

Tolerance limit for fish growth exceeded by warming waters

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Climate change can affect organisms both directly, by affecting their physiology, growth, and behaviour¹, and indirectly, for example through effects on ecosystem structure and function^{1,2}. For ectotherms, or 'cold-blooded' animals, warming will directly affect their metabolism, with growth rates in temperate species predicted to increase initially as temperatures rise, but then decline as individuals struggle to maintain cardiac function and respiration in the face of increased metabolic demands^{3,4}. We provide evidence consistent with this prediction for a marine fish (*Cheilodactylus spectabilis*) in the Tasman Sea; one of the most rapidly warming regions of the Southern Hemisphere ocean⁵. We estimated changes in the species' growth rate over a 90-year period using otoliths—bony structures that fish use for orientation and detection of movement—and compared these changes to temperature trends across the species' distribution. Increasing temperatures coincide with increased growth for populations in the middle of the species range, but with reduced growth for those at the warm northern edge of the species' distribution, indicating that temperatures may have already reached levels associated with increased metabolic costs. If warming continues, the direct metabolic effects of increasing temperatures on this species may lead to declining productivity and range contraction.

In ectotherms, including most fish, environmental temperature dictates reactive, growth and metabolic rates⁶. For most species in their normal temperature range (their so-called thermal window), a slight increase in temperature is likely to be beneficial to growth because it results in more energy, higher rates of diffusion and more enzyme-substrate complexes, which lead to higher reaction rates for growth^{6,7}. However, laboratory studies frequently demonstrate that temperature can increase to the point where it becomes deleterious to growth (Fig. 1a), as cardiac output cannot keep pace with increased metabolic demands^{3,4}. The inflection point is referred to as the pejus temperature⁸ (T_p), and marks the temperature above which increases in temperature lead to decreases in growth (Fig. 1a). Further temperature increases (that is, above the upper critical temperature, T_{CU} , Fig. 1a) lead to growth cessation, anaerobic respiration, protein denaturation, permanent inactivation of enzymes and eventual death^{4,9}.

The Tasman Sea, in the southwest Pacific Ocean (See Supplementary Fig. S1), is one of the fastest warming areas in the Southern Hemisphere ocean^{10,11}, because of both globally increasing sea surface temperatures (SST) and local effects caused by prolonged strengthening of the warm poleward-flowing East Australian Current^{5,11,12}. To assess the impacts of this temperature increase on a marine species, we analysed long-term changes in the growth rates of the long-lived inshore fish species *C. spectabilis*

(banded morwong or red moki), and compared these changes to temperature trends across the species' distribution. Growth rates were estimated from otoliths. These bony structures grow continuously throughout the life of the fish and typically exhibit an incremental structure, analogous to growth rings in trees, which can be counted to determine a fish's age and annual growth rate, the latter estimated by measuring distances between subsequent increments^{13–16}. These methods have been well-validated in the fish literature, including for banded morwong¹⁷ and other long-lived species (see, for example, ref. 18). In our data, correlations were found between otolith radius and fish size (that is, for fish aged seven and nine years; Fig. 2), confirming the expected link between otolith and somatic growth (see Methods). The remaining unexplained variation may result from a combination of biological factors and measurement error.

Banded morwong are a sedentary temperate fish common on rocky reefs at 10–50 m depth along the southeastern coast of Australia and off New Zealand¹⁹. Evidence for a single panmyctic population around the Tasman Sea includes a prolonged planktonic larval stage (~6 months), the fact that pelagic pre-juveniles are typically caught well off the continental shelf, and the results of genetic studies of related species that have similar larval and pre-juvenile stages^{19,20}. Individuals mature early (2–4 years after settlement to the reef) and live for up to 97 years^{17,19}. Adults are sedentary, males are highly territorial, and tagged fish are recaptured in the same region as they are released^{19,21}. Banded morwong populations have been commercially exploited in Australian waters only since 1990 (ref. 19), and harvests in New Zealand are either forbidden (in marine reserves) or restricted to recreational fishing²². The long life span of the species and the availability of specimens spanning a wide size/age and thermal range allowed us to reconstruct variability in age-specific growth rates that cover nearly a century (1910 to 2000; see Supplementary Table S1), following procedures outlined in refs 18 and 17.

Consistent with previous observations¹⁶, inferred growth rates of young adult banded morwong in southeast Australia have increased significantly since 1910, with otolith increments increasing between 0.034 and 0.14 $\mu\text{m yr}^{-1}$ for the four Australian sites ($38 \leq n \leq 79$ year-classes; $0.06 \leq r^2 \leq 0.34$; $P < 0.042$; see Supplementary Fig. S2). However, there is no similar long-term trend for specimens collected at the warm edge of the species range, off northern New Zealand ($n = 29$ year-classes; $P = 0.79$; see Supplementary Fig. S2).

To test whether this difference among sites was related to changes in water temperature, we compared mean growth rates for each year-class with analogous annual mean SSTs for each site. The latter were obtained from the Hadley Centre SST Dataset (HADSST2; ref. 23) and validated against a 60-year coastal

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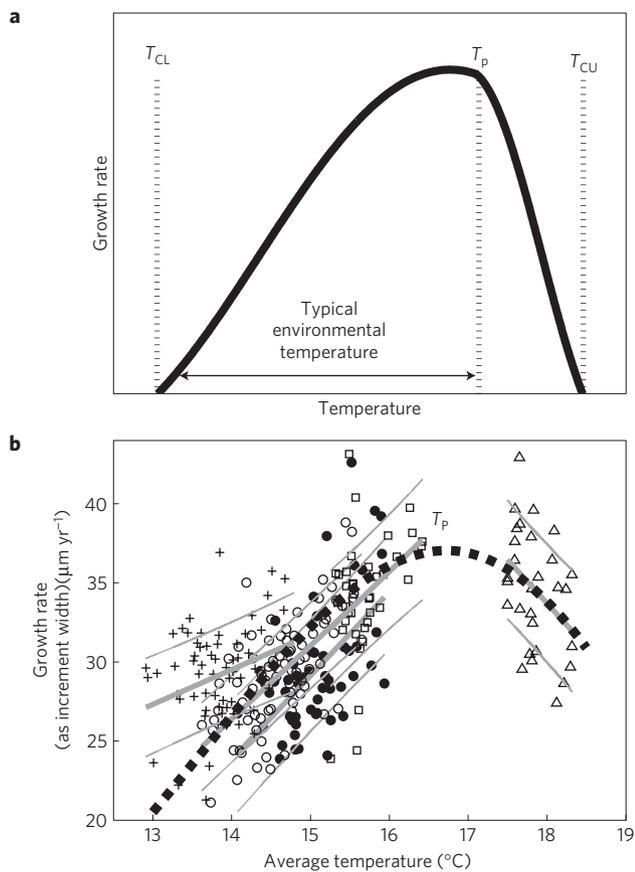


Figure 1 | Theorized and measured effects of temperature on growth.

a, There is a near-linear increase in growth with temperature over a mid-range in temperatures, bounded by the lower critical temperature (T_{CL}) and pejus temperature (T_P). At temperatures above the growth tolerance limit ($> T_P$), growth rate declines with increasing temperature to the upper critical temperature (T_{CU}) whereafter growth ceases. **b**, Mean year-class-specific growth increment (ages seven to nine years) is compared with temperatures over the annual growth period (October to September) for the mid-range Australian (Victoria, squares; northeast coast of Tasmania, closed circles; east coast of Tasmania, open circles; southeast coast of Tasmania, crosses) and extreme New Zealand (North Island, triangles) populations. Trend lines are linear regressions (grey thick lines) with 95% confidence intervals around the predictions (grey thin lines). Positive temperature effects on growth were found for all Australian populations (linear regression; $38 \leq n \leq 79$ year-classes; $0.09 \leq r^2 \leq 0.41$; $P < 0.015$; slope = $2.2\text{--}5.3 \mu\text{m } ^{\circ}\text{C}^{-1}$), whereas negative temperature effects on growth were indicated for the New Zealand population (linear regression; $n = 29$ year-classes; $r^2 = 0.15$; $P = 0.041$; slope = $-5.5 \mu\text{m } ^{\circ}\text{C}^{-1}$). T_P approximates the pejus temperature ($\sim 17^{\circ}\text{C}$) where after increases in temperature result in decreases in growth. We estimate T_P from the maximum of the nonlinear least-squares regression fit (black dashed line): growth rate = $290 \cdot (5.9/17.3 \cdot (\text{temperature}/17.3))^{4.9} \cdot e^{-(\text{temperature}/17.3)^{5.9}}$; $r^2 = 0.29$; $P < 0.0001$.

temperature time-series collected off southeastern Australia¹⁰ (see Methods, Supplementary Fig. S3). Temperatures at all five sites have increased since 1910 (range among sites: 0.010 to $0.016^{\circ}\text{C yr}^{-1}$; linear regression, $n = 108$ years; $0.42 \leq r^2 \leq 0.73$; $P \leq 0.0001$). Mean temperatures have been warmest off New Zealand ($17.7 \pm 0.5^{\circ}\text{C}$, mean \pm standard deviation) and coldest off southeastern Tasmania ($13.6 \pm 0.6^{\circ}\text{C}$) with seasonal temperatures peaking in March–April in each region. A comparison of growth rate and temperature data over all sites shows a strong nonlinear relationship, with an increase in growth rate with temperature for the cooler water Australian

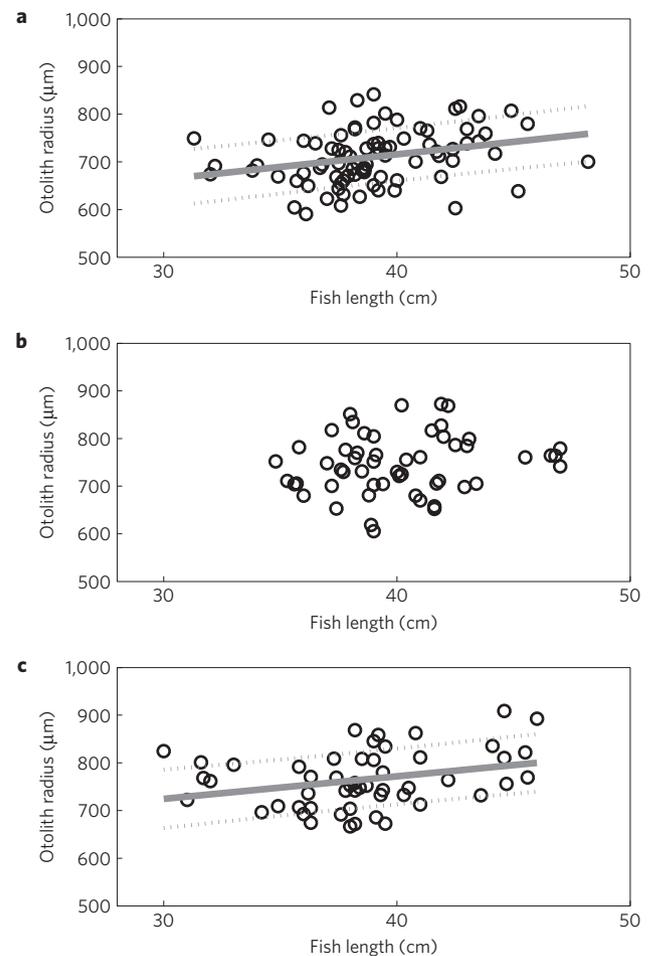


Figure 2 | Otolith radius as a function of fish size.

Otolith radius increases with fish size for **a**, fish aged seven years (linear regression, otolith radius = $5.3 \cdot \text{fish length} + 505 \mu\text{m}$; $n = 82$ fish; $r^2 = 0.083$; $P = 0.0088$) and **c**, nine years (linear regression, otolith radius = $4.7 \cdot \text{fish length} + 583 \mu\text{m}$; $n = 52$ fish; $r^2 = 0.090$; $P = 0.031$). **b**, Effects of other factors are reflected in the residual variability and non-significant relation for fish aged eight years (linear regression, $n = 54$ fish; $P = 0.25$). Trend lines are linear regressions (solid lines) with 95% confidence intervals around the predictions (dashed lines).

populations (range among sites: otolith increment increasing by $2.2\text{--}5.3 \mu\text{m } ^{\circ}\text{C}^{-1}$, linear regression; $38 \leq n \leq 79$ year-classes; $0.09 \leq r^2 \leq 0.41$; $P < 0.015$), but a decrease in growth rate with rising temperature in the warmer water New Zealand population (otolith increment decreasing by $-5.5 \mu\text{m } ^{\circ}\text{C}^{-1}$; $n = 29$ year-classes; $r^2 = 0.15$; $P = 0.041$; Fig. 1b). The New Zealand decrease in growth with temperature is maintained ($r^2 = 0.14$; $P = 0.071$) even when the year-class series is restricted to year-classes 1975 and earlier to avoid the infrequent sampling of year-classes after 1975 (see Supplementary Fig. S2). The correlations reflect in part the long-term trends and in part parallel quasi-decadal variability in SSTs (see Supplementary Fig. S4). Relationships between growth and temperature that are evident at both quasi-decadal and decadal timescales are consistent with a major role of temperature in determining ectotherm growth. Other factors no doubt contribute to variability in individual growth rates, some of which we can discern in the data (see Supplementary Fig. S5), but they all appear to be local and short-term.

The compilation of data across the Tasman Sea strongly suggests the nonlinear relationship between temperature and growth previously demonstrated for ectotherms in the laboratory, and implies a

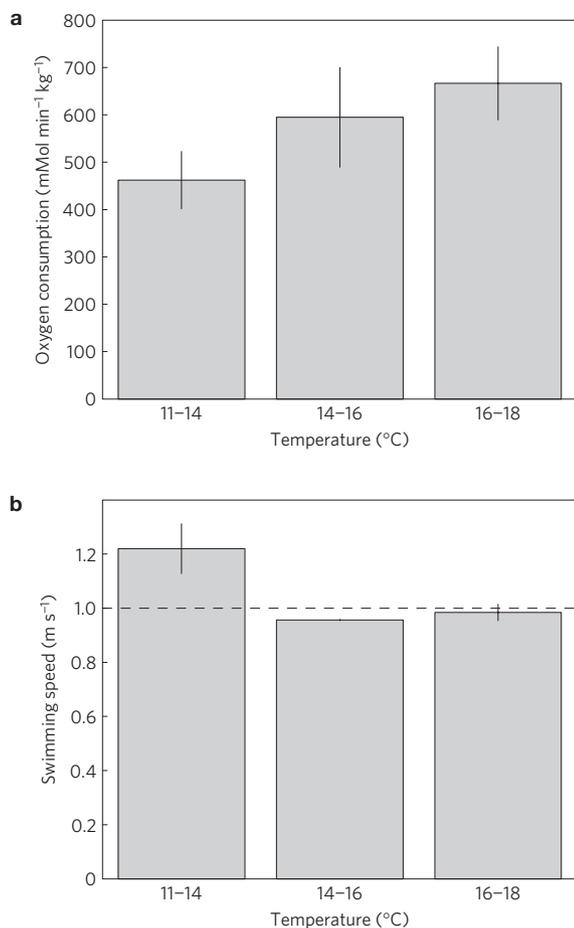


Figure 3 | Preliminary estimates of temperature effects on swimming activity in banded morwong. a, Temperature effects on oxygen consumption at 0.9 m s^{-1} (mean \pm standard error, based on $n = 2$ fish and >12 trials). **b**, The swimming speeds (mean \pm standard error, based on $n = 2$ fish and >12 trials) causing anaerobic stress at different temperatures. Spawning swimming speeds (1 m s^{-1}) were not sustainable at temperatures $>14^\circ\text{C}$, with fish exhibiting signs of anaerobic stress.

T_p (annual mean) for banded morwong of about 17°C (Fig. 1b). This thermal limit is also suggested by results from preliminary ($n = 2$ fish) activity experiments for fish from the southernmost (coldest) population where we observed fish performance at the species' typical spawning swimming speed ($\sim 1 \text{ m s}^{-1}$; period of highest activity) and temperatures ranging from 11 to 18°C (thermal range at sampling site, see Methods). At temperatures above 16°C , the fish seem to consume 44% more oxygen when approaching spawning swimming speeds (that is, $\sim 0.9 \text{ m s}^{-1}$) than fish at temperatures below 14°C (Jarque–Bera test for normality: $P = 0.99$; two-sided t -test: $P = 0.17$; Fig. 3a). Furthermore, fish held above 16°C could not sustain the spawning swimming speed of $\sim 1 \text{ m s}^{-1}$ measured in the field (see Fig. 3b and Methods) and appeared to rapidly go into anaerobic stress. It is important to note, however, that reduced maximum sustainable swimming speed was also found with fish held at temperatures of 14 – 16°C , where the otolith data indicate that fish growth is fastest. This result may reflect the small sample size of our experiments, and further work is needed to determine the effect of increasing temperature on swimming activity in banded morwong. Although these swimming data are preliminary, the patterns of increased stress and reduced maximum sustainable swimming speeds with increasing temperature were consistent in both fish tested, suggesting that the activity results may indicate the increased metabolic costs that appear to be

causing the observed decrease in growth rate in the New Zealand population. Temperatures during spawning time (March–April; ref. 17) now exceed 17°C in four out of five sites examined. A T_p of about 17°C is also suggested by the distribution of banded morwong along the Australian coast, the northern (warmest) extent of which is approximately at the 18 – 19°C SST isotherm.

Our data demonstrate that increasing water temperatures have pushed a species past the point where warming is beneficial to growth, and suggest mechanisms for range contraction as a result of this increase. The distribution of any species is a function of local environmental conditions and the likelihood of spawning and subsequent recruitment of juveniles²⁴. For populations living at the warm-edge of their distribution, temperatures that surpass T_p result in higher metabolic costs and less availability of energy for growth and reproduction³. Declining growth rates are also likely to reduce fecundity and egg quality, both of which vary directly with female size in fish (see, for example, ref. 25), and increase the risk of predation and starvation^{3,26,27}. Additionally, the loss of large fish at high temperatures is expected, as thermal sensitivity (via oxygen supply restriction) increases with body size²⁸. All of these effects imply a reduction in the population's recruitment success²⁴ and productivity²⁸. We speculate that the persistence of banded morwong in northern New Zealand reflects historical recruitment and the buffering capacity of its life history traits (that is, longevity and the fact that the long duration of its planktonic stage may facilitate recruitment from cooler parts of the species' range). In that regard, the factors that stimulate juveniles to recruit to the substratum are likely to be critical in determining the extent and speed of range contraction in the face of increasing water temperatures.

Methods

Banded morwong were sampled between 1984 and 2010 at five sites around southern Australia and New Zealand (see Supplementary Table S1 and refs 19 and 17). Sampling gear included standard commercial gill-nets (mesh size 122–140 mm) and hand-spears^{17,19}. Fish processing and otolith analysis were conducted following the procedures described in refs 16 and 17. Growth estimates were limited to early mature growth (increments seven to nine years) to maximize sample size and avoid the potential confounding effects of maturation on growth rate²⁹. Otolith increments were counted and measured blind (no reference to fish length, locality or date sampled), with $<2.4\%$ average error when compared with replicate blind counts for Australian samples. For correlations against birth year (year-class) and annual temperatures, a mean growth increment was calculated for each year-class.

Temperature estimates were obtained from the Hadley Sea Surface Temperature dataset (HADSST2; ref. 23) for each sample site from 1900 to 2010. The reconstructed temperature series correlated with those measured directly off the east coast of Tasmania¹² (see Supplementary Fig. S3). Annual mean temperature was estimated for each year (averaged from October to September to correspond to increment deposition¹⁹) and a year-class-specific mean temperature was estimated for the years corresponding with growth at ages seven to nine years.

Spawning swimming speeds were determined in the field, off the southeast coast of Tasmania (see Supplementary Fig. S1), using fish fitted with telemetered accelerometer tags. Preliminary observations of swimming performance in the laboratory were conducted at 11 – 14°C , 14 – 16°C and 16 – 18°C for each fish ($n = 2$ fish and >12 trials, weight = 1.8 and 2.7 kg), following the procedures described in ref 30.

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References

- Pörtner, H. O. & Peck, M. A. Climate change effects on fishes and fisheries: Towards a cause-and-effect understanding. *J. Fish. Biol.* **77**, 1745–1779 (2010).
- Brander, K. Impacts of climate change on fisheries. *ICES J. Mar. Sci.* **79**, 389–402 (2010).
- Pörtner, H. O. & Knust, R. Climate change affects marine fishes through the oxygen limitation of thermal tolerance. *Science* **315**, 95–97 (2007).
- Wang, T. & Overgaard, J. The heartbreak of adapting to global warming. *Science* **315**, 49–50 (2007).
- Cai, W., Shi, G., Cowan, T., Bi, D. & Ribbe, J. The response of the Southern Annular Mode, the East Australian Current, and the southern mid-latitude ocean circulation to global warming. *Geophys. Res. Lett.* **32**, L23706 (2005).

6. Fry, F. E. I. in *Fish Physiology Vol. VI Environmental Relations and Behavior* (eds Hoar, W. S. & Randall, D. J.) 1–99 (Academic, 1971).
7. Takasuka, A. & Aoki, I. Environmental determinants of growth rates for larval Japanese anchovy *Engraulis japonicus* in different waters. *Fish. Oceanogr.* **15**, 139–149 (2006).
8. Pörtner, H.-O. & Farrell, A. P. Physiology and climate change. *Science* **322**, 690–692 (2008).
9. Katersky, R. S. & Carter, C. G. High growth efficiency occurs over a wide temperature range for juvenile barramundi *Lates calcarifer* fed a balanced diet. *Aquaculture* **272**, 444–450 (2007).
10. Ridgway, K. R. Long-term trend and decadal variability of the southward penetration of the East Australian Current. *Geophys. Res. Lett.* **34**, L13613 (2007).
11. Pecl, G. *et al.* *The East Coast Tasmanian Rock Lobster Fishery—Vulnerability to Climate Change Impacts and Adaptation Response Options* (Australian Government Department of Climate Change, 2009).
12. Hill, K. L., Rintoul, S. R., Coleman, R. & Ridgway, K. R. Wind forced low frequency variability of the East Australia Current. *Geophys. Res. Lett.* **35**, L08602 (2008).
13. Campana, S. E. & Neilson, J. D. Microstructure of fish otoliths. *Can. J. Fish. Aquat. Sci.* **42**, 1014–1032 (1985).
14. Neilson, J. D. & Geen, G. H. Effects of feeding regimes and diel temperature cycles on otolith increment formation in juvenile chinook salmon, *Oncorhynchus tshawytscha*. *Fish. Bull.* **83**, 91–101 (1985).
15. Chambers, R. C. & Miller, T. J. in *Recent Developments in Otolith Research* (eds Secor, S. H., Dean, J. M. & Campana, S. E.) 155–175 (Univ. South Carolina Press, 1995).
16. Thresher, R. E., Koslow, J. A., Morison, A. K. & Smith, D. C. Depth-mediated reversal of the effects of climate change on long-term growth rates of exploited marine fish. *Proc. Natl Acad. Sci. USA* **104**, 7461–7465 (2007).
17. Ewing, G. P., Lyle, J. M., Murphy, R. J., Kalish, J. M. & Ziegler, P. E. Validation of age and growth in a long-lived temperate reef fish using otolith structure, oxytetracycline and bomb radiocarbon methods. *Mar. Freshwat. Res.* **58**, 944–955 (2007).
18. Armsworthy, S. L. & Campana, S. E. Age determination, bomb-radiocarbon validation and growth of Atlantic halibut (*Hippoglossus hippoglossus*) from the Northwest Atlantic. *Environ. Biol. Fish.* **89**, 279–295 (2010).
19. Ziegler, P. E., Lyle, J. M., Haddon, M. & Ewing, G. P. Rapid changes in life-history characteristics of a long-lived temperate reef fish. *Mar. Freshwat. Res.* **58**, 1096–1107 (2007).
20. Grewe, P. M., Smolenski, A. J. & Ward, R. D. Mitochondrial DNA variation in jackass morwong, *Nemadactylus macropterus* (Teleostei: Cheilodactylidae) from Australian and New Zealand waters. *Can. J. Fish. Aquat. Sci.* **51**, 1101–1109 (1994).
21. Murphy, R. J. & Lyle, J. M. *Impact of Gillnet Fishing on Inshore Temperate Reef Fishes, with Particular Reference to Banded Morwong*. FRDC Project No. 95/145 (Marine Research Laboratories—Tasmanian Aquaculture and Fisheries Institute, University of Tasmania, 1999).
22. McCormick, M. I. & Choat, J. H. Estimating total abundance of a large temperate-reef fish using visual strip-transects. *Mar. Biol.* **96**, 469–478 (1987).
23. Rayner, N. A. *et al.* Improved analyses of changes and uncertainties in sea surface temperature measured *in situ* since the mid-nineteenth century: The HadSST2 Dataset. *J. Clim.* **19**, 446–469 (2006).
24. Rijnsdorp, A. D., Peck, M. A., Engelhard, G. H., Möllmann, C. & Pinnegar, J. K. Resolving the effect of climate change on fish populations. *ICES J. Mar. Sci.* **66**, 1570–1583 (2009).
25. Heinimaa, S. & Heinimaa, P. Effect of the female size on egg quality and fecundity of the wild Atlantic salmon in the sub-arctic River Tenso. *Bor. Environ. Res.* **9**, 55–62 (2004).
26. Mittelbach, G. G. Foraging efficiency and body size: A study of optimal diet and habitat use by bluegills. *Ecology* **62**, 1370–1386 (1981).
27. Beamish, R. J., Mahnken, C. & Neville, C. M. Evidence that reduced early marine growth is associated with lower marine survival of coho salmon. *Trans. Am. Fisheries Soc.* **133**, 26–33 (2004).
28. Pörtner, H.-O. *et al.* Cod and climate in a latitudinal cline: Physiological analyses of climate effects in marine fishes. *Clim. Res.* **37**, 253–270 (2008).
29. Neubeimer, A. B. & Taggart, C. T. Can changes in length-at-age and maturation timing in Scotian Shelf haddock (*Melanogrammus aeglefinus*) be explained by fishing? *Can. J. Fish. Aquat. Sci.* **67**, 854–865 (2010).
30. Clark, T. D. & Seymour, R. S. Cardiorespiratory physiology and swimming energetics of a high-energy-demand teleost, the yellowtail kingfish (*Seriola lalandi*). *J. Exp. Biol.* **209**, 3940–3951 (2006).

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Author contributions

All authors contributed to the design of the study. A.B.N. prepared (where necessary), aged and measured all otoliths, and analysed resulting growth increment and temperature data. J.M.S. designed, implemented and analysed the activity experiments. A.B.N. prepared the manuscript. R.E.T., J.M.L. and J.M.S. edited the manuscript.

Additional information

The authors declare no competing financial interests. Supplementary information accompanies this paper on www.nature.com/natureclimatechange. Reprints and permissions information is available online at <http://npg.nature.com/reprintsandpermissions>. Correspondence and requests for materials should be addressed to A.B.N.