

17. Tong-Dzuy, T. & Janvier, P. Les Vertébrés du Dévonien inférieur du Bac Bo oriental (provinces de Bac Thai et Lang Son, Viêt Nam). *Bull. Mus. Natl. Hist. Nat. Paris* **12**, 143–223 (1990).
18. Johanson, Z. & Ahlberg, P. E. A complete primitive rhizodont from Australia. *Nature* **394**, 569–572 (1998).
19. Long, J. A. A new rhizodontiform fish from the Early Carboniferous of Victoria, Australia, with remarks on the phylogenetic position of the group. *J. Vert. Paleontol.* **9**, 1–17 (1989).
20. Clement, G. Evidence for lack of choanae in the Porolepiformes. *J. Vert. Paleontol.* **21**, 795–802 (2001).
21. Ahlberg, P. E., Clack, J. A. & Lukševičs, E. Rapid braincase evolution between *Panderichthys* and the earliest tetrapods. *Nature* **381**, 61–64 (1996).
22. Chang, M. M. & Yu, X. B. Structure and phylogenetic significance of *Diabolichthys speratus* gen. et sp. nov., a new dipnoan-like form from the early Devonian of southeastern Yunnan, China. *Proc. Linn. Soc. N.S.W.* **107**, 171–184 (1984).
23. Zhu, M., Yu, X. B. & Ahlberg, P. E. A primitive sarcopterygian fish with an eyestalk. *Nature* **410**, 81–84 (2001).
24. Bemis, W. E. & Grande, L. Early development of the actinopterygian head. I. External development and staging of the paddlefish *Polyodon spathula*. *J. Morphol.* **213**, 47–83 (1992).
25. Ashique, A. M., Fu, K. & Richman, J. M. Endogenous bone morphogenetic proteins regulate outgrowth and epithelial survival during avian lip fusion. *Development* **129**, 4647–4660 (2002).
26. Hu, D. & Helms, J. The role of *sonic hedgehog* in normal and abnormal craniofacial morphogenesis. *Development* **126**, 4873–4884 (1999).
27. Zhang, Z. et al. Rescue of cleft palate in *Mx1*-deficient mice by transgenic *Bmp4* reveals a network of BMP and Shh signaling in the regulation of mammalian palatogenesis. *Development* **129**, 4135–4146 (2002).

Supplementary Information accompanies the paper on www.nature.com/nature.

Acknowledgements We thank M. M. Chang for advice and discussions, M. Yang for artwork, and X. Lu for specimen preparation. This work was supported by the Special Funds for Major State Basic Research Projects of China and the Chinese Foundation of Natural Sciences. P.E.A. thanks the Royal Society and Chinese Academy of Sciences for supporting his visit to Beijing in 2002 through their exchange programme.

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

Correspondence and requests for materials should be addressed to M.Z. (zhumin@ivpp.ac.cn).

Ecosystem remodelling among vertebrates at the Permian–Triassic boundary in Russia

M. J. Benton¹, V. P. Tverdokhlebov² & M. V. Surkov²

¹Department of Earth Sciences, University of Bristol, Bristol BS8 1RJ, UK

²Geological Institute of Saratov State University, Ulitsa Moskovskaya 161, Saratov 410075, Russia

The mass extinction at the Permian–Triassic boundary, 251 million years (Myr) ago, is accepted as the most profound loss of life on record^{1–3}. Global data compilations indicate a loss of 50% of families or more, both in the sea^{1,2,4} and on land^{2,5}, and these figures scale to a loss of 80–96% of species, based on rarefaction analyses^{6,7}. This level of loss is confirmed by local and regional-scale studies of marine sections^{3,8}, but the terrestrial record has been harder to analyse in such close detail. Here we document the nature of the event in Russia in a comprehensive survey of 675 specimens of amphibians and reptiles from 289 localities spanning 13 successive geological time zones in the South Urals basin. These changes in diversity and turnover cannot be explained simply by sampling effects. There was a profound loss of genera and families, and simplification of ecosystems, with the loss of small fish-eaters and insect-eaters, medium and large herbivores and large carnivores. Faunal dynamics also changed, from high rates of turnover through the Late Permian period to greater stability at low diversity through the Early Triassic period. Even after 15 Myr of ecosystem rebuilding, some guilds were apparently still absent—small fish-eaters, small insect-eaters, large herbivores and top carnivores.

At a time when there is so much focus on global change and threats to biodiversity, it is surprising how little was known about the Permian–Triassic boundary (PTB) event in 1990 (refs 1, 2, 9). Over the past 15 years, our understanding of this mass extinction has become focused in terms of the timescale (perhaps lasting for 500,000 years (refs 3, 10)), the cause (probably associated with massive outpourings of basalt lava, the Siberian Traps, triggering global warming and anoxia, and possibly a runaway greenhouse effect associated with repeated release of gas hydrates^{2,8–12}), and the nature of the event and the immediate recovery phase (mass extinction followed by rapid turnover of weedy species during the phase of maximum anoxia, and then slow rebuilding of ecosystems^{3,8,9}).

The Permian–Triassic succession of the South Urals is about 6 km thick, thinning to 1–2 km in the Moscow basin^{13–15}, and it is subdivided into 13 successive stratigraphic units (Fig. 1). These units are recognized in the field by changes in sedimentary rock type (svitas), and by particular fossil assemblages (gorizonts); they are correlated with each other, and with the global standard, by means of palynomorphs and ostracods^{13–15}. The age range covers the Kazanian and Tatarian stages of the Late Permian and the Induan to Ladinian stages of the Early and Middle Triassic, a total time span of 25–30 Myr.

The Late Permian to Triassic succession in the South Urals starts with a marine episode in the Kazanian, represented by 200 m of limestone, mudstone and halite, followed by about 1 km of river-deposited mudstone and sandstone. The continental succession extends with relatively continuous deposition from the late Kazanian to the Ladinian (Middle Triassic), and consists of repetitions of four main facies types: mudflats, sandy distributary channels, small gravelly channels and large gravelly channel fluvial systems¹³. The basalmost Triassic is marked by thick sandstone units that document a marked, but short-lived, change in sedimentation style to large gravelly channels, with boulders of more ancient rocks, up to 1 m across, swept down from the Ural mountains. These thick conglomerate units were deposited in large-scale alluvial fans that were part of a much larger terminal fan, about 350–400 km in width.

The abrupt change in the size of the basin and the incoming of coarse-grained alluvial fans all along the western margin of the Urals probably resulted from a peak in mountain-building activity in the core of the Urals, and a change at the PTB towards a more arid climate, with higher sediment yield and greater peak discharges in a drainage basin with reduced vegetation cover¹³. These massive changes in style of sedimentation at the PTB have been seen independently in the continental Karoo succession in South Africa¹⁶ and Australia¹⁷. The changes have been linked to the Siberian basalt eruptions and the consequent marked global warming and acid rain. The acid rain may have killed off the vegetation on land, and soils were stripped from the landscape and swept down rivers on to the plains, and eventually into the sea^{2,8,9}. Mountain uplift and soil stripping, rather than increased rainfall, lies behind the switch from low-energy rivers and cyclical deposition in the latest Permian to massive erosion at the base of the Triassic. Environments and sedimentation styles reverted to pre-PTB conditions higher in the Lower Triassic succession.

The range chart of tetrapods in the Late Permian and Triassic of the South Urals (Fig. 1) shows diverse ecosystems in the Late Permian¹⁵. In the rivers and lakes, four to seven genera of small, medium and large aquatic tetrapods (‘amphibians’) fed on the abundant thick-scaled bony fishes and rarer freshwater sharks and lungfishes. On the wooded banks were 5–11 genera of terrestrial tetrapods (‘reptiles’), ranging in size from tiny insect-eaters to rhino-sized plant-eating pareiasaurs and the wolf-sized to bear-sized sabre-toothed gorgonopsians that fed on them. During the 17–18 Myr of the Kazanian and Tatarian, there was considerable turnover of genera and families through the six time zones (Fig. 2).

The percentage extinction of families at the end of the Permian

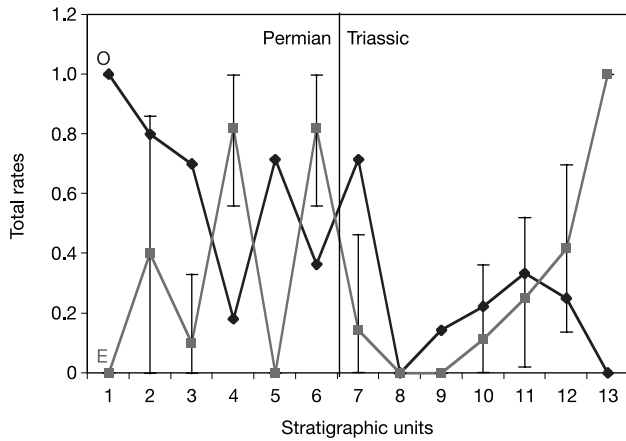


Figure 2 Turnover of tetrapod families through the Late Permian and Early Triassic in the South Urals basin, Russia. Rates are high and variable through the Late Permian, but they are depressed after the end-Permian mass extinction, and pick up slowly thereafter during the Early Triassic recovery phase. Rates of origination (O, diamonds) and extinction (E, squares) are percentage metrics based on all taxa (including Lazarus taxa, but excluding singleton families—families known from a single species or single locality) known from a time bin. Stratigraphic units are the successive svitas of the Upper Permian (1, Osinovskaya; 2, Belebey; 3, Bolshekinelskaya; 4, Amanakskaya; 5, Malokinelskaya/Vyakovskaya; 6, Kutulukskaya/Kulchomovskaya), Lower Triassic (7, Kopanskaya; 8, Staritskaya; 9, Kzylsaiskaya; 10, Gostevskaya; 11, Petropavlovskaya) and Middle Triassic (12, Donguz; 13, Bukobay). Binomial 95% confidence intervals³⁰ are shown for the percentage extinction metrics (confidence intervals are of similar magnitude for the percentage origination metrics, but are omitted for clarity).

familial diversity through time are compared with the distributions of numbers of sites and numbers of specimens in each time bin (Fig. 3c), there is no apparent tracking. Peaks and troughs in the diversity data do not match peaks and troughs in richness of the fossil record. And, crucially, the time of diversity decline across the PTB corresponds to a rising trend in numbers of sites and specimens.

Three sampling standardization protocols were also applied (see Methods) to assess whether the patterns of apparent diversity, and extinction and origination rates, could be determined by sample size. Five of the stratigraphic units are represented by small ($n < 50$) sample sizes, namely the Osinovskaya, Belebey, Bolshekinelskaya, Gostevskaya and Bukobay svitas, of which only the Gostevskaya falls near the PTB (Fig. 1). Ignoring or combining these poorly sampled bins does not affect the patterns of diversity, extinction or origination through time. Rarefaction analysis shows that the better-sampled time units, the Kopanskaya, Kzylsaiskaya and Staritskaya svitas (Fig. 1), may overestimate diversity by one, or at most two, families in comparison with the other time bins. Normalizing all time bin sizes to the range of 49–63 specimens cuts the diversity of the first three Triassic horizons by one or two families, hence making the PTB extinction seem larger (91% instead of 82% extinction rate) and depressing earliest Triassic diversity even more than has been indicated from the raw figures.

Scaling between local-scale or regional-scale observations such as these and the global scale is hard. Nonetheless, just as local-scale studies of marine PTB sections^{3,8} show patterns expected from global-scale studies^{3,20}, so this study, and similar investigations of the PTB in the Karoo basin of South Africa^{16,21}, indicate high familial extinction rates among tetrapods: 74% from a global database⁵, and 82% here. Our most striking finding has been that the high-diversity and complex latest Permian terrestrial ecosystems were volatile in terms of generic and familial turnover, but that when these ecosystems were largely destroyed by the PTB crisis the volatility disappeared, and recovery from low diversity was a slow

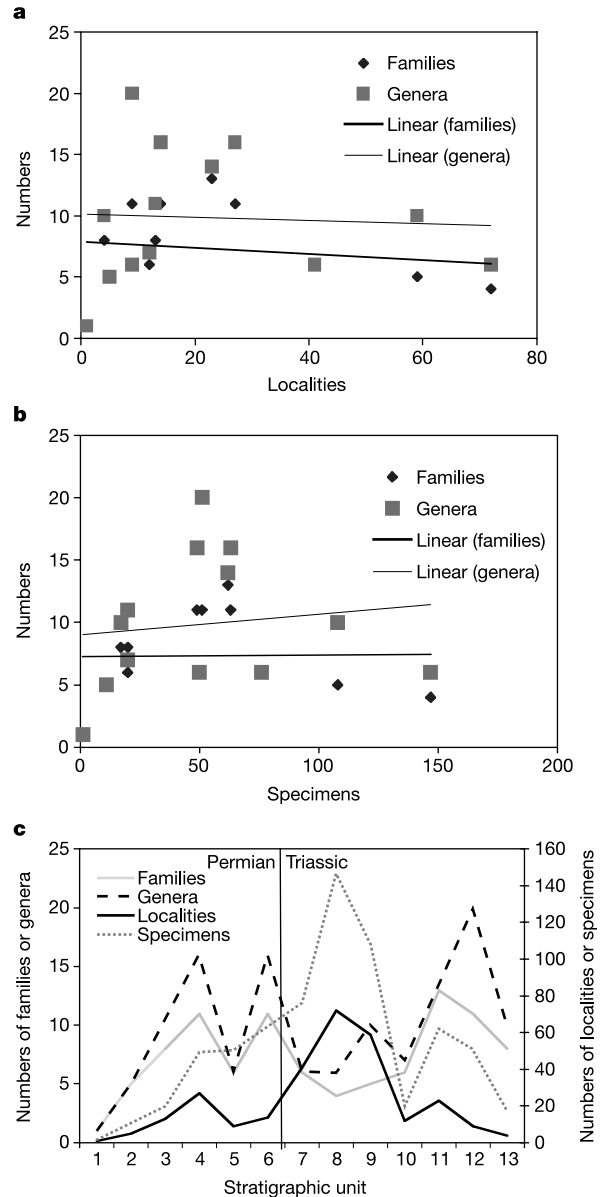


Figure 3 The data on tetrapod distributions from the South Urals are probably reliable, and cannot be accounted for simply by sampling (the patchiness of the rock and fossil record). **a, b.** Numbers of genera and families are not related to numbers of localities (**a**) or numbers of specimens (**b**). Best fitting straight lines show highly insignificant correlation coefficients. **c.** The distributions of generic and familial diversity through time (left-hand y-axis) follow similar curves, but these do not seem to relate to measures of sampling (numbers of localities and specimens per time bin, which themselves are correlated; right-hand y-axis). Stratigraphic units are as in Fig. 2.

process, with longer survivorship of genera and families and less turnover. Within the 15-Myr post-event window, full recovery of the ecosystems had not taken place. □

Methods

Database

The data set consists of records kept by V.P.T. at the Geological Institute of Saratov State University since the 1960s documenting every vertebrate specimen recovered in a broad geographic area about 400 km wide and 200 km long, bounded by Samara in the west and the Ural mountains in the east, and centring on the city of Orenburg. These records document a minimum of 675 specimens (isolated bones, complete skulls and complete skeletons) from 289 localities, each dated to one of the 13 time divisions of the Kazanian to Ladinian interval. The data are listed in refs 14 and 15. Lists of genera and families present in each time bin were compiled, together with the numbers of specimens of each taxon and

a note of the completeness of preservation (isolated bone, group of bones, complete skull, complete skeleton) for each.

In the past, Western authors have tended to rename Russian svitas as 'formations', and horizons as 'horizons', but this masks their true meanings. In Russia, horizons are the main regional stratigraphic units, identified primarily from their palaeontological characteristics, and they do not pertain to lithostratigraphic units. Svitas are largely lithostratigraphic units, given a locality name that is close to their characteristic exposure. The definition of a svita incorporates a mix of field lithological observations and biostratigraphic assumptions.

Analysis

The records were converted into range charts (Fig. 1), including Lazarus taxa²², from which total numbers (*N*) and numbers of originations (*O*) and extinctions (*E*) per time bin were calculated. Percentage origination and extinction metrics (*O/N*, *E/N*) were calculated for each time bin (Fig. 2). There are many other possible measures of extinction and origination rates, most calculated with respect to time; such measures would be inappropriate here because the durations of the svitas are poorly constrained. Boundary-crossing measures of extinction and origination rates were not used because the sample sizes are small, and 10 of the 38 families are restricted to one time bin and would have to be discarded. Generic rates are not presented because many genera are singletons (restricted to one time bin) and most are in need of taxonomic revision. Binomial error bars³⁰ are calculated for the percentage metrics.

The possible influence of sampling was assessed from the raw data (Fig. 3), and by the application of three sampling standardizations. In the first standardization, units that had yielded fewer than 50 specimens were ignored (namely the Osinovskaya, Belebey, Bolshekinelskaya, Gostevskaya and Bukobay svitas); sample sizes then ranged from 49 to 147 specimens. In the second sampling standardization, the two oldest units were ignored, and the others with small sample sizes were combined with adjacent units (Bolshekinelskaya + Amanakskaya, Gostevskaya + Petropavlovskaya, Donguz + Bukobay), yielding a range of sample sizes from 50 to 147 specimens. In the third sampling standardization, rarefaction analysis was applied to the units that had yielded larger samples of specimens (Kopanskaya, Kzylsaiskaya, Staritskaya) to assess what their apparent diversity would have been had the sample size been 50, within the range 49–63 specimens, as for the other moderately well sampled units.

The data sets and analyses are available as Supplementary Data, and may be downloaded at <http://palaeo.gly.bris.ac.uk/Data/RussiaPTR.xls>.

Dating

The timescale indicated in Fig. 1 is based on refs 10, 23, 24 and 25. The date for the Permian–Triassic boundary, 251 Myr, from ref. 10, has been debated²⁶, but is widely accepted and will be the accepted date in the new Cambridge geologic timescale^{27,28}. Other aspects of the scales may seem less familiar, in that the Kazanian and Tatarian are much longer than is often assumed, 16 Myr instead of 4–5 Myr, and the Middle Triassic is dated as older than normally accepted. Should the old dates prove to be correct, and the newer ones incorrect, the conclusions here are not affected because we do not make claims about the longer-term timing of events, nor do we present rates of origination or extinction calculated against time.

Received 2 July; accepted 18 August 2004; doi:10.1038/nature02950.

1. Erwin, D. H. The Permo-Triassic extinction. *Nature* **367**, 231–236 (1994).
2. Benton, M. J. *When Life Nearly Died* (Thames & Hudson, London, 2003).
3. Jin, Y. G. *et al.* Pattern of marine mass extinction near the Permian–Triassic boundary in south China. *Science* **289**, 432–436 (2000).
4. Sepkoski, J. J. Jr in *Global Events and Event Stratigraphy* (ed. Walliser, O. H.) 35–52 (Springer, Berlin, 1996).
5. Maxwell, W. D. Permian and Early Triassic extinction of nonmarine tetrapods. *Palaeontology* **35**, 571–583 (1992).
6. Raup, D. M. Size of the Permo-Triassic bottleneck and its evolutionary implications. *Science* **206**, 217–218 (1979).
7. McKinney, M. L. Extinction selectivity among lower taxa—gradational patterns and rarefaction error in extinction estimates. *Paleobiology* **21**, 300–313 (1995).
8. Twitchett, R. J., Looy, C. V., Morante, R., Visscher, H. & Wignall, P. B. Rapid and synchronous collapse of marine and terrestrial ecosystems during the end-Permian biotic crisis. *Geology* **29**, 351–354 (2001).
9. Benton, M. J. & Twitchett, R. J. How to kill (almost) all life: the end-Permian extinction event. *Trends Ecol. Evol.* **18**, 358–365 (2003).
10. Bowring, S. A. *et al.* U/Pb zircon geochronology of the end-Permian mass extinction. *Science* **280**, 1039–1045 (1998).
11. Wignall, P. B. & Twitchett, R. J. Oceanic anoxia and the end Permian mass extinction. *Science* **272**, 1155–1158 (1996).
12. Berner, R. A. Examination of hypotheses for the Permo-Triassic boundary extinction by carbon cycle modeling. *Proc. Natl Acad. Sci. USA* **99**, 4172–4177 (2002).
13. Newell, A. J., Tverdokhlebov, V. P. & Benton, M. J. Interplay of tectonics and climate on a transverse fluvial system, Upper Permian, Southern Uralian foreland basin, Russia. *Sediment. Geol.* **127**, 11–29 (1999).
14. Tverdokhlebov, V. P., Tverdokhlebova, G. I., Surkov, M. V. & Benton, M. J. Tetrapod localities from the Triassic of the SE of European Russia. *Earth Sci. Rev.* **60**, 1–66 (2003).
15. Tverdokhlebov, V. P., Tverdokhlebova, G. I., Minikh, A. V., Surkov, M. V. & Benton, M. J. Upper Permian vertebrates and their sedimentological context in the South Urals, Russia. *Earth Sci. Rev.* (in press) (2004).
16. Ward, P. D., Montgomery, D. R. & Smith, R. Altered river morphology in South Africa related to the Permian–Triassic extinction. *Science* **289**, 1740–1743 (2000).
17. Michaelsen, P. Mass extinction of peat-forming plants and the effect on fluvial styles across the

- Permian–Triassic boundary, Northern Bowen Basin, Australia. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **179**, 173–188 (2002).
18. Peters, S. E. & Foote, M. Biodiversity in the Phanerozoic: a reinterpretation. *Paleobiology* **27**, 583–601 (2001).
19. Smith, A. B. Large-scale heterogeneity of the fossil record: implications for Phanerozoic biodiversity studies. *Phil. Trans. R. Soc. Lond. B* **356**, 351–367 (2001).
20. Benton, M. J. Diversification and extinction in the history of life. *Science* **268**, 52–58 (1995).
21. Smith, R. M. H. & Ward, P. D. Pattern of vertebrate extinctions across an event bed at the Permian–Triassic boundary in the Karoo Basin of South Africa. *Geology* **29**, 1147–1150 (2001).
22. Jablonski, D. in *Dynamics of Extinction* (ed. Elliott, D. K.) 183–230 (Wiley, New York, 1986).
23. Cassinis, G., Nicosia, U., Lozovsky, V. R. & Gubin, Y. M. A view of the Permian continental stratigraphy of the Southern Alps, Italy, and general correlation with the Permian of Russia. *Permophiles* **40**, 4–16 (2002).
24. Kozur, H. W. Integrated ammonoid, conodont and radiolarian zonation of the Triassic and some remarks to stage/substage subdivision and the numeric age of the Triassic stages. *Albertiana* **28**, 570–574 (2003).
25. Jin, Y., Wardlaw, B. R., Glenister, B. F. & Kotlyar, G. V. Permian chronostratigraphic divisions. *Episodes* **20**, 10–15 (1997).
26. Mundil, R. *et al.* Timing of the Permian–Triassic biotic crisis: implications from new zircon U/Pb age data (and their limitations). *Earth Planet. Sci. Lett.* **187**, 131–145 (2001).
27. Ogg, J. G. Status of divisions of the International Geologic Time Scale. *Lethaia* **37**, 183–199 (2004).
28. Gradstein, F. M., Ogg, J. G. & Smith, A. G. (eds) *A Geologic Time Scale 2004* (Cambridge Univ. Press, in the press).
29. Benton, M. J. Testing the roles of competition and expansion in tetrapod evolution. *Proc. R. Soc. Lond. B* **263**, 641–646 (1996).
30. Raup, D. M. in *Analytical Paleobiology, Short Courses in Paleontology No. 4* (eds Gilinsky, N. L. & Signor, P. W.) 207–216 (Paleontological Society, Knoxville, Tennessee, 1991).

Supplementary Information accompanies the paper on www.nature.com/nature.

Acknowledgements We thank P. Donoghue, S. Braddy, H. Falcon-Lang and R. Twitchett for helpful comments on the manuscript, and S. Powell for Fig. 1. Funding for this work was provided by the Royal Society, INTAS, RFBR, Russian Ministry of Education, the Leverhulme Trust, and the National Geographic Society.

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

Correspondence and requests for materials should be addressed to M.J.B. (mike.benton@bris.ac.uk).

Long-term decline in krill stock and increase in salps within the Southern Ocean

Angus Atkinson¹, Volker Siegel², Evgeny Pakhomov^{3,4} & Peter Rothery⁵

¹British Antarctic Survey, Natural Environment Research Council, High Cross, Madingley Road, Cambridge CB3 0ET, UK

²Sea Fisheries Institute, Palmaille 9, 22767 Hamburg, Germany

³Department of Earth and Ocean Sciences, University of British Columbia, 6339 Stores Rd, Vancouver, British Columbia, V6T 1Z4, Canada

⁴Department of Zoology, Faculty of Science and Technology, University of Fort Hare, Private Bag X1314, Alice 5700, South Africa

⁵NERC Centre for Ecology and Hydrology, CEH Monks Wood, Abbots Ripton, Huntingdon PE28 2LS, UK

Antarctic krill (*Euphausia superba*) and salps (mainly *Salpa thompsoni*) are major grazers in the Southern Ocean^{1–4}, and krill support commercial fisheries⁵. Their density distributions^{1,3,4,6} have been described in the period 1926–51, while recent localized studies^{7–10} suggest short-term changes. To examine spatial and temporal changes over larger scales, we have combined all available scientific net sampling data from 1926 to 2003. This database shows that the productive southwest Atlantic sector contains >50% of Southern Ocean krill stocks, but here their density has declined since the 1970s. Spatially, within their habitat, summer krill density correlates positively with chlorophyll concentrations. Temporally, within the southwest Atlantic, summer krill densities correlate positively with sea-ice extent the