

regulate the timing of sedimentation processes, but through aggregation with sinking particles may also contribute directly to carbon export.

Recent advances in trace metal biogeochemistry have highlighted the importance of dissolved and colloidal organic matter for the cycling of trace nutrients such as Fe and Zn and of the particle reactive tracer  $^{234}\text{Th}$  (ref. 25). Because polysaccharides provide strong binding sites for trace metals, aggregation and sedimentation of polysaccharides are key processes controlling trace metal residence times in the surface ocean. Implemented into larger ecosystem models, our findings could therefore help to reconcile observed dynamics in trace elements with carbon fluxes in the ocean.

Owing to their short-lived nature, the significance of dissolved polysaccharides in marine biogeochemical cycling has previously been overlooked. Whereas phytoplankton exudation has been considered to divert primary production from contributing to vertical flux, the mechanism described here constitutes an effective pathway to channel dissolved matter into the particulate pool. Because PCHO production is not constrained by nutrient supply, this pathway has the potential to modulate the stoichiometry of biogeochemical cycling in the ocean. Its relative contribution to overall primary production thereby strongly depends on the physiology of the phytoplankton and is likely to differ between species and as a function of environmental conditions. Global environmental change and the expected shift in phytoplankton composition are therefore bound to change the relative importance of this pathway, with likely consequences for carbon sequestration in the ocean. □

## Methods

### Determination of TEP, MCHO and PCHO

TEP were determined from 50–100-ml samples filtered onto Nuclepore filters (pore size of 0.4  $\mu\text{m}$ )<sup>26</sup>. All filters were prepared in duplicates and stored at  $-20^\circ\text{C}$  until analysis. A carbon content of TEP of 39% (w/w) was determined<sup>11</sup> from 11 samples (5 l each) taken on different days.

MCHO and PCHO were determined after acidic hydrolysis (1 M HCl for 20 h at  $100^\circ\text{C}$ ) with the 2,4,6-tripyridyl-s-triazine (TPTZ) spectrophotometric method<sup>24</sup> from 30-ml samples, filtered through combusted GF/F filters into combusted glass vials and stored at  $-21^\circ\text{C}$  for less than 4 months. The carbon content of PCHO was calculated assuming a conversion of 30  $\mu\text{g}$  glucose per  $\mu\text{mol C}$ .

### Bacterial abundance

Bacterial abundance was determined at  $\times 1,250$  magnification using an epifluorescent microscope (Zeiss) and 4,6-diamidino-2-phenylindole (DAPI)-stained samples<sup>27</sup>, preserved with 0.2- $\mu\text{m}$ -filtered borax-buffered formalin (2% final concentration). Ten millilitres were stained with 0.2- $\mu\text{m}$ -filtered DAPI solution for 10 min before filtering onto a black 0.2  $\mu\text{m}$  Osmonics filter and stored at  $4^\circ\text{C}$ . Bacterial abundance was estimated from 20–30 randomly selected fields per filter.

Received 24 October 2003; accepted 1 March 2004; doi:10.1038/nature02453.

1. Mc Cave, I. N. Vertical flux of particles in the ocean. *Deep-Sea Res.* **22**, 491–502 (1975).
2. Chin, W., Orellana, M. V. & Verdugo, P. Spontaneous assembly of marine dissolved organic matter into polymer gels. *Nature* **391**, 568–572 (1998).
3. Wells, M. L. A neglected dimension. *Nature* **391**, 530–531 (1998).
4. Volk, T. & Hoffert, M. I. In *The Carbon Cycle and Atmospheric CO<sub>2</sub>: Natural Variations Archaen to Present* (eds Sundquist, E. T. & Broecker, W. S.) 99–110 (Geophys. Monogr. 32, American Geophysical Union, Washington DC, 1985).
5. Dugdale, R. C. & Goering, J. J. Uptake of new and regenerated forms of nitrogen in primary productivity. *Limnol. Oceanogr.* **12**, 196–206 (1967).
6. Eppley, R. W. & Peterson, B. J. Particulate organic matter flux and planktonic new production in the deep ocean. *Nature* **282**, 677–680 (1979).
7. Passow, U. Transparent exopolymer particles (TEP) in the marine environment. *Prog. Oceanogr.* **55**, 287–333 (2002).
8. Engel, A. The role of transparent exopolymer particles (TEP) in the increase in apparent particles stickiness ( $\alpha$ ) during the decline of a diatom bloom. *J. Plankton Res.* **22**, 485–497 (2000).
9. Asper, V. L., Deuser, W. G., Knauer, G. A. & Lorenz, S. E. Rapid coupling of sinking particle fluxes between surface and deep ocean waters. *Nature* **357**, 670–672 (1992).
10. Nanninga, H. J., Ringenaldus, P. & Westbroek, P. Immunological quantification of a polysaccharide formed by *Emiliania huxleyi*. *J. Mar. Syst.* **9**, 67–74 (1996).
11. Engel, A. *et al.* TEP and DOC production by *Emiliania huxleyi* exposed to different CO<sub>2</sub> concentrations: A mesocosm experiment. *Aquat. Microb. Ecol.* **34**, 93–104 (2004).
12. Von Smochulowski, M. Versuch einer mathematischen Theorie der Koagulationskinetik von Kolloidteilchen. *Z. Phys. Chem.* **92**, 129–168 (1917).
13. Ziff, R. M. & Stell, G. Kinetics of polymer gelation. *J. Chem. Phys.* **73**, 3492–3499 (1980).
14. Ruiz, J., Prieto, L. & Ortegón, F. Diatom aggregate formation and fluxes, a modeling analysis under different size-resolution schemes and with empirically determined aggregation kernels. *Deep-Sea Res.* **49**, 495–515 (2002).

15. Geider, R. J., MacIntyre, H. L., Graziano, L. M. & McKay, R. M. L. Responses of the photosynthetic apparatus of *Dunaliella tertiolecta* (Chlorophyceae) to nitrogen and phosphorus limitation. *Eur. J. Phycol.* **33**, 5315–5332 (1998).
16. Carlson, C. A. in *Biogeochemistry of Marine Dissolved Organic Matter* (eds Hansell, D. A. & Carlson, C.) 59–90 (Academic, Amsterdam, 2002).
17. Nielsen, M. V. Growth, dark respiration and photosynthetic parameters of the coccolithophorid *Emiliania huxleyi* (Prymnesiophyceae) acclimated to different day length–irradiance combinations. *J. Phycol.* **33**, 818–822 (1997).
18. Amon, R. M. W. & Benner, R. Rapid cycling of high-molecular-weight dissolved organic matter in the ocean. *Nature* **369**, 549–552 (1994).
19. Benner, R. in *Biogeochemistry of Marine Dissolved Organic Matter* (eds Hansell, D. A. & Carlson, C.) 59–90 (Academic, Amsterdam, 2002).
20. Del Giorgio, P. A. & Duarte, C. M. Respiration in the open ocean. *Nature* **420**, 379–384 (2002).
21. Pakulski, J. D. & Benner, R. Abundance and distribution of carbohydrates in the ocean. *Limnol. Oceanogr.* **39**, 930–940 (1994).
22. Biddanda, B. & Benner, R. Carbon, nitrogen, and carbohydrate fluxes during the production of particulate and dissolved organic matter by marine phytoplankton. *Limnol. Oceanogr.* **42**, 506–518 (1997).
23. Baines, S. B. & Pace, M. L. The production of dissolved organic matter by phytoplankton and its importance to bacteria, patterns across marine and freshwater systems. *Limnol. Oceanogr.* **36**, 1078–1090 (1991).
24. Mykkestad, S. M., Skånøy, E. & Hestmann, S. A sensitive and rapid method for analysis of dissolved mono- and polysaccharides in seawater. *Mar. Chem.* **56**, 279–286 (1997).
25. Wu, J., Boyle, E., Sunda, W. & Wen, L.-S. Soluble and colloidal iron in the oligotrophic North Atlantic and North Pacific. *Science* **293**, 847–849 (2001).
26. Passow, U. & Alldredge, A. L. A dye-binding assay for the spectrophotometric measurement of transparent exopolymer particles (TEP) in the ocean. *Limnol. Oceanogr.* **40**, 1326–1335 (1995).
27. Porter, K. G. & Feig, T. S. The use of DAPI for identifying and counting aquatic microflora. *Limnol. Oceanogr.* **25**, 943–948 (1980).
28. Wells, M. L. & Goldberg, E. D. Marine submicron particles. *Mar. Chem.* **40**, 5–18 (1992).
29. Mari, X. Carbon content and C:N ratio of transparent exopolymer particles (TEP) produced by bubbling of exudates of diatoms. *Mar. Ecol. Prog. Ser.* **33**, 59–71 (1999).
30. Mc Cave, I. N. Size spectra and aggregation of suspended particles in the deep ocean. *Deep-Sea Res.* **31**, 329–352 (1984).

**Acknowledgements** We thank A. Terbrüggen for technical assistance and M. Schartau for discussions. This work was supported by the Large-Scale Facility of the University of Bergen, Norway and the European Commission Human Potential Programme.

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

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## Maturation trends indicative of rapid evolution preceded the collapse of northern cod

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Northern cod, comprising populations of Atlantic cod (*Gadus morhua*) off southern Labrador and eastern Newfoundland, supported major fisheries for hundreds of years<sup>1</sup>. But in the late 1980s and early 1990s, northern cod underwent one of the worst collapses in the history of fisheries<sup>2–4</sup>. The Canadian government closed the directed fishing for northern cod in July 1992, but even after a decade-long offshore moratorium, population sizes remain historically low<sup>4</sup>. Here we show that, up until the moratorium, the life history of northern cod continually shifted towards maturation at earlier ages and smaller sizes.

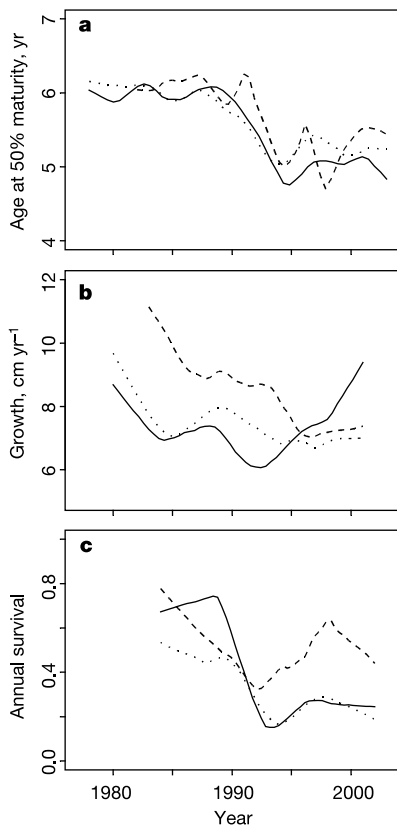
Because confounding effects of mortality changes and growth-mediated phenotypic plasticity are accounted for in our analyses, this finding strongly suggests fisheries-induced evolution of maturation patterns in the direction predicted by theory<sup>5,6</sup>. We propose that fisheries managers could use the method described here as a tool to provide warning signals about changes in life history before more overt evidence of population decline becomes manifest.

Commercially exploited fish stocks often show trends towards earlier maturation<sup>7</sup>, which could involve fisheries-induced evolution<sup>8–10</sup>. Life-history theory predicts that increased mortality at potential ages and sizes at maturation selects for an earlier onset of maturation<sup>5,6</sup>, and experiments with both wild and cultured fish show that the genetic variation needed for age at maturation to evolve clearly resides within populations<sup>11,12</sup>. However, another plausible explanation exists: earlier maturation may simply reflect phenotypic plasticity. Reduced stock biomass resulting from fishing can lead to increased resource availability and thus to accelerated growth for those fish remaining<sup>13</sup>, and faster-growing fish generally mature at an earlier age than do slower-growing fish<sup>14</sup>. Because of the difficulties involved in disentangling plastic and evolutionary components, the nature of phenotypic changes in exploited fish populations remains poorly understood<sup>9</sup>.

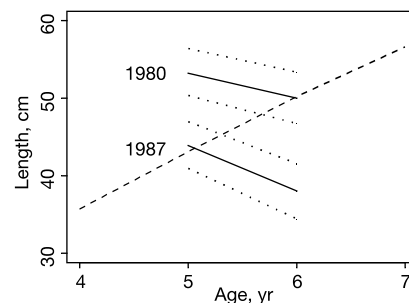
For northern cod, the age at which the proportion of mature females reaches 50% decreased from about 6 yr in the mid-1980s to about 5 yr in the mid-1990s (Fig. 1a). However, it is crucial to realize that this age at 50% maturity will depend not only on the

maturation process itself, but also on conditions for growth and survival<sup>15</sup>. This makes interpretation of the reasons for changes in this quantity ambiguous. The collapse period was characterized by poor conditions for growth and a marked drop in the survival of fish at potential ages of maturation (Fig. 1b, c). Slower growth typically postpones maturation, which is the opposite of what was actually seen. Hence, it has been suggested that the collapse of northern cod was in fact a major selective episode favouring early-maturing relative to late-maturing genotypes<sup>16</sup>. Here we aim to quantitatively test this ‘selective episode’ hypothesis. We use a new method for estimating probabilistic reaction norms for age and size at maturation that overcomes the confounding effects of variation in growth and survival on maturation patterns<sup>15</sup> (see Supplementary Information). Reaction norms in general describe the different phenotypes produced by a genotype under different environmental conditions, and reaction norms for age and size at maturation in particular describe the maturation schedule of a genotype under different growth conditions<sup>17</sup>. So, probabilistic reaction norms for age and size at maturation describe the probability that immature individuals with given age and size will mature during a given time interval. In other words, maturation probability is estimated conditional on the fact that these individuals have reached the considered age and size, the likelihood of which is influenced by growth and survival. Probabilistic maturation reaction norms are thus insensitive to variations in growth and survival (see Supplementary Information). Consequently, a trend in the maturation reaction norm strongly supports the hypothesis of evolutionary change having occurred in the maturation process itself<sup>15</sup>.

We estimated maturation reaction norms for female cod captured during offshore research surveys (1977–2002) off southern Labrador (Northwest Atlantic Fisheries Organization Division 2J) through the Northeast Newfoundland Shelf (Division 3K) to the northern half of the Grand Bank off eastern Newfoundland (Division 3L). Together, these three neighbouring areas encompass the distribution area of a stock complex commonly termed the ‘northern cod’. First, as an illustration, we show the reaction norms for female cod from Division 2J born in 1980 and in 1987. A female growing at a mean rate would intercept the 50% maturation probability contour, the so-called reaction-norm midpoint, of the 1980 cohort at an age of about 6 yr, whereas this age had decreased to about 5 yr for the 1987 cohort (Fig. 2). This illustrates how, for a given growth rate, a lower-positioned reaction norm corresponds to maturation at an earlier age and smaller size. (Note that, technically, the use of reaction-norm terminology is justified as long as a significant proportion of variation in growth is due to environmental variability rather than genetic variance. For northern cod in the 2J and 3K Divisions, body condition was decreasing in parallel with mean length at age during the late 1980s and early 1990s<sup>18</sup>,



**Figure 1** Background information on northern cod (*Gadus morhua*). Temporal trends in the traditional measure of maturation, the age at 50% maturity (a), annual length increments (b) and annual survival probabilities (c) of cod from Northwest Atlantic Fisheries Organization (NAFO) Division 2J (solid lines), 3K (dotted lines) and 3L (dashed lines). Maturity and length increments are from female cod, whereas survival estimates are not sex-specific. Length increments and survival are arithmetic and geometric averages, respectively, for 5- and 6-yr-old fish. Lines represent best fits using a local regression smoother.



**Figure 2** Cod maturation schedules. The reaction norms measure the probabilities for maturing at a certain size and age; here they are illustrated by lines connecting lengths of identical maturation probabilities at ages 5 and 6 yr for female northern cod off southern Labrador (NAFO Division 2J) born in 1980 and 1987 (solid line, reaction-norm midpoints at 50% maturation probability; dotted lines, 25% and 75% maturation probabilities). The dashed line indicates the average growth trajectory.

which suggests an environmental influence on size at age.) More generally, we found that the maturation reaction norm of northern cod shifted continually towards younger ages and smaller sizes throughout the 1980s and early 1990s (Fig. 3). However, from about 1993–1994 onwards, this trend appears to have halted and may even have reversed. In most cases, linear regressions of reaction-norm midpoints—characterizing the age-specific body lengths at which the probability of maturing reaches 50%—on cohort confirmed the statistical significance of these trends (Fig. 4). Because probabilistic maturation reaction norms are independent of variations in survival and growth-mediated phenotypic plasticity, we conclude that our analyses strongly support the hypothesis that early-maturing genotypes were favoured relative to late-maturing genotypes during the collapse of northern cod<sup>16</sup>. Our results agree well with predictions from recent modelling of life-history responses to exploitation: harvesting on both immature and mature individuals—as was the case for northern cod<sup>2,4</sup>—is expected to displace the reaction norm for age and size at maturation towards younger ages and smaller sizes<sup>6</sup>. The positive trend in maturation reaction norms since about 1993 suggests that the moratorium caused a shift in selection regime favouring maturation at older ages and larger sizes. However, the moratorium period so far spans only a decade, northern cod still experience relatively low survival, and population sizes have not been rebuilt<sup>4</sup>. We await the results of future research surveys to confirm whether the trend in maturation schedule has indeed reversed.

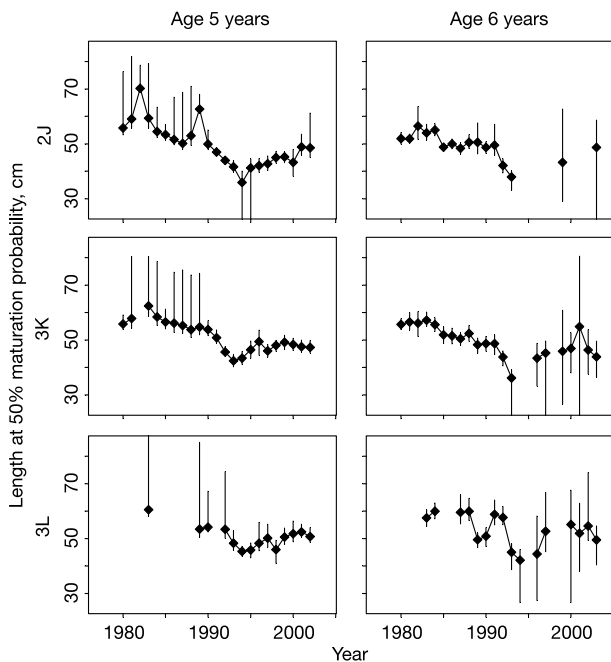
We note that two other processes, in addition to local fisheries-induced evolution, might have contributed to temporal variation in maturation reaction norms. First, gene flow from populations with different genetically determined life histories might have affected the genetic composition of the stock considered. Despite the fact that cod around Newfoundland is structured into genetically recognizable units<sup>19</sup>, there is dispersal among these units<sup>20</sup>: some immigration of genotypes with different maturation schedules therefore cannot be rejected. Second, it is also possible, in principle, that plasticity not mediated by growth, such as social suppression of

maturation<sup>21</sup>, could have influenced the reaction norms.

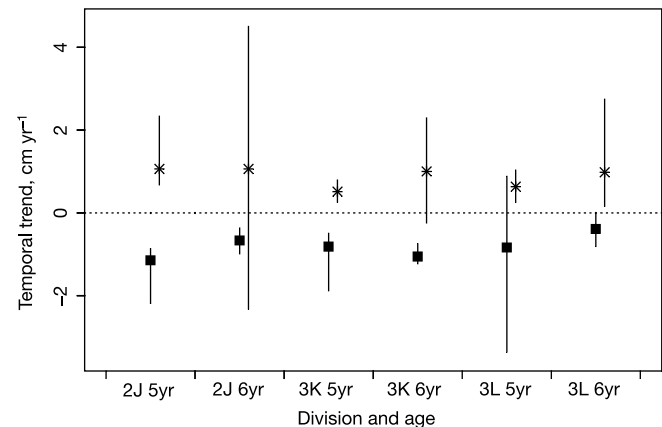
To complete the picture, we estimated rates of phenotypic evolution for the reaction-norm midpoints (body length at 50% probability of maturing) at age 6 yr in the period before the initiation of the moratorium. Such rates can be expressed in two different units. ‘Haldanes’ express evolutionary rates relative to generation length and phenotypic standard deviation of the population in question, whereas ‘darwins’ simply describe the ‘raw’ rate of evolutionary change (see Methods). Estimated rates are as follows: –13,600 (95% confidence limits: –19,100, –8,320) darwins and –1.20 (–1.74, –0.63) haldanes in Division 2J; –18,810 (–24,410, –14,660) darwins and –1.50 (–1.93, –1.20) haldanes in Division 3K; –7,150 (–14,270, –670) darwins and –0.63 (–1.69, 0.26) haldanes in Division 3L. Estimates in darwins are high, but comparable with rates from other studies covering a similar temporal scale<sup>22,23</sup>. In contrast, estimates in haldanes are higher than most previously published rates<sup>22–24</sup>. This is probably explained by estimates in haldanes being normalized relative to a trait’s phenotypic standard deviation<sup>23</sup>: as reaction-norm midpoints are estimated by removing growth-mediated environmental variation from the data, the corresponding phenotypic standard deviations are diminished accordingly, and the resulting estimates in haldanes are therefore bound to systematically exceed those for other quantitative traits sensitive to environmental variation.

Empirical evidence is mounting in support of contemporary evolution in natural populations<sup>25</sup>. Fishing for grayling (*Thymallus thymallus*) in Norwegian mountain lakes has been shown to induce evolutionary changes in grayling maturation comparable to those observed for northern cod<sup>22</sup>. On the Galápagos Islands, body weight and beak size of Darwin’s finches (*Geospiza fortis*) evolved in the course of a single generation in response to a change in the natural mortality regime<sup>26</sup>. Field experiments with a small freshwater fish, the guppy (*Poecilia reticulata*), have documented rapid evolution of life-history traits in response to altered regimes of natural mortality<sup>11</sup>.

We suggest that the reaction-norm approach used here might help fisheries managers by providing warning signals about life-history changes likely to be caused by heavy exploitation. To corroborate this claim, we calculated reaction norms and regression parameters based only on the data that had been available at earlier points in time. Focusing on fish of age 6 yr (which gave the most precise estimates before the moratorium), we estimated the confidence according to which the reaction norms of northern cod were



**Figure 3** Temporal trends in cod maturation schedules. Midpoints of the maturation reaction norms, characterizing the age-specific body lengths at which the probability of maturing reaches 50%, for female northern cod (NAFO Divisions 2J, 3K and 3L) of ages 5 yr (left) and 6 yr (right); vertical lines indicate 95% confidence intervals. Some midpoints are inestimable because of low sample sizes and lack of model fit.



**Figure 4** Statistical significance of temporal trends in cod maturation schedules. Slope parameters with 95% confidence intervals, estimated from linear regression on year of reaction-norm midpoints of female northern cod (NAFO Divisions 2J, 3K, and 3L) at ages 5 and 6 yr (Fig. 3); including years with directed cod fishing (1979–1992, squares), and recent years since the offshore moratorium on directed cod fishing was established (1993–2003, stars).

exhibiting a decline: by 1985 this probability had already risen to above 95% for the 3K Division. The same level of confidence was reached for the 2J Division in 1986, and for the 3L Division in 1989. Although eroding maturation reaction norms can thus signal extreme exploitation pressures, they are not to be misinterpreted as signs of imminent stock collapse. But exploitation pressures so strong that they overturn a species' natural pattern of life-history adaptation certainly ought to be cause for concern.

There is growing anxiety about the consequences of fisheries-induced evolution, because such evolution may ultimately result in lower sustainable yields<sup>9,27</sup> and reduced stock stability. Our study provides new evidence that intense fishing may indeed lead to rapid evolution of key life-history traits in harvested populations. Furthermore, we show that relaxing the selection pressures—in this case through such a drastic measure as closing the fishery—may halt the trend, providing a basis for cautious optimism about practical options for managing fisheries-induced evolutionary change. □

Methods

Sampling

Atlantic cod were caught in spatially stratified random bottom-trawl surveys during autumn and early winter, initiated in 1977 (Division 2J and 3K) and 1981 (Division 3L)<sup>4</sup>. Beyond the age of 2 yr, this sampling is considered representative. Most cod were sampled in the autumn before their spring spawning in the next year. Therefore, age of cod is expressed as if they were sampled after their nominal birthday (1 January)—that is, their age is incremented by 1. Data on 10,778 female Atlantic cod of ages 3 to 6 yr were used in the statistical analyses; younger and older individuals were excluded because of low sample sizes at these ages<sup>4</sup>.

Statistical analyses

Maturation reaction norms, given by the probability  $m(a,s)$  of maturing at age  $a$  and body length  $s$ , were derived from maturity ogives, given by the probability  $o(a,s)$  of being mature at that age and length, using the relationship introduced in ref. 28:  $m(a,s) = [o(a,s) - o(a-1, s - \Delta s(a))]/[1 - o(a-1, s - \Delta s(a))]$ , where  $\Delta s(a)$  is the annual length increment from age  $a - 1$  to age  $a$ . This relationship is exact if immature and mature individuals of a given age and size have the same survival and growth rates, and it has been shown that the estimation of  $m$  is relatively robust to violations of these assumptions<sup>28</sup>. Estimating a maturation reaction norm thus involved five steps: (1) estimation of the required maturity ogives; (2) estimation of the required annual length increments; (3) calculation of the probability to mature; (4) estimation of reaction-norm midpoints; and (5) estimation of confidence intervals around these midpoints. Maturity ogives  $o$  were estimated through logistic regression, with maturity state (juvenile or mature) as a binary response variable. Weighting observations by population abundance at length<sup>28,29</sup> had negligible effect and was not incorporated. Relatively small sample sizes prevented an analysis of the full interaction between cohort  $c$ , age  $a$  and body length  $s$ , when treating both cohort and age as factors. Standard model selection led to the treatment of age as a linear effect while keeping cohort as a factor:  $\text{logit}(o) = \beta_{1c} + \beta_{2ca} + \beta_{3s}$ , with regression coefficients  $\beta_{1c}$ ,  $\beta_{2c}$  and  $\beta_3$ . The second term allows detection of age-dependent temporal changes in the probability of being mature. For each cohort, annual length increments,  $\Delta s(a)$ , were estimated by calculating mean body length at age  $a$  and subtracting mean body length at age  $a - 1$  (ref. 28). Reaction-norm midpoints were estimated, separately for each age and cohort, as  $-\beta_1/\beta_2$  through logistic regression of  $m(a,s)$  on body length  $s$ :  $\text{logit}(m) = \beta_1 + \beta_2 s$ , with regression coefficients  $\beta_1$  and  $\beta_2$  (ref. 28). These midpoints could be estimated for ages 5 and 6 yr; most individuals at ages 3 and 4 yr are immature<sup>4</sup>. Confidence intervals for the reaction-norm parameters were obtained through bootstrap techniques<sup>28,30</sup>. A bootstrapped sample was constructed for each cohort and age, with individuals being chosen at random with replacement from the original data set. The resampling was repeated 1,000 times, and the 2.5% and 97.5% percentiles were extracted as lower and upper confidence limits, respectively, around the reaction-norm midpoints.

Linear regression of reaction-norm midpoints on cohort was used to test for the significance of temporal trends in maturation schedules. Confidence intervals around the regression parameters were generated from bootstrap replicates. Evolutionary rates in darwins were estimated by regressing  $\log(\text{reaction-norm midpoint})$  on time (in millions of years) since the first available data point<sup>23</sup>. Evolutionary rates in halldanes were estimated by regressing the reaction-norm midpoints—rescaled by their pooled phenotypic standard deviation—on the number of generations since the first available data point<sup>23</sup>. Generation length was estimated as the mean age of mature females. Phenotypic standard deviation of reaction-norm midpoints was computed as the square root of the variance of the probabilistic maturation envelope around reaction-norm midpoints. This envelope variance, which comprises genetic variance in the reaction-norm midpoint as well as environmental variance generated by factors other than growth, is the variance of the distribution of body lengths obtained by taking the derivative of the probabilistic maturation reaction norm with respect to body length. Durbin-Watson tests showed that temporal autocorrelations were not significant ( $P > 0.1$ ).

Age at 50% maturity, annual length increments and annual survival rates were estimated for the descriptive illustration in Fig. 1. Age at 50% maturity in year  $y$  was estimated as  $-\beta_1/\beta_2$  through logistic regression on age of the probability  $o$  of females at

ages  $a = 3, \dots, 6$  yr being mature in year  $y$ , using year as a factor:  $\text{logit}(o) = \beta_{1y} + \beta_{2ya}$ , with regression coefficients  $\beta_{1y}$  and  $\beta_{2y}$ . Annual survival probabilities at age  $a$  in year  $y$  were obtained from survey catch data<sup>4</sup> as  $C_{ay}/C_{a-1,y-1}$ , where  $C_{ay}$  denotes the catch abundance per unit effort at age  $a$  in year  $y$ .

Received 8 December 2003; accepted 18 February 2004; doi:10.1038/nature02430.

- Hutchings, J. A. & Myers, R. A. in *The North Atlantic Fisheries: Successes, Failures, and Challenges* (eds Arnason, R. & Felt, L.) 39–93 (The Institute of Island Studies, Charlottetown, Prince Edward Island, 1995).
- Myers, R. A., Hutchings, J. A. & Barrowman, N. J. Why do fish stocks collapse? The example of cod in Atlantic Canada. *Ecol. Appl.* **7**, 91–106 (1997).
- Rose, G. A., deYoung, B., Kulka, D. W., Goddard, S. V. & Fletcher, G. L. Distribution shifts and overfishing the northern cod (*Gadus morhua*): a view from the ocean. *Can. J. Fish. Aquat. Sci.* **57**, 644–663 (2000).
- Lilly, G. R., et al. *An Assessment of the Cod Stock in NAFO Divisions 2J + 3KL* DFO Can. Sci. Adv. Sec. Res. Doc. 2001/044 (2001).
- Gadgil, M. & Bossert, W. Life historical consequences of natural selection. *Am. Nat.* **104**, 1–24 (1970).
- Ernande, B., Dieckmann, U. & Heino, M. Adaptive changes in harvested populations: plasticity and evolution of age and size at maturation. *Proc. R. Soc. Lond. B* **271**, 415–423 (2004).
- Trippel, E. A. Age at maturity as a stress indicator in fisheries. *Bioscience* **45**, 759–771 (1995).
- Stokes, T. K., McGlade, J. M. & Law, R. *The Exploitation of Evolving Resources* (Springer, Berlin, 1993).
- Law, R. Fishing, selection, and phenotypic evolution. *ICES J. Mar. Sci.* **57**, 659–668 (2000).
- Rijnsdorp, A. D. Fisheries as a large-scale experiment on life-history evolution: disentangling phenotypic and genetic effects in changes in maturation and reproduction of North Sea plaice, *Pleuronectes platessa* L. *Oecologia* **96**, 391–401 (1993).
- Reznick, D. N., Shaw, F. H., Rodd, H. F. & Shaw, R. G. Evaluation of the rate of evolution in natural populations of guppies (*Poecilia reticulata*). *Science* **275**, 1934–1937 (1997).
- Roff, D. A. Trade-offs between growth and reproduction: an analysis of the quantitative genetic evidence. *J. Evol. Biol.* **13**, 434–445 (2000).
- Lorenzen, K. & Enberg, K. Density-dependent growth as a key mechanism in the regulation of fish populations: evidence from among-population comparisons. *Proc. R. Soc. Lond. B* **269**, 49–54 (2002).
- Alm, G. Connection between maturity, size and age in fishes. *Rep. Inst. Freshw. Res. Drottningholm* **40**, 5–145 (1959).
- Heino, M., Dieckmann, U. & Godø, O. R. Measuring probabilistic reaction norms for age and size at maturation. *Evolution* **56**, 669–678 (2002).
- Hutchings, J. A. Influence of growth and survival costs of reproduction on Atlantic cod, *Gadus morhua*, population growth rate. *Can. J. Fish. Aquat. Sci.* **56**, 1612–1623 (1999).
- Stearns, S. C. & Koella, J. C. The evolution of phenotypic plasticity in life-history traits: predictions of reaction norms for age and size at maturity. *Evolution* **40**, 893–913 (1986).
- Bishop, C. A. & Baird, J. W. Spatial and temporal variability in condition factors of Divisions 2J and 3KL cod (*Gadus morhua*). *NAFO Sci. Coun. Stud.* **21**, 105–113 (1994).
- Ruzzante, D. E., Taggart, C. T., Doyle, R. W. & Cook, D. Stability in the historical pattern of genetic structure of Newfoundland cod (*Gadus morhua*) despite the catastrophic decline in population size from 1964 to 1994. *Cons. Gen.* **2**, 257–269 (2001).
- Lear, W. H. Discrimination of the stock complex of Atlantic cod (*Gadus morhua*) off southern Labrador and eastern Newfoundland, as inferred from tagging studies. *J. Northwest Atl. Fish. Sci.* **5**, 143–159 (1984).
- Sohn, J. J. Socially induced inhibition of genetically determined maturation in the platyfish, *Xiphophorus maculatus*. *Science* **195**, 199–200 (1977).
- Haugen, T. O. & Vollestad, L. A. A century of life-history evolution in grayling. *Genetica* **112–113**, 475–491 (2001).
- Hendry, A. P. & Kinnison, M. T. The pace of modern life: measuring rates of contemporary microevolution. *Evolution* **53**, 1637–1653 (1999).
- Kinnison, M. T. & Hendry, A. P. The pace of modern life II: from rates of contemporary microevolution to pattern and process. *Genetica* **112–113**, 145–164 (2001).
- Stockwell, C. A., Hendry, A. P. & Kinnison, M. T. Contemporary evolution meets conservation biology. *Trends Ecol. Evol.* **18**, 94–101 (2003).
- Grant, P. R. & Grant, B. R. Unpredictable evolution in a 30-year study of Darwin's finches. *Science* **296**, 707–711 (2002).
- Conover, D. O. & Munch, S. B. Sustaining fisheries yields over evolutionary time scales. *Science* **297**, 94–96 (2002).
- Barot, S., Heino, M., O'Brien, L. & Dieckmann, U. *Estimating Reaction Norms for Age and Size at Maturation when Age at First Reproduction is Unknown*. IIASA Interim Report No. IR-03-043 (2003).
- Morgan, M. J. & Hoenig, J. M. Estimating maturity-at-age from length stratified sampling. *J. Northwest Atl. Fish. Sci.* **21**, 51–63 (1997).
- Manly, F. J. *Randomization, Bootstrap and Monte Carlo Methods in Biology* (Chapman & Hall, London, 1997).

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

**Acknowledgements** We are grateful to the many fisheries biologists and technicians who participated in the data collection underlying this study. We also thank S. Barot, O. R. Godø, T. O. Haugen, N. C. Stenseth and L. A. Vollestad for discussions. S. Barot, W. B. Brodie, O. R. Godø and S. J. Walsh are thanked for their help in initiating the interaction that led to this study. U.D. gratefully acknowledges financial support from the Austrian Science Fund and the Austrian Federal Ministry of Education, Science, and Cultural Affairs. This research has been supported by the European Research Training Network *ModLife* (Modern Life-History Theory and its Application to the Management of Natural Resources), funded through the Human Potential Programme of the European Commission.

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

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