich patches that are trans-ported by tidal currents and move between patches over periods of 1–2 days. We mapped feeding locations of these sharks in two years; the maps show that these sharks indicate broad shifts in front-located secondary production. Foraging behaviour of bask-ing sharks therefore indicates the distribution, density and char-acteristics of zooplankton directly. This makes these sharks unique biological 'plankton recorders', with potential use as detectors of trends in abundance of zooplankton species that are influenced by climatic fluctuations of the North Atlantic Oscillation[7].

Natural foraging behaviour of filter-feeding marine fishes is poorly understood because of the problems associated with tracking them and quantifying food abundance simultaneously. However, the basking shark spends long periods feeding at the waters' surface, a behaviour that allows study of this shark by tracking, observation of active feeding, and sampling of zooplankton prey. During May–July in 1996 and 1997, we tracked visually the movements of aggregations of feeding sharks ($n = 13$ groups) and the fine-scale foraging movements of individual basking sharks ($n = 14$), and measured zooplankton density on their swimming paths off Plymouth, southwest England (50° 16 N 004° 09 W). We also recorded the positions of basking sharks sighted in addition to those tracked. During 1996 and 1997, we observed 58 and 54 different sharks, respectively.

Foraging locations of basking sharks seen during May–July in 1996–97 were orientated along a seasonal boundary separating coastal inshore water off Plymouth from fully stratified water of the

northern side of the western English Channel (Fig. 1). The Plymouth front has been characterized by previous studies[8–14] and lies approximately 8 km offshore, defined by the 14–16 °C contours that outcrop at the sea's surface[14,15]. The front's approximate position in 1996 was determined from an infrared image of sea surface temperature (SST) taken on 6 June 1996, when we tracked 11 sharks.

A temperature transect across this position confirmed the presence of the front, with a gradient of 1.5 °C (between mean temperatures 12.3 °C and 13.8 °C) over a horizontal distance of 4.1 km, corroborating the remotely sensed determinations (Fig. 1). Close to, we could see the front by the presence of narrow strips of flat water (slicks) next to rippled water[16–18].
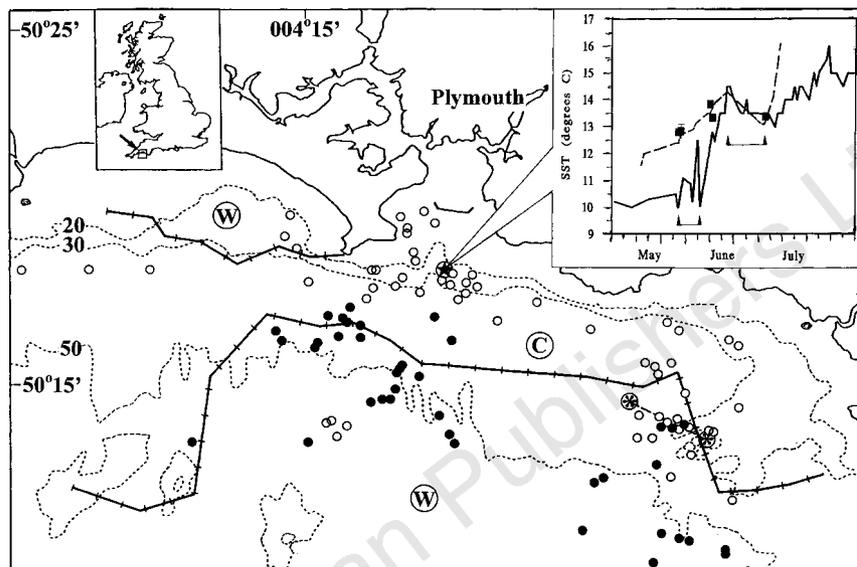
Figure 1 Distribution of surface-foraging basking sharks and changes in summer SST. The main figure shows the distribution of surface-foraging basking sharks in May–July, 1996 (open small circles, $n = 58$) and 1997 (filled circles, $n = 39$). Location points mark the extent of foraging locations. Bold ticked lines represent thermal-front boundaries between warm stratified water (W, 14–16 °C) and cooler mixed water (C, 12–13 °C) drawn from an infrared SST image from AVHRR channel 4 (NOAA-14 satellite) at 12:31, 6 June 1996. Tick marks are 1 km apart. Circled asterisks joined by a dashed line indicate the SST (5 m depth) transect position across the front at 12:00–13:00, 17 June 1996. The top right inset shows the change in summer SST at the SST-sampling station, S1, in 1996 and 1997. Horizontal square brackets delimit periods of SST fluctuation. Filled squares represent mean SST while we were tracking individual basking sharks in 1997. Vertical bars denote ± 1 s.e.m. Dashed line, 1997 (2 m depth); complete line, 1996 (5 m depth). Dotted lines denote contour depths (20, 30, 50 m) and ticked lines are frontal boundaries.
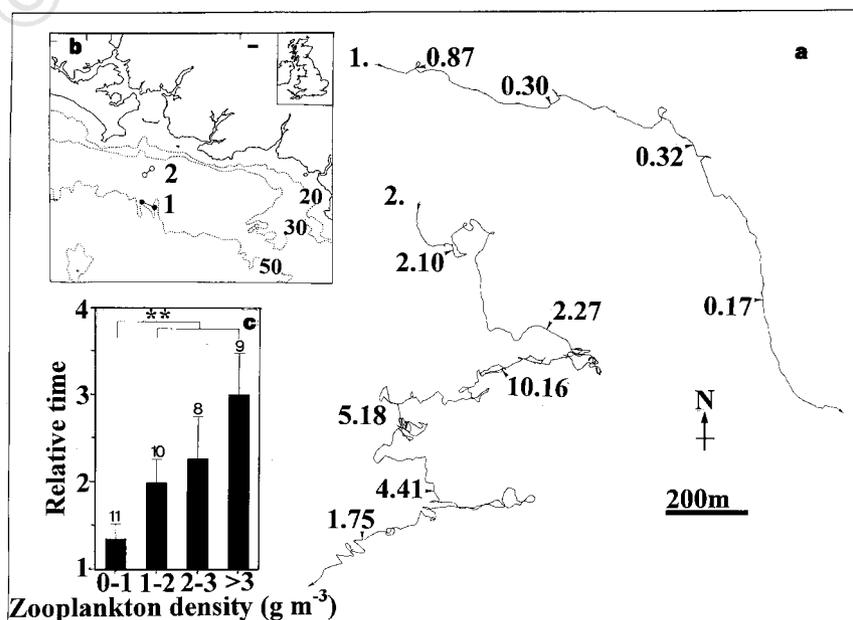
Figure 2 Feeding behaviour of basking sharks in relation to zooplankton density. **a**, Representative fine-scale-foraging tracks of two basking sharks responding to the zooplankton densities that they encountered. Track 1, swimming path of a shark (4 m L_T); L_T is total length) tracked for 0.5 h (11:40–12:10, 30 May 1997). Track 2, foraging path for a different shark (4 m L_T) tracked for 1.7 h (08:20–10:02 h, 12 June 1997). Numbers along each track denote zooplankton densities sampled in the sharks' paths in g wet weight per m³. **b**, Positions of trackings in relation to coastline and bathymetry off Plymouth. **c**, Relationship between zooplankton-density class and the time that 14 basking sharks spent filter-feeding within 25 m of the zooplankton-sample locations. A relative time of 1 equals 50 s. Vertical bars denote ± 1 s.e.m. Figures above bars represent n zooplankton samples. Two asterisks represent $P < 0.01$.

The distribution of basking sharks off Plymouth reflected broadly the front's known geographic position, indicating that the sharks may have concentrated their foraging activity along the boundary, generally in well mixed, cooler water (Fig. 1). However, in 1996, 91.5% of foraging locations were closest to the depth contours at 20–30 m, whereas in 1997 87.2% of locations were nearer to the 50-m contour, a further 4–7 km offshore (Fig. 1). Plymouth frontal sharpness varies according to the weather, as mixed inshore water becomes partly stratified, and hence warmer, in calm conditions[13,14]. The predominance of strong easterly winds in May and early June 1997 may have extended the inshore zone of vertically mixed water, thereby locating the front further offshore. Later in the summer in both years, temperature fluctuations of 2.6–3.0 °C at the SST-sampling station, S1 (Fig. 1, inset), followed by large increases in SST, coincided with periods of calm weather, which would be consistent with decreased front sharpness as inshore water stratified. Sharks were seldom seen when high SSTs (indicative of front breakdown) were recorded at S1. Hence, foraging basking sharks may indicate weather-induced changes in location and persistence of the front between years, as well as indicating the broad position of the front.

Surface-feeding basking sharks followed convoluted swimming paths along tidal slicks associated with the front, exhibiting area-restricted searching (ARS) behaviour where zooplankton densities were measured to be high ($>1\,\mathrm{g\,m^{-3}}$) (Fig. 2a, b). As a consequence of this localized feeding response, the 14 sharks tracked spent 48%, 69% and 123% longer time feeding in locations where zooplankton densities were 1–2, 2–3, and $>3\,\mathrm{g\,m^{-3}}$, respectively, compared with the time spent in areas with $<1\,\mathrm{g\,m^{-3}}$ zooplankton (Kruskal-Wallis test: $H_c = 11.22$, $\chi^2_{0.05,3} = 7.82$, $P < 0.025$; with multiple comparisons, $Q_{0.05,4} = 2.64$, $Q = 3.32$, $P < 0.01$; Fig. 2c). Densities of $<1\,\mathrm{g\,m^{-3}}$ did not produce well defined ARS behaviour in six different sharks (Fig. 2c), which generally continued swimming on a relatively straight, non-convoluted course (see, for example, track 1 in Fig. 2a). Thus, zooplankton densities close to $1\,\mathrm{g\,m^{-3}}$ could represent the threshold below which it becomes increasingly less profitable to filter-feed.

Although time spent foraging by ten different sharks in zooplankton densities above the observed threshold showed a graded increase with productivity, mean times were not significantly different (multiple comparison: $Q = 1.51$, $P > 0.50$; Fig. 2c) because of greater temporal variability in ARS behaviour. We speculate that sharks already feeding on dense patches of zooplankton showed greater variability in food-orientated activity because prey was not limiting. Sharks feeding in zooplankton densities below $1\,\mathrm{g\,m^{-3}}$ exhibited less variable foraging responses (that is, they swam in a straight course), a behaviour that could act to increase the horizontal distance covered and consequently their chances of encountering new, more productive patches.

Basking sharks surface-feed in areas in which the dominant calanoid copepod prey, *Calanus helgolandicus*, is 2.5 times as numerous (~1,500 organisms per m^3) and 50% longer (~2 mm),
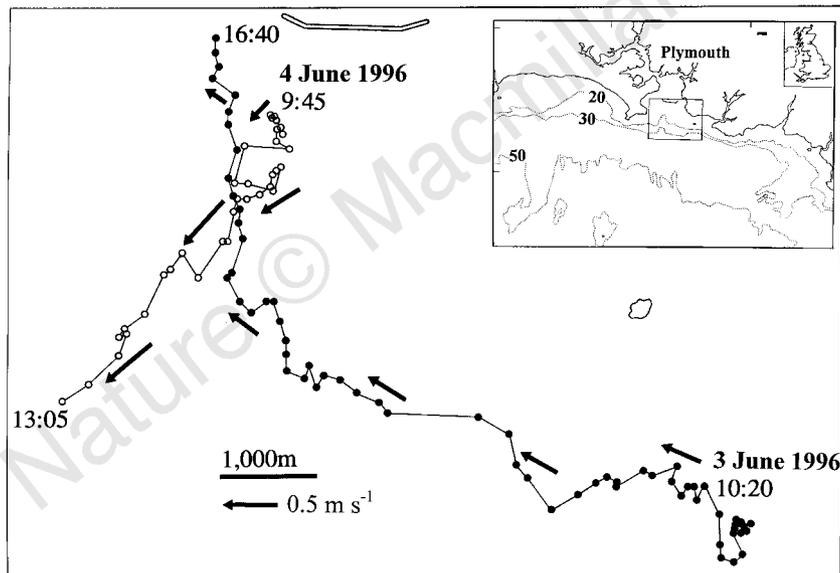
Figure 3 Movements of a feeding group of basking sharks over two consecutive days (3 June 1996, filled circles, and 4 June 1996, open circles). Position markers are given for every 5–10 min, with arrows denoting the direction of the tidal stream at hourly intervals during tracking. Tidal-stream speed is proportional to the length of the arrow.

Table 1 Group tracking data

Track date	Duration (h)	Number of sharks	Minimum distance covered (km)	Mean tidal-stream speed (m s⁻¹)	Mean shark heading (degrees)	Mean tidal-stream direction (degrees)	Difference between shark heading and tidal-stream direction (degrees)
10.5.96	1.9	3	1.9	0.2	62.7	59.8	2.9
17.5.96	3.6	5	7.1	0.3	264.3	261.7	2.6
28.5.96	2.9	2	4.2	0.2	–	–	–
3.6.96	6.3	5	12.6	0.3	317.6	318.2	0.6
4.6.96	3.3	3	6.2	0.5	200.2	223.7	23.5
5.6.96	2.5	6	4.7	0.2	271.5	267.3	4.2
6.6.96	4.2	11	7.2	0.3	151.3	133.8	17.5
7.6.96	3.0	12	7.4	0.2	133.3	147.6	14.3
12.6.96	0.8	3	1.2	0.2	233.5	251.5	18.0
8.7.96	1.3	2	2.3	0.2	102.2	98.7	3.5
9.7.96	1.1	2	2.0	0.2	82.7	75.0	7.7
17.7.96	3.0	4	5.4	0.2	–	–	–
13.6.97	1.4	6	1.8	0.1	116.5	149.6	33.1

than in areas in which sharks do not feed[19]. In the feeding areas there are also fewer numbers of smaller zooplankton species, and therefore the biomass per cubic metre where sharks' forage is significantly increased[19]. These and our present results indicate that basking sharks may orientate to specific zooplankton prey by exhibiting ARS behaviour in response to fine-scale variations in zooplankton quantity and quality. In this way the basking sharks could locate the densest, most energy-rich patches. The sensory systems used by basking sharks to achieve these behaviours are unknown, but could involve electroreception[20] of copepod muscle activity and olfaction of dimethyl sulphide, which is produced by phytoplankton when grazed by zooplankton and is used as a foraging cue by some seabirds[21].

Course headings of groups of foraging basking sharks followed closely the directions of tidal streams, indicating that they remained in, and tracked the movements of, productive patches transported by currents for at least 0.8–6.3 h (Fig. 3 and Table 1). Over distances travelled daily of 1.2–12.6 km, the headings of basking sharks compared with tidal-stream directions showed a mean difference of only 11.6° (±3.2 s.e.m., $n = 11$; Table 1). One feeding group followed a productive patch as it was transported towards Plymouth Sound (Fig. 3), and, after one tidal cycle, was found to be tracking the patch back out to sea with the second outgoing tide. The minimum estimated time over which this feeding group remained in this patch was 27 h and the minimum distance that the patch and sharks moved was 18.8 km (track dates 3.6.96 and 4.6.96 in Table 1).

Our tracking studies also indicated movements of sharks between patches over periods of 1–2 days. Along the Plymouth front during 1996–97 (Fig. 1a), we relocated (separately) three sharks feeding in different patches 18–28 h after our first trackings and 5–11 km distant from initial foraging areas of the previous day. Two sharks that originally fed in the same patch moved in similar directions along a zooplankton gradient from low to higher density (range: 0.47–1.11 g m^{-3} to 1.06–1.43 g m^{-3}), covering minimum distances of 9.5 km and 10.6 km in 27.6 h and 23 h respectively. The third shark was relocated feeding in slightly lower densities than 17.9 h earlier, and 4.7 km distant from the calculated new position of the first patch. These results indicate that basking sharks may move between patches, probably in response to low zooplankton densities encountered previously, minimizing travelling time between patches by using frontal boundaries to find successive patches in close proximity.

The areas where basking sharks foraged were also used by commercially important shoaling fishes. When tracking sharks along tidal slicks, large fish shoals appeared frequently on our echosounder, and fish were often seen thrashing the water's surface when feeding, sometimes doing so immediately ahead of feeding sharks. We identified large shoals of mackerel (*Scomber scombrus*), small whiting (*Merlangius merlangus*) and grey mullet (*Chelon labrosus*) near sharks. We also noted the activity of the northern gannet (*Sula bassana*) when tracking sharks. Around Britain and Ireland, gannets feed on shoaling fishes (length range 2.5–30.5 cm), primarily herring (*Clupea harengus*), sprat (*Sprattus sprattus*), mackerel, cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*) and small whiting[22]. We saw gannets diving and resting at the surface within the sharks' foraging areas during 22 of our 27 trackings (82%). This indicates that western Channel fronts are important hydrographic features for commercial teleosts as well as sharks.

Thus, basking sharks foraged for longer periods in patches with high zooplankton density above a threshold density of 1 g m^{-3}; these patches contained more numerous large prey. The highest densities produced the most prolonged ARS responses. Basking sharks also tracked tidally transported planktonic patches and moved between patches within fronts over broader temporal and spatial scales (10–20 km in 1–2 days). Mapping their foraging locations indicated the position of a seasonal front, and indicated a westward shift in

biological front location between 1996 and 1997, perhaps because of weather conditions. Basking sharks exhibit predictable ARS behaviour in response to specific zooplankton densities and characteristics[19] and follow and move between tidally transported patches in fronts, identifying the basking shark as a selective forager on zooplankton assemblages; this behaviour was previously unknown.

As fronts show enhanced production of plankton[16,23,24], attended by increased fish stocks[15,17,25], identifying frontal regions from new satellite-derived ocean-colour data of phytoplankton abundance (for example, using SeaWiFS) may help indirectly in studies of zooplankton and fish distribution[26]. However, basking sharks integrate a planktivorous fish's behaviour with zooplankton abundance directly. In addition, fluctuations in the abundance of two *Calanus* species (upon which basking sharks feed) are closely linked to the state of the North Atlantic Oscillation[7], emphasizing the influence of climate variations on zooplankton. Thus we propose that basking sharks are potentially useful detectors of the distribution, density and characteristics of these zooplankton in fronts, and could provide cheap, high-trophic-level biological indication of fluxes in zooplankton assemblages that are affected by oceanographic and climatic fluctuations in the North Atlantic. □

Methods

Fish tracking. We located surface-foraging basking sharks by visual survey from a 10-m research vessel. We stayed within 10–50 m of sharks during tracking, except when zooplankton sampling, plotting our location using a global positioning system (GPS) (Garmin 120S) every 5–10 min. Fine-scale-foraging routes were determined by vectors, using the time each shark spent on successive course headings (obtained from a hand-held digital compass, with headings recorded in real time on audiotape) multiplied by the mean feeding-swimming speed, to calculate estimated distance travelled between course deviations. Feeding-cruising speeds were measured for six sharks using onboard differential GPS (Valsat 03, MLR Electronics, France) and a digital flowmeter (Solomat 520c) attached to a towed propellor (General Oceanics 2030R, USA). Under the feeding conditions observed, basking shark swimming speeds remained relatively constant at 0.97 m s^{-1} (±0.03 s.e.m., $n = 59$ determinations; mean shark length = 4.7 m ± 1.1 s.e.m.). Tracks were reconstructed graphically using the compass headings and data on distance travelled. Data on tidal-stream direction and speed for each track were calculated from data given on Admiralty Chart number 1613 (Crown Copyright 1995, Hydrographic Office, UK) made at tidal-stream recording stations A–D, located at: A, 50° 18.3 N 4° 10.8 W; B, 50° 18.3 N 4° 07.7 W; C, 50° 12.5 N 4° 05.2 W; and D, 50° 07.7 N 3° 55.2 W. Recording stations A and B are positioned on the 20-m contour in the western and eastern approaches to Plymouth Sound, respectively. The SST sampling station (S1) lies at a position equidistant to A and B at a distance of 1.8 km. Tidal-stream recording stations C and D are located near the frontal boundary.

Zooplankton and water-temperature sampling. Zooplankton samples were taken within 3 m of feeding paths of sharks and analysed using described methods[1,19]. One to six samples were taken per individual fish track. Water temperature was taken with a Yellow Springs Instruments model 58 meter and a standard mercury thermometer with minimum–maximum markers.

Track analysis. The time sharks spent foraging near measured zooplankton densities was quantified by drawing a circular area of interest (AOI) around each sample location on each shark's graphically reconstructed foraging track. The AOI radius was set at 25 m; this area was to analyse activity at each zooplankton-sample location on all tracks. The length of track falling within each AOI, indicating the degree of localization of foraging responses, was measured (in mm) on track reconstructions and converted to time in seconds, as distance covered at a uniform cruising speed was directly proportional to time. The degree of dispersion of foraging time between zooplankton-density classes was examined with a Kruskal-Wallis test with tied ranks, performed with non-parametric multiple comparisons for unequal sample sizes[27].

1. Sims, D. W., Fox, A. M. & Merrett, D. A. Basking shark occurrence off south-west England in relation to zooplankton abundance. *J. Fish Biol.* **51,** 436–440 (1997).

2. Matthews, L. H. & Parker, H. W. Notes on the anatomy and biology of the basking shark (*Cetorhinus maximus* (Gunner)). *Proc. Zool. Soc. Lond.* **120**, 535–576 (1950).

3. Kenney, R. D., Owen, R. E. & Winn, H. E. Shark distributions off the northeast United States from marine mammal surveys. *Copeia* 1985, 220–223 (1985).

4. Berrow, S. D. & Heardman, C. The basking shark *Cetorhinus maximus* (Gunnerus) in Irish waters—patterns of distribution and abundance. *Proc. R. Irish Acad. B* **94**, 101–107 (1994).

5. Priede, I. G. A basking shark (*Cetorhinus maximus*) tracked by satellite together with simultaneous remote sensing. *Fish. Res.* **2**, 201–216 (1984).

6. Choy, B. K. & Adams, D. H. An observation of a basking shark, *Cetorhinus maximus*, feeding along a thermal front off the east-central coast of Florida. *Florida Sci.* **58**, 313–319 (1995).

7. Fromentin, J.-M. & Planque, B. *Calanus* and environment in the eastern North Atlantic. II. Influence of the North Atlantic Oscillation on *C. finmarchicus* and *C. helgolandicus*. *Mar. Ecol. Prog. Ser.* **134**, 111–118 (1996).

8. Harvey, H. W., Cooper, L. H. N., Lebour, M. V. & Russell, F. S. Plankton production and its control. *J. Mar. Biol. Assoc. UK* **20**, 407–441 (1935).

9. Southward, A. J. On changes of sea temperature in the English Channel. *J. Mar. Biol. Assoc. UK* **39**, 449–458 (1960).

10. Armstrong, F. A. J., Butler, E. I. & Boalch, G. T. Hydrographic and nutrient chemistry surveys in the western English Channel during 1963 and 1964. *J. Mar. Biol. Assoc. UK* **52**, 915–930 (1972).

11. Southward, A. J. & Butler, E. I. A note on further changes of sea temperature in the Plymouth area. *J. Mar. Biol. Assoc. UK* **52**, 931–937 (1972).

12. Southward, A. J. & Demir, N. The abundance and distribution of eggs and larvae of some teleost fishes off Plymouth in 1969 and 1970. *J. Mar. Biol. Assoc. UK* **52**, 987–996 (1972).

13. Southward, A. J. The western English Channel—an inconstant ecosystem? *Nature* **285**, 361–366 (1980).

14. Southward, A. J. Fluctuations in the 'indicator' chaetognaths *Sagitta elegans* and *Sagitta setosa* in the western Channel. *Oceanol. Acta* **7**, 229–239 (1984).

15. Robinson, I. S. *Satellite Oceanography* (Wiley, Chichester, 1994).

16. Wolanski, E. & Hamner, W. M. Topographically controlled fronts in the ocean and their biological significance. *Science* **241**, 177–181 (1988).

17. Kingsford, M. J., Wolanski, E. & Choat, J. H. Influence of tidally induced fronts and Langmuir circulations on distribution and movements of presettlement fishes around a coral reef. *Mar. Biol.* **109**, 167–180 (1991).

18. Le Fèvre, J. Aspects of the biology of frontal systems. *Adv. Mar. Biol.* **23**, 163–299 (1986).

19. Sims, D. W. & Merrett, D. A. Determination of zooplankton characteristics in the presence of surface feeding basking sharks, *Cetorhinus maximus*. *Mar. Ecol. Prog. Ser.* **158**, 297–302 (1997).

20. Kalmijn, A. J. Electric and magnetic field detection in elasmobranch fishes. *Science* **218**, 916–918 (1982).

21. Nevitt, G. A., Veit, R. R. & Kareiva, P. Dimethyl sulphide as a foraging cue for Antarctic Procellariiform seabirds. *Nature* **376**, 680–682 (1995).

22. Cramp, S. *et al. Handbook of the Birds of Europe the Middle East and North Africa: The Birds of the Western Palearctic* Vol. 1 (Oxford Univ. Press, Oxford, 1977).

23. Pingree, R. D., Pugh, P. R., Holligan, P. M. & Forster, G. R. Summer phytoplankton blooms and red tides along tidal fronts in the approaches to the English Channel. *Nature* **258**, 672–677 (1975).

24. Yoder, J. A. *et al.* A line in the sea. *Nature* **371**, 689–692 (1994).

25. Fiedler, P. C., Smith, G. B. & Laurs, R. M. Fisheries applications of satellite data in the eastern north Pacific. *Mar. Fish. Rev.* **46**, 1–13 (1984).

26. Southwell, K. Oceanography: Shades of the sea. *Nature* **389**, 444 (1997).

27. Zar, J. H. *Biostatistical Analysis* (Prentice-Hall, Englewood Cliffs, 1984).

Physiology and molecular phylogeny of coexisting *Prochlorococcus* ecotypes

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The cyanobacterium *Prochlorococcus*[1,2] is the dominant oxygenic phototroph in the tropical and subtropical regions of the world's oceans[1,3,4]. It can grow at a range of depths over which light intensities can vary by up to 4 orders of magnitude. This broad depth distribution has been hypothesized to stem from the coexistence of genetically different populations adapted for growth at high- and low-light intensities[4–6]. Here we report

direct evidence supporting this hypothesis, which has been generated by isolating and analysing distinct co-occurring populations of *Prochlorococcus* at two locations in the North Atlantic. Co-isolates from the same water sample have very different light-dependent physiologies, one growing maximally at light intensities at which the other is completely photoinhibited. Despite this ecotypic differentiation, the co-isolates have 97% similarity in their 16S ribosomal RNA sequences, demonstrating that molecular microdiversity, commonly observed in microbial systems[7–12], can be due to the coexistence of closely related, physiologically distinct populations. The coexistence and distribution of multiple ecotypes permits the survival of the population as a whole over a broader range of environmental conditions than would be possible for a homogeneous population.

Using sea-going flow cytometry for studying picoplankton populations, we and others[4,13,14] have observed multiple populations of *Prochlorococcus* in single water samples, as distinguished by their chlorophyll fluorescence intensities. These populations could be derived from the mixing together of genetically identical *Prochlorococcus* cells which have acclimated to different past light
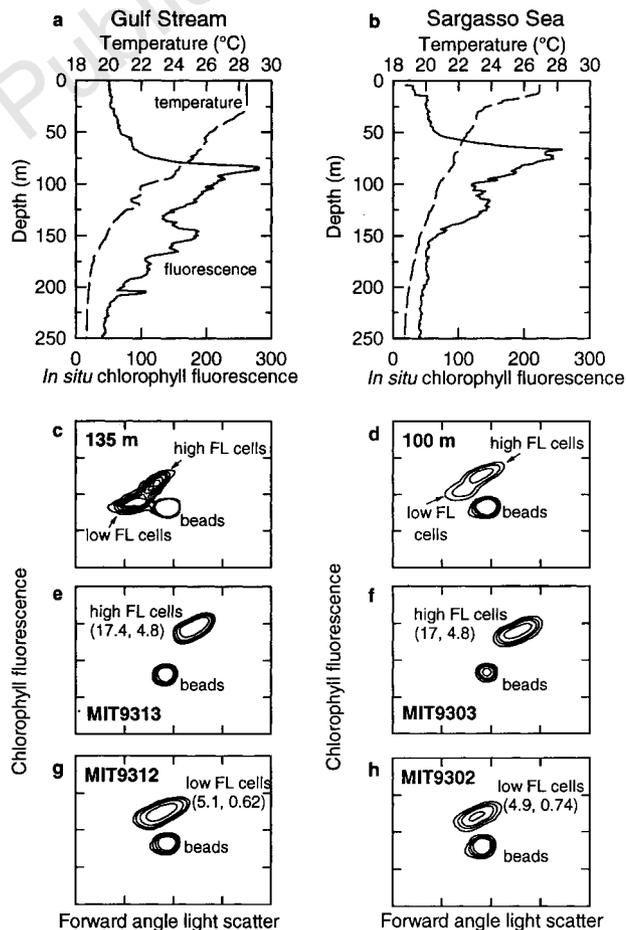
Figure 1 Properties of the euphotic zone and flow cytometric signatures of the *Prochlorococcus* populations and isolates. **a**, **b**, The physical features of the water columns were similar at the Gulf Stream station, 37° 30.8′N, 68° 14.4′W, and the Sargasso Sea station, 34° 45.5′N, 66° 11.1′W. **c**, **d**, Flow cytometry signatures of coexisting *Prochlorococcus* populations from 135 m in the Gulf Stream and 100 m in the Sargasso Sea from which the isolates were obtained. **e–h**, Flow cytometry signatures of the cultured isolates maintained at an irradiance of 9 μmol Q m^{-2} s^{-1}. Numbers in parentheses refer to the mean chlorophyll fluorescence per cell (FL) and FALS per cell. Differences in the absolute values of the flow cytometry parameters between natural populations and isolates result from unmatched growth conditions.