

Humans are apex predators

In their recent paper, Bonhommeau et al. (1) calculate human trophic levels (HTL) as fractional trophic levels (FTL), which is the mean trophic level of all species in a consumer's diet weighted according to their proportions in the diet. Producer species are assigned FTL 1, and consumer values range from 2 (primary consumers) to 5 or greater. The authors conclude that HTL varies globally between 2.04 and 2.57. The mean HTL of 2.21 has increased over time as societies trend toward meatier diets. The authors also assert that humans, therefore, are not apex predators nor at the top of the food chain, being more comparable to low FTL omnivores.

This finding is problematic, however, because HTL captures the broad composition and multiple sources of human diets, not the roles that humans play in particular ecosystems. The HTL values reflect significant proportions of farmed producers and primary consumers. The impact of farming on ecosystems is primarily through land use and pollution, and the ecosystems are overwhelmingly terrestrial. In contrast, HTL components from marine ecosystems are

dominated by directly harvested wild species. There, humans affect populations and communities as consumers. Although suitable for the comparison of human diets, HTL does not measure human trophic levels in natural ecosystems.

For example, I inserted humans into two marine food webs: a northern Caribbean coral reef food web (2) and a food web of the Benguela system off southern Africa (3). The reef web is a high-resolution network comprising 267 nodes (representing 758 species) and 3,800 trophic links. Data necessary for FTL calculations are lacking for most links, so a network trophic level (NTL) was calculated as one plus the mean shortest distance of a consumer's prey species to a producer node. Producers are therefore NTL 1, primary consumers are NTL 2, and so forth. Resulting NTL values are significantly correlated with FTL, as determined by comparison with global fish FTL data ($r^2 = 0.75$, $P < 0.0001$) (4). The reef web has an NTL range of 1–4.8 (blacktip shark) and humans, linked to 15 commercially exploited fish species, are NTL 4.27, equivalent to a FTL of 4.65 (model II regression, $P < 0.0001$). Species in the

Benguela web are aggregated into 29 nodes, but commercially important species are resolved. Human NTL there is 3.82, equivalent to a FTL of 4.50. Thus, humans are apex predators in those systems.

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1 Bonhommeau S, et al. (2013) Eating up the world's food web and the human trophic level. *Proc Natl Acad Sci USA* 110(51):20617–20620.

2 Roopnarine PD, Hertog R (2012) Detailed food web networks of three Greater Antillean coral reef systems: The Cayman Islands, Cuba and Jamaica. *Dataset Papers in Ecology* 2013. Available at www.hindawi.com/journals/dpis/2013/857470/. Accessed December 16, 2013.

3 Yodzis P (1998) Local trophodynamics and the interaction of marine mammals and fisheries in the Benguela ecosystem. *J Anim Ecol* 67(4):635–658.

4 Romanuk TN, et al. (2011) Trophic level scales positively with body size in fishes. *Glob Ecol Biogeogr* 20(2):231–240.

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