CellPress REVIEWS

Letter

Aquatic Predators Influence Micronutrients: Important but Understudied

Alexander S. Flecker,[1,*,@] Cornelia W. Twining,[2,3,@] Oswald J. Schmitz,[4] Steven J. Cooke,[5,@] and Neil Hammerschlag [6,7,@]

In a recent paper on ecosystem function and services of aquatic predators in the Anthropocene [1], Hammerschlag and colleagues highlight a set of 16 outstanding research needs, including strengthening our understanding of the mechanisms and extent to which aquatic predators influence micronutrient and trace element fluxes within ecosystems. Závorka *et al.* [2] persuasively point out that within the realm of micronutrients, there is strong evidence that aquatic predators play a central role in the transfer of essential fatty acids (EFAs) such as docosahexaenoic acid (DHA, 22:6ω3) and eicosapentaenoic acid (EPA, 20:5ω3) in food webs, and that EFAs are vitally important neurologically for many consumers including humans. We agree that EFAs are an exciting and significant area of research, and we embrace their suggestion to extend the social and ecological framework presented in [1] to incorporate what is known about fluxes of EFAs as micronutrients.

EFAs have been studied in aquatic systems from a variety of perspectives [3]. Linkages between photoautotrophs and lower trophic levels have been studied for some time [4], and recent work on egg-rafts in the ocean provide a fascinating mechanism for satisfying EFA demands of some consumers [5]. Future EFA research can increase its impact on research across ecological subdisciplines by including a broader set of taxa within aquatic systems and by moving beyond the water's edge to examine linkages between aquatic and terrestrial systems. Moreover, most experimental studies evaluating EFA limitation on consumer growth and productivity have been conducted in laboratory settings, and ecologists should work to link analogous effects on organism performance in nature, with studies that quantify natural EFA sources and fluxes. For example, recent work by Twining and colleagues [6,7] on aquatic sources of EFAs as food web subsidies for riparian bird species illustrates some of the exciting insights as well as the challenges of thoroughly understanding complex interactions involving EFAs and aquatic predators. Through integrated laboratory and field studies based on bulk and compound-specific isotope analyses, this work demonstrated how EFA sources for tree swallows (*Tachycineta bicolor*) and Eastern phoebes (*Sayornis phoebe*) originate from aquatic primary producers, with emerging aquatic insects enriched in EFAs serving as micronutrient conveyor belts to riparian consumers [6,7]. Moreover, controlled diet experiments revealed that chick growth rate and condition were substantially improved when diets were supplemented by EFAs [6], and extensive field observations over a 24-year period suggested that EFA-rich aquatic insects are fundamental to bird population success [7].

Even with recent progress in EFA studies, micronutrients remain highly understudied in food webs, and our knowledge about interactions involving many key elements, including predator effects, is woefully inadequate, despite their importance as vital building blocks for life [8,9]. Fatty acids are just one of many physiologically important and potentially limiting organic compounds, including amino acids, sterols, and vitamins, that remain understudied in natural ecosystems. For example, thiamine (vitamin B_1) deficiency is also known to impair neurological function, which can result in high mortality of early life stages in fishes [10], and has been hypothesized as a driver of extirpation of some predators [11]. Nevertheless, there are still remarkably large knowledge gaps about thiamine in ecosystems, starting with the range of natural concentrations found in most natural waters, thiamine requirements of aquatic predators from wild populations, especially those found high in food chains, and how thiamine deficiency can affect predator secondary production [12].

Závorka *et al.* [2] correctly emphasize how the decline of predators in aquatic food webs has critical implications for human health through the loss of vital sources of micronutrients such as EFAs. Indeed, aquatic predators represent a key provisioning ecosystem service via linkages with human nutrition, which serves as a major rationale as to why further research aimed at elucidating mechanisms and extent to which aquatic predators influence micronutrients and trace element fluxes within ecosystems is an urgent priority [1].

[1]Department of Ecology and Evolutionary Biology, Cornell University, Ithaca, NY, 14853, USA
[2]Limnological Institute, University of Konstanz, 78464 Konstanz, Germany
[3]Max Planck Institute for Animal Behavior, 78315 Radolfzell, Germany
[4]School of Forestry and Environmental Studies, Yale University, New Haven, CT, 06511, USA
[5]Fish Ecology and Conservation Physiology Laboratory, Carleton University, Ottawa, ON, K1S 5B6, Canada
[6]Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami, FL, 33149, USA
[7]Leonard and Jayne Abess Center for Ecosystem Science and Policy, University of Miami, Coral Gables, FL, 33146, USA

*Correspondence:
asf3@cornell.edu (A.S. Flecker).
[@]Twitter: @DrNeilHammer (N. Hammerschlag), @SJC_Fishy (S.J. Cooke), @SchmitzLab (O.J. Schmitz), @Cornell (A.S. Flecker), and @twisci1 (C.W. Twining)

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Forum

Niche Modification, Human Cultural Evolution and the Anthropocene

Felicia M. Low,[1,2] Peter D. Gluckman,[1,2,*,@] and Mark A. Hanson[3]

Niche-constructing organisms actively modify their environments with adaptive consequences, sustaining a new equilibrium. Modern humans are instead niche modifiers, continually changing their environments irrespective of adaptive pressures. The nature, scale, and speed of such modifications have potential ill effects that need to be addressed with multilevel societal initiatives.

Humans as Niche Constructors – Is a Rethink Needed?

The concept of the Anthropocene has focused attention on the far-reaching impact of human activity on many aspects of the planetary environment. In this forum we discuss the evolutionary implications of contemporary human–environment interactions, not only in terms of our unique capacity to change our environment, but also in terms of the possible effects of the environment on our biology and culture.

A widely accepted and important concept in evolutionary biology is that of niche construction [1] – the process whereby organisms actively construct environments that establish an evolutionary equilibrium by sustaining their fitness. Frequently cited examples of niche-constructing species are beavers (*Castor* spp.) and termites (Isoptera) [2]. Niche construction may involve the proactive initiation of changes in the immediate environment by the organism, or the reactive changing of the niche in direct response to prior environmental changes. The latter strategy, termed counteractive niche construction, stabilizes local environments in an adaptive way and buffers against the effects of variations in the wider environment; an example is temperature regulation of the nests of bees and wasps.

These processes of niche construction lead to the attainment of equilibrium between the organism's constructed niche and its reaction norm of phenotypes. They thus confer an adaptive benefit. As Laland and Brown [3] pointed out, niche construction can serve to reduce the 'adaptive lag' that would otherwise challenge fitness due to the time required for a new genotype to evolve following substantial environmental change. Humans are often considered an example of niche constructors [4]. The question we ask is: to what extent do modern human activities relating to the Anthropocene present a challenge to this viewpoint?

Humans as Niche Modifiers in the Anthropocene

We argue that humans are not just counteractive niche constructors, but rather now cumulative and progressive niche modifiers, continually changing their environment irrespective of adaptive need or pressures [5] (Table 1). Our evolution, and in particular our cultural evolution, is characterized by unique innovative capacities, including our manual dexterity and ability to learn and to communicate through complex language, building expertise cumulatively over time [5]. Thus, our environments in the world change dramatically, unlike the relatively

Table 1. Relative Differences between Niche Construction and Niche Modification

	Niche construction	Niche modification
Biologically heritable phenotype/genotype	Yes	Not necessarily
Enhances or sustains fitness	Yes	Not necessarily
Behavioral characteristics	Stereotyped	Innovative
Effectively creates environmental equilibrium	Yes	No
Relative pace	Slow	Rapid
Relative impact	Small (local) – generally the subpopulations that engaged in niche construction	Large (even global) – wider populations, including those far removed from actual niche modifiers