

Reply to Koons: Harvest-related trait changes in an increasingly variable world

Koons (1) offers welcome insight into an additional threat to sustainability that could arise from harvest-driven trait changes. His contribution stems from our finding that shifts to life-history traits (e.g., reproduction at earlier ages and/or smaller sizes) in harvested populations averaged $\approx 25\%$ and were among the most rapid changes we observed in our dataset of 40 human-harvest systems (2).

Koons (1) frames his concern as evolutionary. We had not distinguished evolutionary from phenotypically plastic effects on trait expression but reasoned that the implications we identified hold irrespective of this distinction (2). How the implication Koons highlights might vary under differing degrees of genetic or plastic control is less clear, given that plasticity is itself an adaptation for variable environments.

Although not central to his contribution, Koons (1) suggests that shifts to faster reproductive tempos can increase maximum yield in terms of numbers of individuals. This is possible, but we suspect that, for aquatic communities in particular, such shifts might lead to declines in harvestable biomass (2), in part because younger, smaller breeders are often less fecund (3), with offspring less likely to survive (e.g., ref. 4).

Koons offers an important bridge between previously isolated literatures relating to contemporary life-history evolu-

tion and joins others in suggesting that harvest-related trait change might compound stochastic threats to populations (5). Such scenarios in which human-induced organismal changes interact with environmental perturbations could become increasingly common, cumulatively exposing populations to greater peril than predicted by the sum of independent threats.

Chris T. Darimont^{a,b,1}, Stephanie M. Carlson^c, Michael T. Kinnison^d, Paul C. Paquet^e, Thomas E. Reimchen^a, and Christopher C. Wilmers^b
^aDepartment of Biology, University of Victoria, P.O. Box 3020, Station CSC, Victoria, BC, V8W 3N5, Canada; ^bEnvironmental Studies Department, University of California, 405 Interdisciplinary Sciences Building, 1156 High Street, Santa Cruz, CA 95060; ^cDepartment of Environmental Science, Policy and Management, University of California, 137 Mulford Hall #3114, Berkeley, CA 94720; ^dSchool of Biology and Ecology, University of Maine, 321 Murray Hall, Orono, ME 04469; and ^eEnvironmental Design, University of Calgary, 2500 University Drive NW, Calgary, AB, T2N 1N4, Canada

1. Koons DS (2009) Does harvest select for maladaptation in an increasingly variable world? *Proc Natl Acad Sci USA* 106:E32.
2. Darimont CT, et al. (2009) Human predators outpace other agents of trait change in the wild. *Proc Natl Acad Sci USA* 106:952–954.
3. Venturelli PA, Shuter BJ, Murphy CA (2009) Evidence for harvest-induced maternal influences on the reproductive rates of fish populations. *Proc R Soc London Ser B* 276:919–924.
4. Berkeley SA, Chapman C, Sogard SM (2004) Maternal age as a determinant of larval growth and survival in a marine fish, *Sebastes melanops*. *Ecology* 85:1258–1264.
5. Anderson CNK, et al. (2008) Why fishing magnifies fluctuations in fish abundance. *Nature* 452:835–839.

Author contributions: C.T.D., S.M.C., M.T.K., P.C.P., T.E.R., and C.C.W. wrote the paper.

The authors declare no conflict of interest.

¹To whom correspondence should be addressed. E-mail: darimont@ucsc.edu.