Fishing Down Marine Food Webs
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PRP24 fragment or a 1.4-kb Apa I–Sal I *PRP24-Pya* fragment (*13*). Both constructs overexpressed Prp24p when transformed into PRY98 as determined by Western blotting with anti-Prp24 polyclonal antibodies.

19. Three liters of each strain, PRY115 (PRY98 with *pG1-PRP24* as sole *PRP24* gene) and PRY116 (PRY98 with *pG1-PRP24-Pya* as sole *PRP24* gene), were harvested in late logarithmic phase. Whole cell extract was prepared (*15*), and 150 mg of each was subjected to 30 to 55% ammonium sulfate precipitation. The precipitates were resuspended in 40 ml of AGK 200 [10 mM Hepes (pH 7.9), 200 mM KCl, 1.5 mM $MgCl_2$, 10% glycerol, 0.2 mM EDTA, 0.1% Triton X-100, 0.5 mM DTT, 1 mM phenylmethylsulfonyl fluoride, 1 mM benzamidine, pepstatin A (1 μg/ml), leupeptin (1 μg/ml)] and incubated with 150 μl of protein G–Sepharose (washed in AGK 200) on a nutator at 4°C for 30 min. (This step removed proteins that bound nonspecifically to the resin.) The supernatants were added to 1 ml of protein G–Sepharose coupled to anti-polyoma antibodies (beads: AGK 200 = 1:1) as in (*32*). After 1.5 hours nutating at 4°C, the supernatants were removed, and the beads were washed 5 × 20 ml of AGK 700 (AGK buffer with 700 mM KCl), 1 × 15 ml of AGK 200, and 1 × 15 ml of AGK 50 (AGK buffer with 50 mM KCl). The washed beads were eluted twice by nutating at 23°C for 10 min with 2 × 400 μl (1 mg/ml) of peptide EYMPME (Glu-Tyr-Met-Pro-Met-Glu) (*32*) in AGK 50. Each eluate was dialyzed against 2 × 2 liters of buffer D at 4°C for 3.5 hours. The dialyzates were microcentrifuged 10 min, and the supernatants were collected. Approximately 15 μg of Prp24 was recovered, and no snRNAs copurified under these conditions (with a sensitivity to ~1 fmol of U6, no U6 was detected in 1 pmol of Prp24 protein).
20. D. S. Horowitz and J. Abelson, *Genes Dev.* **7**, 320 (1993).
21. A typical splicing reaction mixture may contain ~3 nM U4 and ~6 nM U6 snRNAs, compared with 0.2 to 0.5 nM pre-mRNA. (It is not known what fraction of the snRNAs is competent for splicing.) Levels of U6 snRNA are constitutively lower in PRY112 (*13*) (Fig. 3), so sensitivity to snRNP recycling defects may be enhanced in this extract.
22. R. J. Lin *et al.*, *J. Biol. Chem.* **260**, 14780 (1985).
23. U. Vijayraghavan, M. Company, J. Abelson, *Genes Dev.* **3**, 1206 (1989); J. Banroques and J. N. Abelson, *Mol. Cell. Biol.* **9**, 3710 (1989); J. D. Brown and J. D. Beggs, *EMBO J.* **11**, 3721 (1992); F. Galisson and P. Legrain, *Nucleic Acids Res.* **21**, 1555 (1993); S. W. Ruby, T.-H. Chang, J. Abelson, *Genes Dev.* **7**, 1909 (1993).
24. Additional figures are available to readers at the URL www.sciencemag.org/feature/data/972699/shl
25. Supershifted free U6 snRNP did not hybridize to U4, appeared in Prp24-3HA extract and not in untagged Prp24 extract, and increased with antibody concentration. Only the faster migrating, diffuse supershift was observed at lower antibody concentrations, suggesting that multiple antibody molecules may bind the 3HA epitope (*17*).
26. Splicing reaction mixtures (80 μl) (*22*) containing extract, ATP, and unlabeled actin pre-mRNA as noted were incubated 30 min at 25°C. After nutating for 1 hour at 4°C with 3.2 μg of 12CA5 antibody and 400 μl of NET 50 [50 mM tris-HCl (pH 7.4), 50 mM NaCl, 0.05% NP-40], antibody complexes were mixed with protein A–Sepharose (Pharmacia) for 1 hour at 4°C. The bound complexes were washed three times with 800 μl of NET 50, extracted on ice twice with phenol chloroform, and ethanol-precipitated to isolate RNAs.
27. S. M. Noble and C. Guthrie, *Genetics* **143**, 67 (1996); J. Lauber *et al.*, *EMBO J.* **15**, 4001 (1996).
28. P. L. Raghunathan, thesis, University of San Francisco (1997).
29. On a glycerol gradient, the vast majority of Prp24-3HA comigrates with U6 and U4/U6 snRNPs and away from triple snRNPs and spliceosomes (*17*). Also, Prp24 is not detected in Prp8-3HA immunoprecipitates that contain U4, U6, and U5 snRNAs (*17*). Thus, we have no evidence indicating that Prp24 is a component of U4/U6.U5 snRNPs or of the spliceosome.
30. J. Valcárcel, R. K. Gaur, R. Singh, M. R. Green, *Science* **273**, 1706 (1996).
31. M. Altmann, B. Wittmer, N. Méthot, N. Sonenberg, H. Trachsel, *EMBO J.* **14**, 3820 (1995).
32. K. R. Schneider, R. L. Smith, E. K. O'Shea, *Science* **266**, 122 (1994).
33. S. M. Noble and C. Guthrie, *EMBO J.* **15**, 4368 (1996); R. Bordonné, J. Banroques, J. Abelson, C. Guthrie, *Genes Dev.* **4**, 1185 (1990).
34. Blots were stripped for 1 hour at 65°C in 0.9 M NaCl and 0.09 M sodium citrate containing 0.2% SDS to remove probes. Subsequent probings were performed as described (*33*).
35. Z. Li and D. A. Brow, *Nucleic Acids Res.* **21**, 4645 (1993).
36. U4/U6 snRNPs were coimmunoprecipitated with polyoma-tagged Brr2 (*28*). The bound complexes were washed with 3 × 500 μl of NET 50 and then incubated for 10 min at 23°C with 150 μl of buffer (40% buffer D, 2.5 mM $MgCl_2$, 3% PEG 8000, 60 mM potassium phosphate, with or without 2 mM ATP). The supernatants were separated from the beads, and the beads were washed with 1 × 500 μl of NET 50. For Fig. 4A, the samples were directly deproteinized for nondenaturing gel analysis of U4 and U6 snRNAs. For Fig. 4, B and C, 1 μl of purified Prp24 was added to 11 μl of supernatant containing ATP (~0.4 nM each U4 and U6) and incubated for 2 min at 23°C unless otherwise stated. Reactions were stopped by the addition of 200 μl of 0.3 M sodium acetate, 6 mM EDTA, and 0.5% SDS on ice. RNAs were isolated by proteinase K digestion (*3*) or by phenol chloroform extraction and ethanol precipitation. To deproteinize U4 and U6 snRNPs before annealing, 100 μl of supernatant containing ATP was incubated at 23°C for 30 min with 10 mg of proteinase K beads (Sigma) washed in buffer D. The deproteinized supernatant was carefully collected for annealing reactions.
37. We thank A. Ghetti and J. Abelson for recombinant Prp24 protein; M. Lenburg, B. O'Neill, and E. O'Shea for advice on immunoaffinity purification; J. Brown for the anti-polyoma hybridoma line; C. Collins and S. Rader for advice and assistance; past and present members of the Guthrie laboratory for constructive criticism; and E. Blackburn, C. Collins, A. Frankel, H. Madhani, S. Rader, C. Siebel, J. Staley, O. Uhlenbeck, and K. Zingler for comments on the manuscript. We are indebted to L. Esperas, C. Pudlow, and H. Roiha for matchless technical assistance. P.L.R. was supported by a Howard Hughes Medical Institute predoctoral fellowship. C.G. is an American Cancer Society Research Professor of Molecular Genetics. Supported by NIH grant GM21119 to C.G.

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Fishing Down Marine Food Webs

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The mean trophic level of the species groups reported in Food and Agricultural Organization global fisheries statistics declined from 1950 to 1994. This reflects a gradual transition in landings from long-lived, high trophic level, piscivorous bottom fish toward short-lived, low trophic level invertebrates and planktivorous pelagic fish. This effect, also found to be occurring in inland fisheries, is most pronounced in the Northern Hemisphere. Fishing down food webs (that is, at lower trophic levels) leads at first to increasing catches, then to a phase transition associated with stagnating or declining catches. These results indicate that present exploitation patterns are unsustainable.

Exploitation of the ocean for fish and marine invertebrates, both wholesome and valuable products, ought to be a prosperous sector, given that capture fisheries—in contrast to agriculture and aquaculture—reap harvests that did not need to be sown. Yet marine fisheries are in a global crisis, mainly due to open access policies and subsidy-driven over-capitalization (*1*). It may be argued, however, that the global crisis is mainly one of economics or of governance, whereas the global resource base itself fluctuates naturally. Contradicting this more optimistic view, we show here that landings from global fisheries have shifted in the last 45 years from large piscivorous fishes toward smaller invertebrates and planktivorous fishes, especially in the Northern Hemisphere. This may imply major changes in the structure of marine food webs.

Two data sets were used. The first has estimates of trophic levels for 220 different species or groups of fish and invertebrates, covering all statistical categories included in the official Food and Agricultural Organization (FAO) landings statistics (*2*). We obtained these estimates from 60 published mass-balance trophic models that covered all major aquatic ecosystem types (*3*, *4*). The models were constructed with the Ecopath software (*5*) and local data that included detailed diet compositions (*6*). In such models, fractional trophic levels (*7*) are estimated values, based on the diet compositions of all ecosystem components rather than assumed values; hence, their precision and accuracy are much higher than for the integer trophic level values used in

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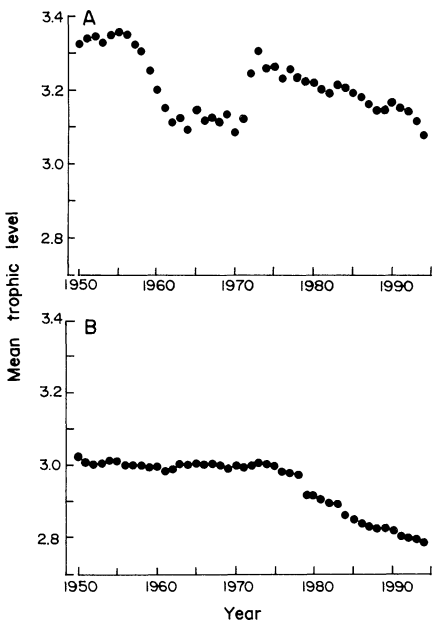

Fig. 1. Global trends of mean trophic level of fisheries landings, 1950 to 1994. (**A**) Marine areas; (**B**) inland areas.

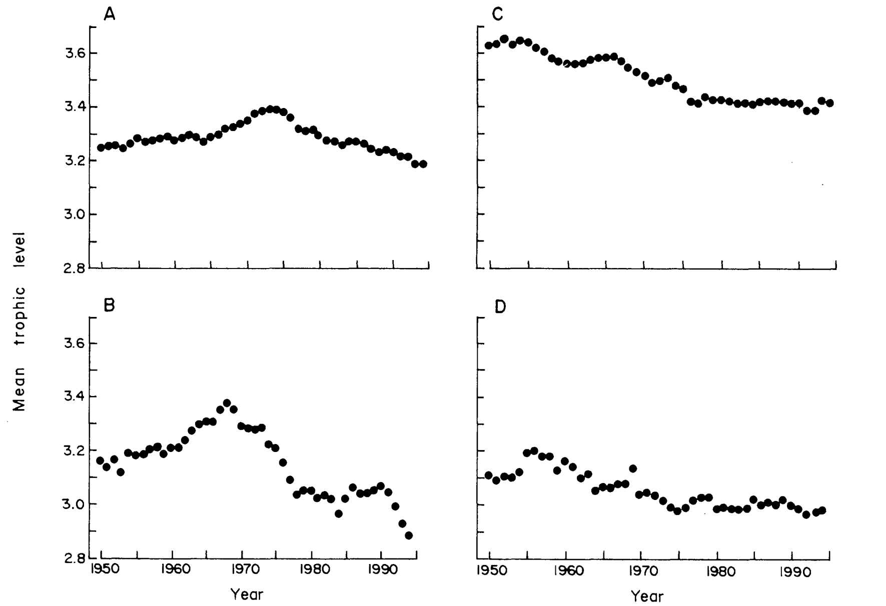

Fig. 2. Trends of mean trophic level of fisheries landings in northern temperate areas, 1950 to 1994. (**A**) North Pacific (FAO areas 61 and 67); (**B**) Northwest and Western Central Atlantic (FAO areas 21 and 31); (**C**) Northeast Atlantic (FAO area 27); and (**D**) Mediterranean (FAO area 37).

earlier global studies (*8*). The 220 trophic levels derived from these 60 Ecopath applications range from a definitional value of 1 for primary producers and detritus to 4.6 (± 0.32) for snappers (family Lutjanidae) on the shelf of Yucatan, Mexico (*9*). The second data set we used comprises FAO global statistics (*2*) of fisheries landings for the years from 1950 to 1994, which are based on reports submitted annually by FAO member countries and other states and were recently used for reassessing world fisheries potential (*10*). By combining these data sets we could estimate the mean trophic level of landings, presented here as time series by different groupings of all FAO statistical areas and for the world (*11*).

For all marine areas, the trend over the past 45 years has been a decline in the mean trophic level of the fisheries landings, from slightly more than 3.3 in the early 1950s to less than 3.1 in 1994 (Fig. 1A). A dip in the 1960s and early 1970s occurred because of extremely large catches [>12 × 10^6 metric tons (t) per year] of Peruvian anchoveta with a low trophic level (*12*) of 2.2 (± 0.42). Since the collapse of the Peruvian anchoveta fishery in 1972–1973, the global trend in the trophic level of marine fisheries landings has been one of steady decline. Fisheries in inland waters exhibit, on the global level, a similar trend as for the marine areas (Fig. 1B): A clear decline in average trophic level is apparent from the early 1970s, in parallel to, and about 0.3 units below, those of marine catches. The previous plateau, from 1950 to 1975, is due to insufficiently detailed fishery statistics for the earlier decades (*10*).

In northern temperate areas where the fisheries are most developed, the mean trophic level of the landings has declined steadily over the last two decades. In the North Pacific (FAO areas 61 and 67; Fig. 2A), trophic levels peaked in the early 1970s and have since then decreased rapidly in spite of the recent increase in landings of Alaska pollock, *Theragra chalcogramma*, which has a relatively high trophic level of 3.8 (± 0.24). In the Northwest Atlantic (FAO areas 21 and 31; Fig. 2B), the fisheries were initially dominated by planktivorous menhaden, *Brevoortia* spp., and other small pelagics at low trophic levels. As their landings decreased, the average trophic level of the fishery initially increased, then in the 1970s it reversed to a steep decline. Similar declines are apparent throughout the time series for the Northeast Atlantic (FAO area 27; Fig. 2C) and the Mediterranean (FAO area 37; Fig. 2C), although the latter system operates at altogether lower trophic levels.

The Central Eastern Pacific (FAO area 77; Fig. 3A), Southern and Central Eastern Atlantic (FAO areas 41, 47, and 34; Fig. 3B), and the Indo-Pacific (FAO areas 51, 57, and 71; Fig. 3C) show no clear trends over time. In the southern Atlantic this is probably due to the development of new fisheries, for example, on the Patagonian shelf, which tends to mask declines of trophic levels in more developed fisheries. In the Indo-Pacific area, the apparent stability is certainly due to inadequacies of

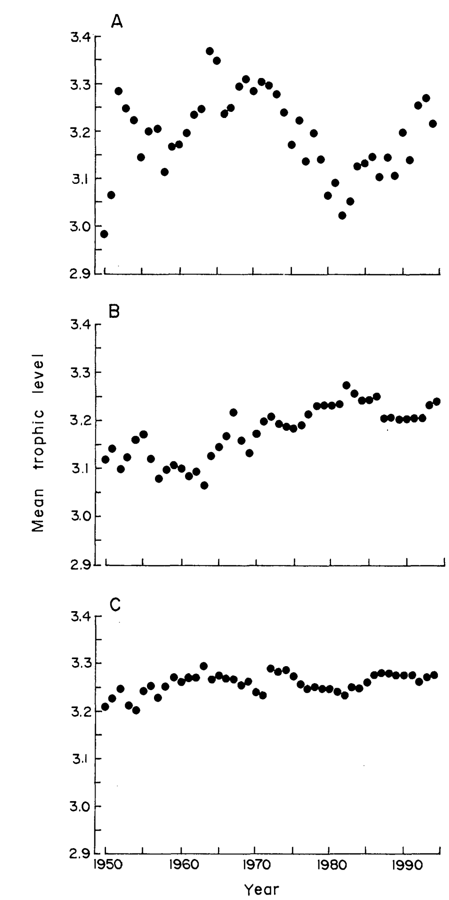

Fig. 3. Trends of mean trophic levels of fisheries landings in the intertropical belt and adjacent waters. (**A**) Central Eastern Pacific (FAO area 77); (**B**) Southwest, Central Eastern, and Southeast Atlantic (FAO areas 41, 34, and 47); and (**C**) Indo (west)-Pacific (FAO areas 51, 57, and 71).

the statistics, because numerous accounts exist that document species shifts similar to those that occurred in northern temperate areas (*13*).

The South Pacific areas (FAO areas 81 and 87; Fig. 4A) are interesting in that they display wide-amplitude fluctuations of trophic levels, reflecting the growth in the mid-1950s of a huge industrial fishery for Peruvian anchoveta. Subsequent to the anchoveta fishery collapse, an offshore fishery developed for horse mackerel, *Trachurus murphyi*, which has a higher trophic level (3.3 ± 0.21) and whose range extends west toward New Zealand (*14*). Antarctica (FAO areas 48, 58, and 88; Fig. 4B) also exhibits high-amplitude variation of mean trophic levels, from a high of 3.4, due to a fishery that quickly depleted local accumulations of bony fishes, to a low of 2.3, due to *Euphausia superba* (trophic level 2.2 ± 0.40), a large krill species that dominated the more recent catches.

The gross features of the plots in Figs. 2 through 4, while consistent with previous knowledge of the dynamics of major stocks, may provide new insights on the effect of fisheries on ecosystems. Further interpretation of the observed trends is facilitated by plotting mean trophic levels against catches. For example, the four systems in Fig. 5 illustrate patterns different from the monotonous increase of catch that may be expected when fishing down food webs (*15*). Each of the four systems in Fig. 5 has a signature marked by abrupt phase shifts. For three of the examples, the highest landings are not associated with the lowest trophic levels, as the fishing-down-the-food-web theory would predict. Instead, the time series tend to bend backward. The exception (where landings continue to increase as trophic levels decline) is the Southern Pacific (Fig. 5C), where the westward expansion of horse mackerel fisheries is still the dominant feature, thus masking more local effects.

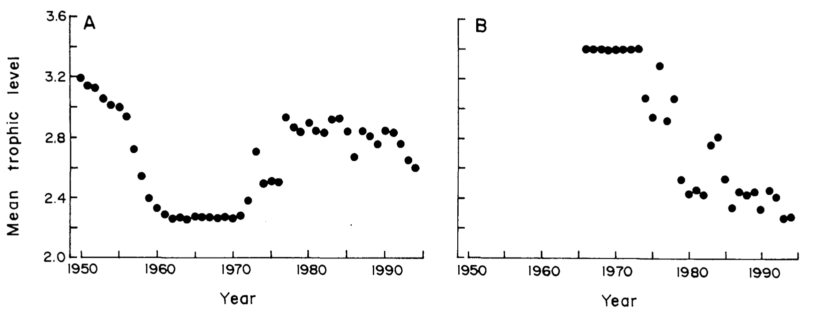

Fig. 4. High-amplitude changes of mean trophic levels in fisheries landings. (**A**) South Pacific (FAO areas 81 and 87); (**B**) Antarctica (FAO areas 48, 58, and 88).

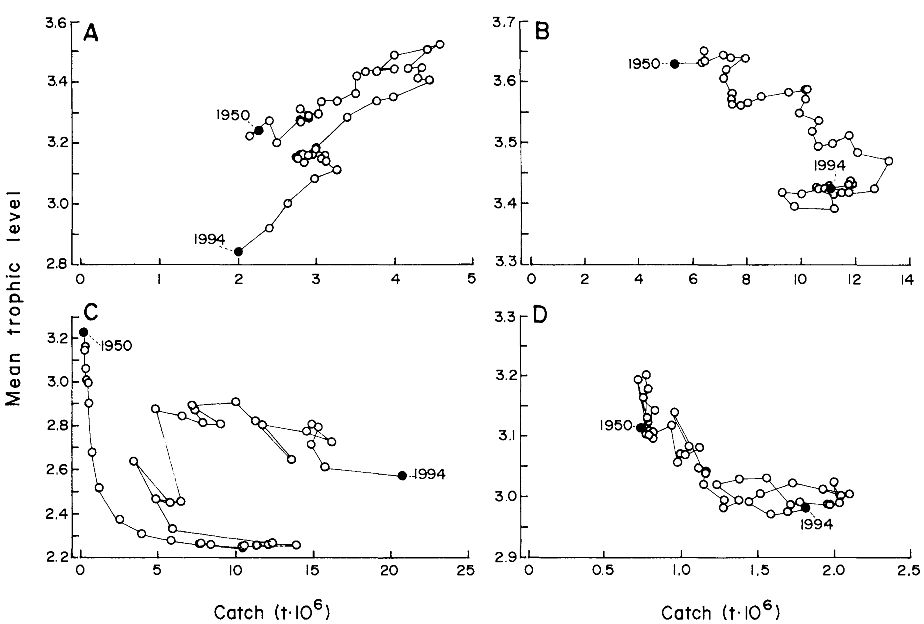

Fig. 5. Plots of mean trophic levels in fishery landings versus the landings (in millions of metric tons) in four marine regions, illustrating typical backward-bending signatures (note variable ordinate and abcissa scales). (**A**) Northwest Atlantic (FAO area 21); (**B**) Northeast Atlantic (FAO area 27); (**C**) Southeast Pacific (FAO area 87); (**D**) Mediterranean (FAO area 37).

The backward-bending feature of the plots of trophic levels versus landings, which also occurs in areas other than those in Fig. 5, may be due to a combination of the following: (i) artifacts due to the data, methods, and assumptions used; (ii) large and increasing catches that are not reported to FAO; (iii) massive discarding of bycatches (*16*) consisting predominantly of fish with low trophic levels; (iv) reduced catchability as a result of a decreasing average size of exploitable organisms; and (v) fisheries-induced changes in the food webs from which the landings were extracted. Regarding item (i), the quality of the official landing statistics we used may be seen as a major impediment for analyses of the sort presented here. We know that considerable under- and misreporting occur (*16*). However, for our analysis, the overall accuracy of the landings is not of major importance, if the trends are unbiased. Anatomical and functional considerations support our assumption that the trophic levels of fish are conservative attributes and that they cannot change much over time, even when ecosystem structure changes (*17*). Moreover, the increase of young fish as a proportion of landings in a given species that result from increasing fishing pressure would strengthen the reported trends, because the young of piscivorous species tend to be zooplanktivorous (*18*) and thus have lower trophic levels than the adults. Items (ii) and (iii) may be more important for the overall explanation. Thus, for the Northeast Atlantic, the estimated (*16*) discard of 3.7×10^6 t year^{-1} of bycatch would straighten out the backward-bending curve of Fig. 5B.

Item (iv) is due to the fact that trophic levels of aquatic organisms are inversely related to size (*19*). Thus, the relation between trophic level and catch will always break down as catches increase: There is a lower size limit for what can be caught and marketed, and zooplankton is not going to be reaching our dinner plates in the foreseeable future. Low catchability due to small size or extreme dilution (<1 g m^{-3}) is, similarly, a major reason why the huge global biomass ($\approx 10^9$ t) of lanternfish (family Myctophidae) and other mesopelagics (*20*) will continue to remain latent resources.

If we assume that fisheries tend to switch from species with high trophic levels to species with low trophic levels in response to changes of their relative abundances, then the backward-bending curves in Fig. 5 may be also due to changes in ecosystem structure, that is, item (v). In the North Sea, Norway pout, *Trisopterus esmarkii*, serves as a food source for most of the important fish species used for human consumption, such as cod or saithe. Norway pout is also the most important predator on euphausiids (krill) in the North Sea (*3*).

We must therefore expect that a directed fishery on this small gadoid (landings in the Northeast Atlantic are about 3×10^5 t year^{-1}) will have a positive effect on the euphausiids, which in turn prey on copepods, a much more important food source for commercial fish species than euphausiids. Hence, fishing for Norway pout may have a cascading effect, leading to a build-up of nonutilized euphausiids. Triangles such as the one involving Norway pout, euphausiids, and copepods, and which may have a major effect on ecosystem stability, are increasingly being integrated in ecological theory (*21*), especially in fisheries biology (*22*).

Globally, trophic levels of fisheries landings appear to have declined in recent decades at a rate of about 0.1 per decade, without the landings themselves increasing substantially. It is likely that continuation of present trends will lead to widespread fisheries collapses and to more backward-bending curves such as in Fig. 5, whether or not they are due to a relaxation of top-down control (*23*). Therefore, we consider estimations of global potentials based on extrapolation of present trends or explicitly incorporating fishing-down-the-food-web strategies to be highly questionable. Also, we suggest that in the next decades fisheries management will have to emphasize the rebuilding of fish populations embedded within functional food webs, within large "no-take" marine protected areas (*24*).

REFERENCES AND NOTES

1. S. M. Garcia and C. Newton, in *Global Trends in Fisheries Management*, E. Pikitch, D. D. Hubert, M. Sissenwine, Eds. (American Fisheries Society Symposium 20, Bethesda, MD, 1997), pp. 3–27.
2. FAO, *FISHSTAT-PC: Data Retrieval, Graphical and Analytical Software for Microcomputers* (FAO, Rome, 1996).
3. V. Christensen, *Dana* **11**, (1995).
4. The bulk of the 60 published models are documented in (*25*); D. Pauly and V. Christensen, in *Large Marine Ecosystems: Stress, Mitigation and Sustainability Stratified*, K. Sherman, L. M. Alexander, B. D. Gold, Eds. (AAAS Publication, Washington, DC, 1993), pp. 148–174; D. Pauly and V. Christensen, *Nature* **374**, 255 (1995). References to the remaining models are given in FishBase 97 (*9*).
5. V. Christensen and D. Pauly, *Ecol. Model.* **61**, 169 (1992).
6. The documentation of the Ecopath models in (*3*) and (*4*) includes sources of diet compositions of all consumer groups in each ecosystem. These diet compositions are rendered mutually compatible when mass-balance within each model is established.
7. As initially proposed by W. E. Odum and E. J. Heald, in *Estuarine Research*, L. E. Cronin, Ed. (Academic Press, New York, 1975), vol. 1, pp. 265–286.
8. J. H. Ryther, *Science* **166**, 72 (1969).
9. All trophic level estimates are fully documented on the home pages of the Fisheries Centre, University of British Columbia, (www.fisheries.com) and of the FishBase project (www.fishbase.org), and on the FishBase 97 CD-ROM {R. Froese and D. Pauly, *FishBase 97, Concepts, Design and Data Sources* [International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines, 1997]}, where references to the 60 published Ecopath applications are given as well. FishBase 97 also includes the FAO statistics (*2*), so Figs. 1 through 5 can be reproduced straightforwardly. To estimate the standard error (SE) we used the square root of the variance of the estimate of trophic level, in agreement with S. Pimm (*21*), who defined an omnivore as "a species which feeds on more than one trophic level." Thus, our estimates of SE do not necessarily express uncertainty about the exact values of trophic level estimates; rather, they reflect levels of omnivory. We do not present SE for the trophic levels of fisheries landings, as fisheries are inherently "omnivorous."
10. R. J. R. Grainger and S. M. Garcia, *FAO Fish. Tech. Pap. No. 359* (1996).
11. Mean trophic level, $\overline{TL}_i$, for year *i* is estimated by multiplying the landings (Y_i) by the trophic levels of the individual species groups *j*, then taking a weighted mean, that is, $\overline{TL}_i = \Sigma_{ij} TL_{ij} Y_{ij} / \Sigma Y_{ij}$.
12. A. Jarre, P. Muck, D. Pauly, *ICES Mar. Sci. Symp.* **193**, 171 (1991).
13. J. R. Beddington and R. M. May, *Sci. Am.* **247**, 42 (November 1982); P. Dalzell and D. Pauly, *Neth. J. Sea Res.* **24**, 641 (1989); contributions in G. Silvestre and D. Pauly, Eds., *Status and Management of Tropical Coastal Fisheries in Asia* (Conf. Proc. 53, ICLARM, Manila, Philippines, 1997).
14. R. Parrish, in *Peruvian Upwelling Ecosystem: Dynamics and Interactions*, D. Pauly, P. Muck, J. Mendo, I. Tsukayama, Eds. (Conf. Proc. 18, ICLARM, Manila, Philippines, 1989).
15. V. Christensen, *Rev. Fish Biol. Fish.* **6**, 417 (1996).
16. D. L. Alverson, M. H. Freeberg, S. A. Murawski, J. G. Pope, *FAO Fish. Tech. Paper 339* (1994).
17. We refer here to gill rakers, whose spacing determines the sizes of organisms that may be filtered, the length of the alimentary canal, which determines what may be digested, or the caudal fin aspect ratio, which determines attack speed and, hence, which prey organisms that may be consumed. See S. J. de Groot [*Neth. J. Sea Res.* **5**, 121 (1981)] for an example for flatfish (order Pleuronectiformes).
18. A. R. Longhurst and D. Pauly, *Ecology of Tropical Oceans* (Academic Press, San Diego, CA, 1987); A. P. Robb and J. R. G. Hislop, *J. Fish. Biol.* **16**, 199 (1980).
19. Contributions in (*25*) document the strong correlation between size and trophic level in aquatic ecosystems, a case also made for the North Sea by J. Rice and H. Gislason [*ICES J. Mar. Sci.* **53**, 1214 (1996)].
20. J. Gjøsaeter and K. Kawaguchi, *FAO Fish. Tech. Paper No. 193* (1980).
21. S. Pimm, *Food Webs* (Chapman & Hall, London, 1982).
22. R. Jones, in *Theory and Management of Tropical Fisheries*, D. Pauly and G. I. Murphy, Eds. (Conf. Proc. 9, ICLARM, Manila, Philippines, 1982), pp. 195–240; E. Ursin, *Dana* **2**, 51 (1982).
23. M. E. Power, *Ecology* **73**, 733 (1992).
24. A. C. Alcala and G. R. Russ, *J. Cons. Cons. Int. Explor. Mer* **46**, 40 (1990); M. H. Carr and D. C. Reed, *Can. J. Fish. Aquat. Sci.* **50**, 2019 (1993); J. E. Dugan and G. E. Davis, *ibid.*, p. 2029; C. M. Roberts and N. V. C. Polunin, *Ambio* **6**, 363 (1993).
25. V. Christensen and D. Pauly, Eds., *Trophic Models of Aquatic Ecosystems* (Conf. Proc. 26, ICLARM, Manila, Philippines, 1993).

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Impaired Locomotion and Dopamine Signaling in Retinoid Receptor Mutant Mice

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In the adult mouse, single and compound null mutations in the genes for retinoic acid receptor β and retinoid X receptors β and γ resulted in locomotor defects related to dysfunction of the mesolimbic dopamine signaling pathway. Expression of the D1 and D2 receptors for dopamine was reduced in the ventral striatum of mutant mice, and the response of double null mutant mice to cocaine, which affects dopamine signaling in the mesolimbic system, was blunted. Thus, retinoid receptors are involved in the regulation of brain functions, and retinoic acid signaling defects may contribute to pathologies such as Parkinson's disease and schizophrenia.

The retinoic acid (RA) signal is transduced by two nuclear receptor families, the retinoic acid receptors (RARα, RARβ, and RARγ) and the retinoid X receptors (RXRα, RXRβ, and RXRγ), which function as RAR-RXR heterodimers and play important roles during mouse embryonic development and postnatal life [(*1–4*) and references therein]. The high levels of expression of retinoid receptors in the brain and spinal cord (*5*), together with the RA responsiveness of various neurotransmitter pathways in vitro (*6, 7*), suggest that retinoid signaling might be involved in the regulation of neural functions. The locomotor skills of knockout mice for the genes encoding RARβ, RARγ, RXRβ, and RXRγ, all of which are normally expressed in the striatum (*5*), were analyzed by open

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