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Aquatic food webs will need to stand on giants' shoulders

Teias tróficas aquáticas precisarão se apoiar sobre os ombros dos gigantes

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Abstract: Aquatic food webs have been especially impacted in the last thirty years. This is particularly true for trophic webs with Mobile Generalist Species (MGS), which are species with high mobility (movement and dispersal) and flexibility in both foraging and habitat use. In general, MGS are large-sized species with the ability to move long distances, and they may be top predators (Large Generalist Predator; LGP) or feed lower in the food web than predicted from their size (Giant Secondary Consumers; GSCs). These species groups will play a fundamental role in connecting and rewiring human-impacted food webs, however this may be challenging because the stream network connectivity in most of the world's largest river basins has been severely fragmented by dams.

Keywords: reservoir; hydropower impact; top predators; trophic pyramid.

Resumo: As teias tróficas têm sido impactadas especialmente nos últimos 30 anos. Isto ocorre em especial para teias tróficas com Espécies Generalistas Viajantes (MGS) que são espécies com alta mobilidade (movimento e dispersão) e flexibilidade em forrageamento e uso do habitat. Em geral, MGS são espécies de grande tamanho com habilidade de se mover longas distâncias como predadores de topo (Grande Predador Generalista, LGP) ou de se alimentar em estratos mais baixos da teia trófica do que o predito pelo seu tamanho, são espécies chamadas Consumidoras Secundárias Gigantes (GSC). Estes grupos de espécies terão papel fundamental em conectar e reestruturar as teias tróficas impactadas pelo homem. Entretanto, isto pode ser um desafio devido ao fato que as conectividades das redes hidrográficas nas maiores bacias do mundo têm sido severamente fragmentadas por barramentos.

Palavras-chave: reservatórios; impacto de hidrelétricas; predadores de topo; pirâmide trófica.

Despite being an old warning since the 1980s, only recently have climate change issues become prevalent in scientific literature and spread quickly on the news and Internet. In the last ten years, people have come to understand that climate change affects not only animals and plants, but could also affect people and their ways of living.

Nowadays humans know that they are a fragile part of a big web of interactions with other species and the environment. This global food web, including the human species, allows a Brazilian citizen to eat wild buffalo meat from South Africa and a Chinese citizen to eat sea cucumber from the Caribbean region. However, this lifestyle can intensify climate change effects, because, at least, the release of atmospheric CO_2 is increased from the long-distance transportation of those products.

Climate change is likely exacerbated by human activities. However, before the current level of global impact, humans had already disturbed aquatic food webs with dam construction, invasive species release, pollution, and fishing. The latter is one of the most ancient impact on aquatic species and, consequently, their food webs (Fagan, 2017; Bieg et al., 2018). In the last one hundred years, technological developments have permitted a huge increase in fish catch values. In 1950, the global fish catch was around 20 million tons per year, and, 40 years later, the value was more than four times higher, remaining consistent (90 million tons) as of 2018 (FAO, 2018). Between 2011 and 2016, inland waters alone produced almost 70 million fish tons (yearly mean = 11 million tons).

Overfishing has collapsed several fish stocks around the world, and some of them are considered irreversible (Allan et al., 2005; Le Pape et al., 2017). Closing fishing areas and reducing fishing efforts are the most common strategies to recover fish stocks; however, when a stock collapses, fishing vessels generally start looking for other species (stocks) from lower trophic levels, a phenomenon called fishing down food web, which is observed in several parts of the world (Pauly et al., 1998).

The change in fishing targets is due to economic issues but also because fishermen have faith that the collapsed stock can be recovered once catches stop. It could call this capacity of recovery “resilience”, which depends, in large part, on the food web. Researchers, in general, believe that when humans impact one component of the food web, all others are directly or indirectly affected, sometimes positively, in a process called trophic cascade. To begin, we need to better qualify the definition of a food web.

A food web has two main components: nodes (species or groups; named topology, i.e., “who eats whom”) and direct strength interactions (consumer-prey relationship). The food web controls the flux of nutrients (or energy) from decomposing material and recycling nutrients to primary (plant and algal growth) and secondary (animal growth) production (Bartley et al., 2019). There are lots of drivers, including climate change, acting together on aquatic food webs and their components; however, it is extremely difficult to isolate the influence of each driver on the food web’s components. Nevertheless, science is trying to forecast food web rewiring under climate change scenarios. This way, we can start to think about species (food-web nodes) and how species could maintain consumer-prey relations, especially species which could be considered as key-species which play an important role on food webs stability (Libralato et al., 2006).

Regarding, *Mobile Generalist Species* (MGS) are species with high mobility (movement and dispersal) and flexibility in both foraging and habitat use. They have a large dietary breadth, allowing movement to new ecosystems and rewiring of food webs, changing interaction strengths, adding new interactions, and influencing indirect interactions (trophic cascade). In general, Mobile Generalist Species are large-sized species with the ability to move long distances, such as Amazon catfish that migrate from estuarine water to Andean foothills, bears, and sharks (Bartley et al., 2019).

It is well known that body size can control consumer-resource interactions (Ou et al., 2017; Romanuk et al., 2011), with the biggest species being top predators and feeding on a wide range of prey sizes (*Large Generalist Predator*; LGP). However, there are also large-sized species that feed lower in the food web than predicted from their size (e.g., baleen whales, whale sharks, manatees), called *Giant Secondary Consumers* (GSCs). These animals evolved mainly in tropical areas because, in higher temperatures, the relative demand for carbon is higher than for nutrients and digestion of plant tissue is easier, inducing higher rates of herbivory and omnivory (Woodson et al., 2018).

In food webs with LGPs and GSCs, the classic trophic pyramid of Lindeman (1942) can change to an “hourglass shape” (in Portuguese, *forma de pilão*), with the most biomass accounted for by the largest animals in the top (LGP) and bottom (GSC) positions. This unusual shape is especially likely in pristine ecosystems (Woodson et al., 2018).

Ecology textbooks teach that specialist species do better in stable environmental conditions. However, in a climate change scenario with unforeseeable variations, there are no steady conditions, and it seems logical that generalist species could adapt better under these circumstances. Accordingly, the expected food webs tend to be dominated by generalist species in a broad sense: large dietary breadth (omnivory; LGP), able to disperse (migratory species; MGS), and flexible in habitat use to consume relatively more carbon than nutrients (GSC).

Thus, food webs will tend to get more complex even with lower number of nodes, and a meta-food web approach (an analysis of many local food webs in order to find patterns) will be necessary to analyze the role of big mobile species in the interchange and exchange of several connected local food webs. Unfortunately, the biggest marine species are constantly endangered by fishing and hunting; however, there are no enormous obstacles in the sea, and fish species could swim to colder (deeper or distant) or more productive waters, especially if members of the species have large-sized bodies.

Conversely, the prospect is worse for freshwater species, even the large-sized ones, because they have no escape route. Small streams tend to be isolated or dry and lakes tend to be shallow (no deep or cold waters) with climate change (Dantas et al., 2019). In addition, the big rivers, typically the most resilient freshwater environments to climate change, are suffering an unprecedented boom in the construction of hydropower dams, stopping migration of the mobile species (generally the biggest species, such as tropical catfish; LGP) because many kinds of fish-passage facilities do not work (Pelicice & Agostinho, 2008; Noonan et al., 2012). Dams heavily modify the surrounding habitat (flood pulse, nursery areas), making it almost impossible for mobile and large-native species to adapt themselves to this new environment (Winemiller et al., 2016). Regarding, the main paradox is that hydropower is often promoted as a carbon-free energy; however, although most dams tend to produce low-carbon energy, some dams may emit more greenhouse gases per unit electricity generated than fossil fuel-based electricity (Almeida et al., 2019). Still, dams are worse than global warming for freshwater fish species because they do not give mobile generalist species a chance to adapt their own behavioral responses.

The rewiring of our future food webs stands on giant species' shoulders, because they could connect several ecosystems since they have high mobility and large feeding adaptability. Global warming could induce a decrease of trophic position of larger fish due to the higher carbon demand under higher temperatures (probably, Giant Secondary Consumer will replace Large Generalist Predator species), consequently reducing the length of food webs ("adaptive-down-food-web"). This trend is stronger in freshwater ecosystem because marine systems have larger space and no barriers to dispersion (Dantas et al., 2019).

Unfortunately, dam construction has been increasing since the 1970s, and is predicted to continue proliferating at a fast pace in the next decades (Zarfl et al., 2015). Thus, more than giant species, we will need a huge courage to move away from hydropower and its dams. After all, the human being is the giant with clay feet who depends on global food webs.

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