

Current Biology

Old-Growth Fishes Become Scarce under Fishing

Highlights

- Fishing reduced the proportion of old fish in 79% to 97% of populations
- The magnitude of decline was greater than 90% in 32% to 41% of populations
- US Southeast and West Coast had the most pronounced and consistent age truncation
- Shifting baselines and recruitment variation can bias estimates of age truncation

Authors

Lewis A.K. Barnett, Trevor A. Branch,
R. Anthony Ranasinghe,
Timothy E. Essington

Correspondence

lewisab@uw.edu

In Brief

Barnett et al. show that age truncation is prevalent and often severe in exploited marine fish populations. These changes in age structure likely reduce trait diversity and thus may reduce stability of fish populations and marine communities.



Old-Growth Fishes Become Scarce under Fishing

Lewis A.K. Barnett,^{1,2,4,*} Trevor A. Branch,¹ R. Anthony Ranasinghe,^{2,3} and Timothy E. Essington¹¹School of Aquatic & Fishery Sciences, University of Washington, Seattle, WA 98195, USA²Visiting Scientist at Northwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 2725 Montlake Boulevard East, Seattle, WA 98112, USA³Virginia Polytechnic Institute and State University, Blacksburg, VA 24061, USA⁴Lead Contact

*Correspondence: lewisab@uw.edu

<http://dx.doi.org/10.1016/j.cub.2017.07.069>

SUMMARY

Researchers have long recognized the importance of ecological differences at the species level in structuring natural communities yet until recently have often overlooked the influence of intraspecific trait variation, which can profoundly alter community dynamics [1]. Human extraction of living resources can reduce intraspecific trait variation by, for example, causing truncation of age and size structure of populations, where numbers of older individuals decline far more with exploitation than younger individuals. Age truncation can negatively affect population and community stability, increasing variability in population and community biomass [2–6], reducing productivity [7–10] and life-history diversity in traits such as the spatial and temporal pattern of reproduction and migration [4, 11–16]. Here, we quantified the extent of age truncation in 63 fished populations across five ocean regions, as measured by how much the proportions of fish in the oldest age groups declined over time. The proportion of individuals in the oldest age classes decreased significantly in 79% to 97% of populations (compared to historical or unfished values, respectively), and the magnitude of decline was greater than 90% in 32% to 41% of populations. The pervasiveness and intensity of age truncation indicates that fishing is likely reducing the stability of many marine communities. Our findings suggest that more emphasis should be given to management measures that reduce the impact of fishing on age truncation, including no-take areas, slot limits that prohibit fishing on all except a narrow range of fish sizes, and rotational harvesting.

RESULTS

We estimated the prevalence and severity of age truncation in marine fishes with empirical estimates from 63 fisheries stock assessments that spanned 24–140 years. These stock assessments contain calculations of annual numbers at age, which we analyzed using two methods of estimating age truncation. In the first estimation method, we compared the initial age

structure (the distribution of abundance by individual age at the beginning of the time series) from each stock assessment to the final age structure (the begin-end approach). In the second, we compared the age structure at the end of each time series with an estimate of age structure at the unfished equilibrium (i.e., the steady state where the population size remains constant), in which all mortality is due to a natural death rate at the level assumed in the stock assessment (the unfished-end approach). We calculated the change in the proportion of individuals in the oldest age class as our primary metric of age truncation.

We found that age truncation is widespread and often severe, with the proportion of old individuals most commonly reduced by 90% or more (Figures 1A and 1C; Table S1). The begin-end approach revealed statistically significant declines in old fish in 79% of populations (versus 5% expected from Pearson's chi-square tests on the log response ratio of the proportion of old fish), and 32% declined by more than 90%, while 19% significantly increased, and 2% did not significantly change (Figure 1A). When compared to estimated unfished conditions, effects were even more substantial: the unfished-end approach found that 97% of old fish significantly declined in proportional abundance, 41% by more than 90%, and only 3% significantly increased (Figure 1C). The begin-end estimates of age truncation are likely biased low, given the presence of some short model output time series and our finding that age truncation was weakly negatively correlated with time series duration ($r = -0.35$, $p = 0.0048$; Figure S1).

While age truncation was common in all ocean regions, we found significant regional differences in the magnitude of age truncation (Figures 1B and 1D; ANOVA, begin-end $p = 0.0016$, unfished-end $p = 0.0075$). The Southeast US had significantly more severe reductions in the proportion of old fish than Alaska, as indicated by both approaches (Tukey honest significant difference [HSD]: begin-end $p = 0.0086$; unfished-end $p = 0.0030$), and more severe reductions than the Northeast US ($p = 0.0318$) and Icelandic and northern European (ICES: International Council for the Exploration of the Sea) regions ($p = 0.0481$) under the begin-end approach (Figure 1B). The Southeast US and the West Coast US had the most pronounced and consistent age truncation across estimation methods, whereas Alaska had populations without age truncation regardless of method (1–5 out of 17 populations, 6%–29%).

To confirm that the above analyses of changes in the proportion of fish in the oldest age classes was due to a decline in old fish abundance (not only an increase in young fish abundance),

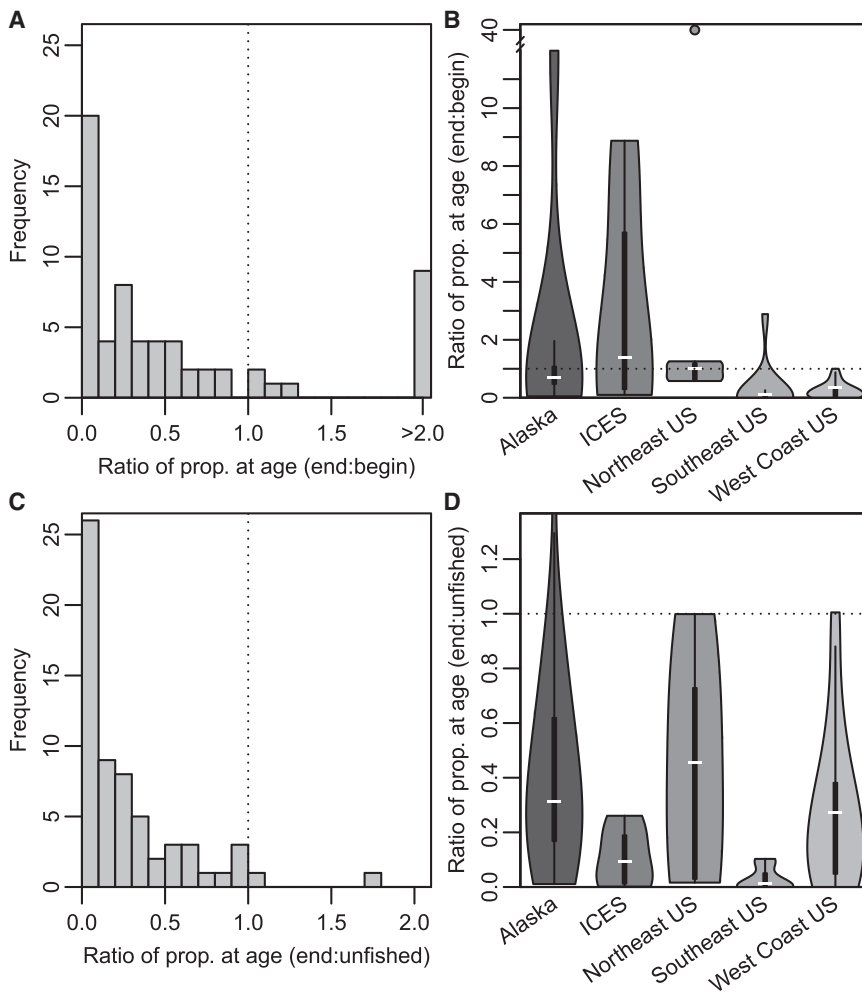


Figure 1. Change in the Proportion of Old Fish with Exploitation for the Populations in Table S1

(A) Distribution of the ratio of the proportion of individuals in the oldest age class between the beginning and end of the stock assessment model output time series (begin-end estimate) across all populations. The dotted line indicates no change, where values above (below) one indicate an increase (decrease) with time.

(B) Violin plots (boxplots, in addition to kernel density estimates) showing regional comparisons of the ratio of the proportion of individuals in the oldest age class between the beginning and end of the stock assessment model output time series (begin-end estimate).

(C) Distribution of the ratio of the proportion of individuals in the oldest age class between the unfished equilibrium and the end of the stock assessment model output time series (unfished-end estimate) across all populations.

(D) Violin plots showing regional comparisons of the proportion of individuals in the oldest age class between the unfished equilibrium and the end of the stock assessment model output time series (unfished-end estimate).

DISCUSSION

The widespread age truncation we reveal among exploited fish populations has implications for the persistence and dynamics of fish populations and the ecosystems in which they live, by potentially reducing productivity, trait diversity, resilience, and community stability. Age truncation can reduce productivity by

causing declines in rates of birth and offspring survival due to the presence of maternal effects, such as the positive relationship between maternal age or size and the number and/or size of offspring, which is prevalent in many fishes, birds, and mammals [8, 17]. The prevalence of maternal effects in fishes has led to claims that old fish have disproportionate effects on population productivity [8, 18, 19]. Although this premise is intuitive, population-scale evidence to support this claim has been inconsistent and difficult to obtain. Some studies have found a relationship between age structure and egg production [9] or recruitment [7], leading to increased recovery time (i.e., population growth rate) or “engineering resilience” [10], whereas others predict that maternal effects have limited influence on long-term population dynamics [7, 20–22].

Fished populations are more variable than unfished populations [6, 23], or at least more sensitive to environmental variability [24–27], and this influence of fishing on population stability can be caused by age truncation [4, 28]. Making the specific, mechanistic connection between age truncation and population variability is difficult because responses depend on life history, management strategy, and the stage and form of density dependence [29–31]. However, theoretical evidence indicates that age truncation contributes to increased variability in recruitment by

we also estimated the change in the numbers of individuals at age rather than the proportions. The numerical abundance of old fish decreased by more than 90% in 38% (begin-end) and 51% (unfished-end) of populations. These declines in old fish abundance were only slightly greater than declines in the proportions of old fish, thereby confirming that the number of individuals at age did not decline uniformly with fishing and the changes we report resulted from disproportionate declines in old fish.

In addition to calculating changes in old fish representation, we quantified the effect of fishing across the entire age structure (Figure 2) to see whether fishing effects changed smoothly with age, as expected without temporal environmental variation in death or birth rates. We did observe this pattern of smooth change in fishing effect on age-specific proportional abundance in populations from the Southeast and West Coast US. These regions were characterized by increased proportions of the youngest individuals and decreased proportions of nearly all other age classes regardless of estimation method, with an increasing or constant magnitude of change with increasing age (Figure 2, compare medians). In other regions, the changes across age classes were less consistent; for example, fishing effects in Alaska and ICES regions alternated between increases and decreases across the many of the younger age classes (Figure 2B).

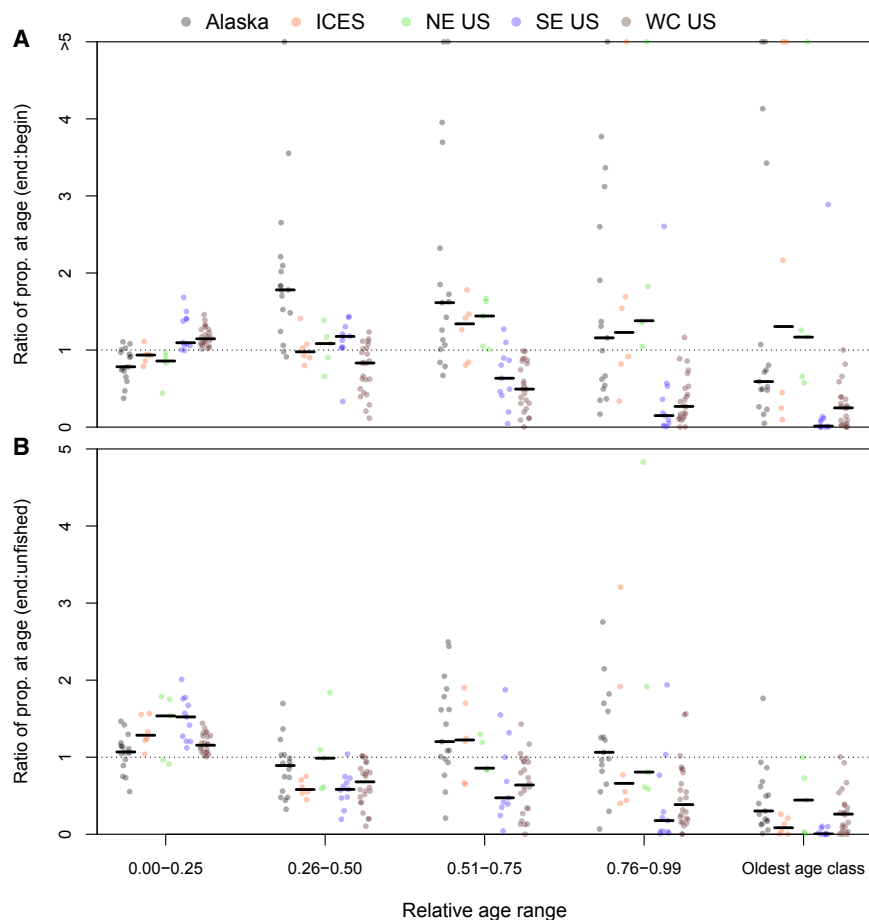


Figure 2. Change in the Proportion of Individuals with Exploitation among All Age Groups, by Ocean Region, for the Populations in Table S1

(A) Ratio of the proportion of individuals in each age class (denoted by the range of ages relative to the initial age of the “old fish” grouping, or oldest age class) between the beginning and end of the stock assessment model output time series (begin-end estimate). Lines indicate group medians. The horizontal dotted line indicates no change, where values above (below) one indicate an increase (decrease) with time.

(B) Ratio of the proportion of individuals in each age class between the unfished equilibrium state and that at the end of the stock assessment model output time series (unfished-end estimate).

narrowing the range of ages contributing to reproduction and thereby strengthening an “echo” of past recruitment ([5] and references therein). Alternatively, age truncation could lead to increases in maximum reproductive rates, causing instability arising from overcompensatory density dependence and environmental stochasticity ([2, 3], but also see [30]). The output we present here could be paired with data on recruitment variation to test these emerging hypotheses.

Age truncation can affect community stability by reducing trait diversity. Biodiversity and community stability are often positively related [32–35], particularly when stability is measured as variability in abundance over time [36]. Age truncation can reduce stability by decreasing life-history diversity, influencing key drivers of positive diversity-stability relationships, such as response diversity [36–38], food web complexity, and the presence of numerous weak interactions [39, 40]. Life-history diversity, which is often related to individual age or size, likely enhances stability by increasing asynchrony among groups through mechanisms such as increased response diversity to fishing and environmental variation [13, 41]. For example, variability in the timing [15, 16] or location [4] of reproduction and the timing and extent of movements and migrations [11–13] is attributable to age diversity in many species and increases response diversity, engineering resilience, and stability [15, 28]. Homogenization of population spatial structure has been linked to age truncation based on evidence that the distribution of

fished populations are more sensitive to environmental variation than unfished populations, and such responses can increase variation in community structure and erode ecological stability by increasing synchrony [4, 42–44]. In addition, age truncation can affect community structure by reducing the prevalence and strength of ontogenetic diet shifts (e.g., [45]) and omnivory, which are hypothesized to stabilize food webs [40, 46].

Although here we revealed much evidence for age truncation, demonstrating the severity of effects suggested by changes in mean age and size [4], we

found notable exceptions that highlight the role of natural variability and shifting baselines in affecting the estimation and interpretation of changes in age structure over time. Most notably, the signal of age truncation was weakest in Alaska, and it was stronger in most regions under the unfished-end approach than the begin-end approach: under the latter approach 12 of 63 populations had statistically significant increases in the proportion of old fish. Such anomalies were likely caused by several factors: interannual variability in reproductive success resulting in occasional huge year classes that temporarily increase proportions of old fish (after a time lag); decadal environmental regime shifts, such as those leading to favorable conditions for juvenile survival in Alaska [47–49] and Icelandic and northern European waters [50, 51] in recent decades; and short time series encompassing recent years with fisheries recovery but excluding previous decades of extensive exploitation (shifting baselines; [52]). Shifting baselines were particularly evident for Icelandic and northern European populations (consistent with a parallel phenomenon in changing distributions of body size structure at the community scale [53]), along with those in the Northeast US, because stock assessment output began long after development of large-scale commercial fisheries and exploitation rates have declined in recent years [54] (Figure S1). Our results comparing unfished age distributions to current age distributions suggest the issues discussed above have likely caused underestimation of age truncation in previous

studies inferring age truncation from changes in mean age over time [4]. For example, Hsieh et al. [4] estimated an average relative change in mean age of 10 stocks as roughly -25% , whereas the average relative change in the proportion of old fish we calculated was -72% .

Globally, the magnitude of reduction of old fishes is likely larger than the estimates we present here based on information from fisheries in developed nations. Regional differences in management capacity, fishing power, and fishery selectivity are all likely to govern the extent of age truncation, and the populations examined here are not a random sample. For example, models indicate that reductions in old fish are greater when a fishery targets a greater range of ages, due to the accumulation of deaths caused by being exposed to fishing over a longer duration (L.A.K.B., unpublished data). Fisheries in developing nations are typically less selective on size or age than those in developed nations [55, 56], thus we expect that they would cause greater reductions in old fishes per unit of fishing intensity. In addition, there is likely regional bias in data availability and management quality, where developed nations with data-rich age-structured stock assessments have better management outcomes because they are more intensively managed than developing regions where management is guided by data-poor assessments (or simply fewer assessments) and are otherwise lacking management capacity [54, 57, 58].

A number of fisheries management tools are available to reduce age truncation, notably marine reserves, rotational harvests, and slot limits. No-take marine reserves can restore a broad age structure within protected areas [59] and can buffer against destabilizing effects of fishing and environmental variability through overall increases in multiple forms of resilience [14, 60–62]. Rotational harvests are an effective mechanism for sedentary species, where fishing alternates among areas over time, allowing each individual area to develop a broad age structure before harvest occurs [63]. An additional approach is to modify the ages or sizes selected by the fishery by imposing both maximum and minimum size limits to form a “slot” fishery, so that fishing only affects a small range of ages. Slot fisheries can preserve age structure while increasing catch numbers, including catches of large “trophy” fish in recreational fisheries [64], but will likely be difficult to implement in many large-scale commercial fisheries. Gear restrictions and time-area closures can have analogous effects to slot limits in certain cases. These management approaches often produce complex trade-offs and thus the effectiveness and appropriateness of these tools will depend on the biological, technological, cultural, and socio-economic factors in a fishery.

In summary, we found that age truncation was prevalent and typically severe across a wide array of species and regions. The implications of truncated age structure with few old individuals are obvious: fish traits often vary with age, and thus phenotypic and life-history diversity will decline when age structure is truncated. Similar deleterious effects are observed in other natural systems, most prominently when old-growth forests are clear cut or when long-lived corals and other living habitats are damaged by bottom trawling [65]. Given the growing body of research demonstrating the specific relationship between age structure and population dynamics, and the general relationship between biodiversity at multiple scales, community stability and ecosystem function (e.g.,

[34, 35]), our results imply that fishing has decreased the productivity and stability of many fish populations and aquatic communities [4, 5, 13–15, 42].

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

- KEY RESOURCES TABLE
- CONTACT FOR REAGENT AND RESOURCE SHARING
- METHOD DETAILS
 - Age Truncation Estimation Approaches
 - Age Truncation Metric Development and Analysis
- QUANTIFICATION AND STATISTICAL ANALYSIS
- DATA AND SOFTWARE AVAILABILITY
 - Data and Code

SUPPLEMENTAL INFORMATION

Supplemental Information includes two figures and one table and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2017.07.069>.

AUTHOR CONTRIBUTIONS

Conceptualization, L.A.K.B., T.A.B., and T.E.E.; Methodology, L.A.K.B. and T.A.B.; Software, L.A.K.B. and T.A.B.; Investigation, L.A.K.B., R.A.R., and T.A.B.; Data Curation, R.A.R. and L.A.K.B.; Writing – Original Draft, L.A.K.B.; Writing – Reviewing & Editing, L.A.K.B., T.A.B., and T.E.E.; Funding Acquisition, T.A.B., T.E.E., and L.A.K.B.

ACKNOWLEDGMENTS

We thank Michelle McClure for helpful discussions and for contributing resources that facilitated this research. We also thank Jason Cope, Jim Thorson, Chantel Wetzel, Ian Taylor, and the entire NWFSC stock assessment team for data access, assistance interpreting stock assessment output, and helpful discussions; Jim Ianelli, Arni Magnusson, Erik Williams, Rob Cheshire, Gary Fitzhugh, and Patrick Lynch for providing access to stock assessment output; and Ole Shelton and one anonymous reviewer for comments that improved the manuscript. Funding was provided by the Joint Institute for the Study of the Atmosphere and Ocean (JISAO) under NOAA Cooperative Agreement No. NA15OAR4320063, Contribution No. 2017-081. T.A.B. was supported in part by the Richard C. and Lois M. Worthington Endowed Professor in Fisheries Management. R.A.R. was supported by the Ernest F. Hollings Undergraduate Scholarship Program.

Received: April 13, 2017

Revised: July 4, 2017

Accepted: July 28, 2017

Published: September 14, 2017

REFERENCES

1. Bolnick, D.I., Amarasekare, P., Araújo, M.S., Bürger, R., Levine, J.M., Novak, M., Rudolf, V.H.W., Schreiber, S.J., Urban, M.C., and Vasseur, D.A. (2011). Why intraspecific trait variation matters in community ecology. *Trends Ecol. Evol.* 26, 183–192.
2. Sugihara, G., Beddington, J., Hsieh, C.H., Deyle, E., Fogarty, M., Glaser, S.M., Hewitt, R., Hollowed, A., May, R.M., Munch, S.B., et al. (2011). Are exploited fish populations stable? *Proc. Natl. Acad. Sci. USA* 108, E1224–E1225, author reply E1226.
3. Anderson, C.N.K., Hsieh, C.H., Sandin, S.A., Hewitt, R., Hollowed, A., Beddington, J., May, R.M., and Sugihara, G. (2008). Why fishing magnifies fluctuations in fish abundance. *Nature* 452, 835–839.

4. Hsieh, C.-h., Yamauchi, A., Nakazawa, T., and Wang, W.-F. (2010). Fishing effects on age and spatial structures undermine population stability of fishes. *Aquat. Sci.* *72*, 165–178.
5. Botsford, L.W., Holland, M.D., Field, J.C., and Hastings, A. (2014). Cohort resonance: a significant component of fluctuations in recruitment, egg production, and catch of fished populations. *ICES J. Mar. Sci.* *71*, 2158–2170.
6. Hsieh, C.H., Reiss, C.S., Hunter, J.R., Beddington, J.R., May, R.M., and Sugihara, G. (2006). Fishing elevates variability in the abundance of exploited species. *Nature* *443*, 859–862.
7. Shelton, A.O., Hutchings, J.A., Waples, R.S., Keith, D.M., Akçakaya, H.R., and Dulvy, N.K. (2015). Maternal age effects on Atlantic cod recruitment and implications for future population trajectories. *ICES J. Mar. Sci.* *72*, 1769–1778.
8. Hixon, M.A., Johnson, D.W., and Sogard, S.M. (2014). BOFFFFs: on the importance of conserving old-growth age structure in fishery populations. *ICES J. Mar. Sci.* *71*, 2171–2185.
9. Stige, L.C., Yaragina, N.A., Langangen, Ø., Bogstad, B., Stenseth, N.C., and Ottersen, G. (2017). Effect of a fish stock's demographic structure on offspring survival and sensitivity to climate. *Proc. Natl. Acad. Sci. USA* *114*, 1347–1352.
10. Barnett, L.A.K., Baskett, M.L., and Botsford, L.W. (2015). Quantifying the potential for marine reserves or harvest reductions to buffer temporal mismatches caused by climate change. *Can. J. Fish. Aquat. Sci.* *72*, 376–389.
11. Moore, J.W., Yeakel, J.D., Peard, D., Lough, J., and Beere, M. (2014). Life-history diversity and its importance to population stability and persistence of a migratory fish: steelhead in two large North American watersheds. *J. Anim. Ecol.* *83*, 1035–1046.
12. Jonsson, N., Jonsson, B., and Hansen, L.P. (1990). Partial segregation in the timing of migration of Atlantic salmon of different ages. *Anim. Behav.* *40*, 313–321.
13. Schindler, D.E., Hilborn, R., Chasco, B., Boatright, C.P., Quinn, T.P., Rogers, L.A., and Webster, M.S. (2010). Population diversity and the portfolio effect in an exploited species. *Nature* *465*, 609–612.
14. Barnett, L.A.K., and Baskett, M.L. (2015). Marine reserves can enhance ecological resilience. *Ecol. Lett.* *18*, 1301–1310.
15. Greene, C.M., Hall, J.E., Guilbault, K.R., and Quinn, T.P. (2010). Improved viability of populations with diverse life-history portfolios. *Biol. Lett.* *6*, 382–386.
16. Wright, P.J., and Trippel, E.A. (2009). Fishery-induced demographic changes in the timing of spawning: consequences for reproductive success. *Fish Fish.* *10*, 283–304.
17. Bernardo, J. (1996). Maternal effects in animal ecology. *Am. Zool.* *36*, 83–105.
18. Law, R. (2000). Fishing, selection, and phenotypic evolution. *ICES J. Mar. Sci.* *57*, 659–668.
19. Berkeley, S.A., Hixon, M.A., Larson, R.J., and Love, M.S. (2004). Fisheries sustainability via protection of age structure and spatial distribution of fish populations. *Fisheries* *29*, 23–32.
20. Le Bris, A., Pershing, A.J., Hernandez, C.M., Mills, K.E., and Sherwood, G.D. (2015). Modelling the effects of variation in reproductive traits on fish population resilience. *ICES J. Mar. Sci.* *72*, 2590–2599.
21. Shelton, A.O., Munch, S.B., Keith, D., and Mangel, M. (2012). Maternal age, fecundity, egg quality, and recruitment: linking stock structure to recruitment using an age-structured Ricker model. *Can. J. Fish. Aquat. Sci.* *69*, 1631–1641.
22. O'Farrell, M.R., and Botsford, L.W. (2006). The fisheries management implications of maternal-age-dependent larval survival. *Can. J. Fish. Aquat. Sci.* *63*, 2249–2258.
23. Minto, C., Myers, R.A., and Blanchard, W. (2008). Survival variability and population density in fish populations. *Nature* *452*, 344–347.
24. Perry, R.I., Cury, P., Brander, K., Jennings, S., Möllmann, C., and Planque, B. (2010). Sensitivity of marine systems to climate and fishing: concepts, issues and management responses. *J. Mar. Syst.* *79*, 427–435.
25. Planque, B., Fromentin, J.-M., Cury, P., Drinkwater, K.F., Jennings, S., Perry, R.I., and Kifani, S. (2010). How does fishing alter marine populations and ecosystems sensitivity to climate? *J. Mar. Syst.* *79*, 403–417.
26. Lobón-Cerviá, J. (2011). Why fishing does not magnify temporal fluctuations in the population abundance of stream-living salmonids. *Rev. Fish. Sci.* *19*, 246–256.
27. Cameron, T.C., O'Sullivan, D., Reynolds, A., Hicks, J.P., Pieltney, S.B., and Benton, T.G. (2016). Harvested populations are more variable only in more variable environments. *Ecol. Evol.* *6*, 4179–4191.
28. McGilliard, C.R., Punt, A.E., Hilborn, R., and Essington, T. (2017). Modeling the impacts of two age-related portfolio effects on recruitment variability with and without a marine reserve. *Ecol. Appl.* <http://dx.doi.org/10.1002/eap.1593>.
29. Wikström, A., Knape, J., Casini, M., Gårdmark, A., Cardinale, M., Hjelm, J., and Jonzén, N. (2016). Fishing, reproductive volume and regulation: population dynamics and exploitation of the eastern Baltic cod. *Popul. Ecol.* *58*, 199–211.
30. Shelton, A.O., and Mangel, M. (2011). Fluctuations of fish populations and the magnifying effects of fishing. *Proc. Natl. Acad. Sci. USA* *108*, 7075–7080.
31. Okamoto, D.K., Schmitt, R.J., and Holbrook, S.J. (2015). Stochastic density effects on adult fish survival and implications for population fluctuations. *Ecol. Lett.* *19*, 153–162.
32. Gross, K., Cardinale, B.J., Fox, J.W., Gonzalez, A., Loreau, M., Polley, H.W., Reich, P.B., and van Ruijven, J. (2014). Species richness and the temporal stability of biomass production: a new analysis of recent biodiversity experiments. *Am. Nat.* *183*, 1–12.
33. Campbell, V., Murphy, G., and Romanuk, T.N. (2011). Experimental design and the outcome and interpretation of diversity–stability relations. *Oikos* *120*, 399–408.
34. Worm, B., Barbier, E.B., Beaumont, N., Duffy, J.E., Folke, C., Halpern, B.S., Jackson, J.B.C., Lotze, H.K., Micheli, F., Palumbi, S.R., et al. (2006). Impacts of biodiversity loss on ocean ecosystem services. *Science* *314*, 787–790.
35. Micheli, F., Mumby, P.J., Brumbaugh, D.R., Broad, K., Dahlgren, C.P., Harborne, A.R., Holmes, K.E., Kappel, C.V., Litvin, S.Y., and Sanchirico, J.N. (2014). High vulnerability of ecosystem function and services to diversity loss in Caribbean coral reefs. *Biol. Conserv.* *171*, 186–194.
36. Ives, A.R., and Carpenter, S.R. (2007). Stability and diversity of ecosystems. *Science* *317*, 58–62.
37. Elmquist, T., Folke, C., Nyström, M., Peterson, G., Bengtsson, J., Walker, B., and Norberg, J. (2003). Response diversity, ecosystem change, and resilience. *Front. Ecol. Environ.* *1*, 488–494.
38. Baskett, M.L., Fabina, N.S., and Gross, K. (2014). Response diversity can increase ecological resilience to disturbance in coral reefs. *Am. Nat.* *184*, E16–E31.
39. McCann, K.S. (2000). The diversity-stability debate. *Nature* *405*, 228–233.
40. Polis, G.A., and Strong, D.R. (1996). Food web complexity and community dynamics. *Am. Nat.* *147*, 813–846.
41. Hilborn, R., Quinn, T.P., Schindler, D.E., and Rogers, D.E. (2003). Biocomplexity and fisheries sustainability. *Proc. Natl. Acad. Sci. USA* *100*, 6564–6568.
42. Hsieh, C.-h., Reiss, C.S., Hewitt, R.P., and Sugihara, G. (2008). Spatial analysis shows that fishing enhances the climatic sensitivity of marine fishes. *Can. J. Fish. Aquat. Sci.* *65*, 947–961.
43. Kuo, T.C., Mandal, S., Yamauchi, A., and Hsieh, C.H. (2016). Life history traits and exploitation affect the spatial mean-variance relationship in fish abundance. *Ecology* *97*, 1251–1259.
44. Ciannelli, L., Fisher, J.A., Skern-Mauritzen, M., Hunsicker, M.E., Hidalgo, M., Frank, K.T., and Bailey, K.M. (2013). Theory, consequences and evidence of eroding population spatial structure in harvested marine fishes: a review. *Mar. Ecol. Prog. Ser.* *480*, 227–243.
45. Selden, R.L., Gaines, S.D., Hamilton, S.L., and Warner, R.R. (2017). Protection of large predators in a marine reserve alters size-dependent prey mortality. *Proc. Biol. Sci.* *284*, 20161936.

46. McCann, K., and Hastings, A. (1997). Re-evaluating the omnivory-stability relationship in food webs. *Proc. R. Soc. Lond. B Biol. Sci.* *264*, 1249–1254.
47. Hollowed, A.B., Hare, S.R., and Wooster, W.S. (2001). Pacific Basin climate variability and patterns of Northeast Pacific marine fish production. *Prog. Oceanogr.* *49*, 257–282.
48. Wilderbuer, T., Hollowed, A., Ingraham, W., Spencer, P., Conners, M., Bond, N., and Walters, G. (2002). Flatfish recruitment response to decadal climatic variability and ocean conditions in the eastern Bering Sea. *Prog. Oceanogr.* *55*, 235–247.
49. Mueter, F.J., Boldt, J.L., Megrey, B.A., and Peterman, R.M. (2007). Recruitment and survival of Northeast Pacific Ocean fish stocks: temporal trends, covariation, and regime shifts. *Can. J. Fish. Aquat. Sci.* *64*, 911–927.
50. Brander, K.M. (2005). Cod recruitment is strongly affected by climate when stock biomass is low. *ICES J. Mar. Sci.* *62*, 339–343.
51. Hislop, J.R.G. (1996). Changes in North Sea gadoid stocks. *ICES J. Mar. Sci.* *53*, 1146–1156.
52. Pauly, D. (1995). Anecdotes and the shifting baseline syndrome of fisheries. *Trends Ecol. Evol.* *10*, 430.
53. Jennings, S., and Blanchard, J.L. (2004). Fish abundance with no fishing: predictions based on macroecological theory. *J. Anim. Ecol.* *73*, 632–642.
54. Worm, B., Hilborn, R., Baum, J.K., Branch, T.A., Collie, J.S., Costello, C., Fogarty, M.J., Fulton, E.A., Hutchings, J.A., Jennings, S., et al. (2009). Rebuilding global fisheries. *Science* *325*, 578–585.
55. Van Zwieten, P., Béné, C., Kolding, J., Brummett, R., and Valbo-Jorgensen, J. (2011). Review of Tropical Reservoirs and Their Fisheries: The Cases of Lake Nasser, Lake Volta and Indo-Gangetic Basin Reservoir (Food and Agriculture Organization of the United Nations).
56. Misund, O.A., Kolding, J., and Fréon, P. (2002). Fish capture devices in industrial and artisanal fisheries and their influence on management. In *Handbook of Fish Biology and Fisheries 2*, P.J.B. Hart, and J.D. Reynolds, eds. (Blackwell Publishing), pp. 13–36.
57. Costello, C., Ovando, D., Hilborn, R., Gaines, S.D., Deschenes, O., and Lester, S.E. (2012). Status and solutions for the world's unassessed fisheries. *Science* *338*, 517–520.
58. Worm, B., and Branch, T.A. (2012). The future of fish. *Trends Ecol. Evol.* *27*, 594–599.
59. White, J.W., Botsford, L.W., Hastings, A., Baskett, M.L., Kaplan, D.M., and Barnett, L.A.K. (2013). Transient responses of fished populations to marine reserve establishment. *Conserv. Lett.* *6*, 180–191.
60. Takashina, N., and Mougi, A. (2014). Effects of marine protected areas on overfished fishing stocks with multiple stable states. *J. Theor. Biol.* *341*, 64–70.
61. Micheli, F., Saenz-Arroyo, A., Greenley, A., Vazquez, L., Espinoza Montes, J.A., Rossetto, M., and De Leo, G.A. (2012). Evidence that marine reserves enhance resilience to climatic impacts. *PLoS ONE* *7*, e40832.
62. Baskett, M.L., and Barnett, L.A.K. (2015). The ecological and evolutionary consequences of marine reserves. *Annu. Rev. Ecol. Evol. Syst.* *46*, 49–73.
63. Plagányi, É.E., Skewes, T., Murphy, N., Pascual, R., and Fischer, M. (2015). Crop rotations in the sea: Increasing returns and reducing risk of collapse in sea cucumber fisheries. *Proc. Natl. Acad. Sci. USA* *112*, 6760–6765.
64. Gwinn, D.C., Allen, M.S., Johnston, F.D., Brown, P., Todd, C.R., and Arlinghaus, R. (2015). Rethinking length-based fisheries regulations: the value of protecting old and large fish with harvest slots. *Fish Fish.* *16*, 259–281.
65. Watling, L., and Norse, E.A. (1998). Disturbance of the seabed by mobile fishing gear: a comparison to forest clearcutting. *Conserv. Biol.* *12*, 1180–1197.
66. R Core Team (2016). R: A Language and Environment for Statistical Computing, 3.3.2 Edition (R Foundation for Statistical Computing).

STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited Data		
Estimated numbers-at-age from stock assessment models	GitHub (this will also be available within the larger RAM Legacy database: http://ramlegacy.org/)	https://github.com/lewisab/age-truncation/tree/master/Data
Software and Algorithms		
Code for performing the analyses in this study	GitHub	https://github.com/lewisab/age-truncation/blob/master/R/AgeTruncationAnalysis_pub_code.R
Other		
List of populations and assessments used in this analysis	Supplementary Information of this study	Table S1

CONTACT FOR REAGENT AND RESOURCE SHARING

Further information and requests for resources should be directed to and will be fulfilled by the Lead Contact, Lewis A.K. Barnett (lewisab@uw.edu).

METHOD DETAILS

Age Truncation Estimation Approaches

We quantified the effect of fishing on age structure (the distribution of proportional abundance over ages within a population) with two estimation approaches, relying on a metaanalysis of fish stock assessment model results. In the first estimation approach (the “begin-end” approach), we compared the historical age structure to its present condition. As an alternative (the “unfished-end” approach), we compared the present age structure to that based on age-specific death rates without fishing (i.e., the stable age distribution, the constant age structure approached in the long run). The strength of the begin-end approach is that it requires no additional assumptions beyond those included in the stock assessments. The disadvantage of the begin-end approach is that it may not represent a true comparison of fished to unfished conditions, given that the estimate of historical age structure might be from a period after the onset of intensive fishing (i.e., the baseline might have shifted). The unfished-end approach circumvents this shifting baselines problem, but it requires a greater dependence on assumptions of death rate values.

In our begin-end and unfished-end approaches, we analyzed the model-estimated age structure from the most recent stock assessments of 63 populations spanning five ocean regions (Table S1; Alaska: Eastern Bering Sea, Aleutian Islands, Gulf of Alaska; ICES [International Council for the Exploration of the Sea]: Icelandic and northern European waters; northeast US: including the mid-Atlantic US; southeast US: Atlantic coast; west coast US). In our begin-end approach, we compared the age structure estimated by the stock assessment model at the time of the latest stock assessment (2008–2016) to the earliest estimates of abundance at age, smoothing over recruitment anomalies by computing the mean age structure from the first and last five years of the stock assessment model output.

For many stocks and regions, the unfished-end estimates of abundance-at-age were not available for periods prior to development of large-scale fisheries. Short durations of model output relative to the history of intensive fishing were particularly noticeable for Alaska (mean: 41.9 y; 95% CI: [41.9–46.3] y), the ICES region (39.7 [28.9–50.5] y), the northeast US (30.4 [24.2–36.6] y), and to some extent the southeast US (51.5 [43.1–60.0] y), compared to the west coast US (95.5 [84.4–106.5] y). We expected that stocks with shorter durations of model output would have less severe age truncation than those with longer time series, so we tested for correlation between model output time series duration and the magnitude of age truncation, as estimated by the begin-end approach. To remove the dependence of the results on time series length, we developed an unfished-end approach to compare the present age structure to an estimate of the stable age distribution without fishing, derived from the stock assessment parameter M_x , the rate of mortality due to natural causes (e.g., predation) at age x . Given that the probability of surviving from age x to age $x + 1$ is $\exp(-M_x)$, the stable age distribution is $\{1, \exp(-M_1)\lambda^{-1}, \exp(-M_1 - M_2)\lambda^{-2}, \dots, \exp(-M_1 - M_2 \dots - M_{X-1})\lambda^{-(X-1)}\}$, where λ is the asymptotic population growth rate, X is the maximum age, and the relative abundance in the first age class is scaled to one. By assuming that the population is at equilibrium, and therefore $\lambda = 1$, we can estimate the proportion of individuals in each age class

before fishing $\hat{P}_{x,0}$ by scaling the stable age distribution to sum to one, dividing each element of the stable age distribution by P^* , the sum of the sequence $\{\exp(-M_1), \exp(-M_1 - M_2), \dots, \exp(-M_1 - M_2 \dots - M_{X-1})\}$:

$$\hat{P}_{x,0} = \frac{\exp(-\sum_{i=1}^x M_i)}{P^*}.$$

Age Truncation Metric Development and Analysis

To evaluate the change in older age classes in particular, we focused on the so-called “plus group” (the oldest age classes modeled as a single group in stock assessments) after verifying that the age at which the plus group begins is positively correlated with the maximum observed age across stocks ($r = 0.73$, $p < 0.0001$, Figure S2). For each stock, we computed the log ratio of the proportion of individuals in the plus group P_X at the end of the stock assessment period T , $P_{X,T}$, and the plus group proportion at either the beginning of the stock assessment period $t - T$, $P_{X,t-T}$ [begin-end approach: $\log(P_{X,T}/P_{X,t-T})$], or the initial unfished condition $\hat{P}_{X,0}$ [unfished-end approach: $\log(P_{X,T}/\hat{P}_{X,0})$]. We tested for change in plus group proportion with fishing for each stock, and tested for regional differences in mean proportions.

QUANTIFICATION AND STATISTICAL ANALYSIS

Data are presented as described in the text and figure legends. We tested for change in plus group proportion with fishing for each stock by performing Pearson’s Chi-square tests of the null hypothesis of no difference before and after fishing, and tested for regional differences in mean log ratios using ANOVA, with Tukey Honest Significant Differences as a post hoc test of pairwise differences among regions. To assess correlation between plus group age and maximum age, and between model output time series duration and age truncation, we computed Pearson’s product moment correlation coefficients and tested whether these differed from 0. We considered differences to be statistically significant if $p < 0.05$. Sample sizes can be discerned from Table S1. In tests for regional differences in the log ratio of the proportion of old individuals, the sample size is defined as the number of stocks. In tests for changes in log ratios of proportions of old individuals, the sample size is defined as the total number of individuals in each population as estimated within the stock assessment (these numbers are not reported here due to their large magnitude, but can be easily found within the publicly-available data). Statistical tests were performed using the functions *prop.test*, *aov*, *TukeyHSD*, and *cor.test* in the base *stats* package of R, version 3.3.2 [66].

DATA AND SOFTWARE AVAILABILITY

Data and Code

The data (<https://github.com/lewisab/age-truncation/tree/master/Data>) and code (https://github.com/lewisab/age-truncation/blob/master/R/AgeTruncationAnalysis_pub_code.R) are publicly available. The data can also be accessed through the larger RAM Legacy Stock Assessment Database: <http://ramlegacy.org/>.