Trophic Cascades

T Ramakrishna Rao

In many ecosystems, apex consumers (top predators) play a crucial role in food web dynamics. Their top-down impacts are known to spread downwards through the food webs in a cascading fashion. Trophic cascades manifest when top predators are excluded from an ecosystem or introduced into a system lacking them. Two such case studies are described here. Trophic cascades are generally more pronounced in the aquatic than in the terrestrial ecosystems, which in turn is related to the differences in the average body sizes of herbivores relative to the plant resources they feed upon and in the structure of their food webs. Scientists express concern that human activities have been leading to planet-wide trophic downgrading (loss of apex consumers) which could affect vital ecological processes of the biosphere.

After retiring in 2004 from the University of Delhi where he was Professor and Director of the School of Environmental Studies, T Ramakrishna Rao served as a visiting Professor for six years (2010–2016) at the Indian Institute of Science Education and Research (IISER), Mohali. He received his PhD from the University of California and conducted postdoctoral research in British Columbia (Canada) and Hawaii (USA). His research interests are in the roles of competition and predation in the life of freshwater zooplankton.

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1. Introduction

Everything in nature is connected directly or indirectly with everything else. Francis Thompson's famous aphorism: "Thou canst not stir a flower without troubling a star" may be a poetic hyperbole, but nearly 200 years ago, the Native American Chief Seattle conveyed its essence more eloquently:

> "*Humankind has not woven the web of life,*
> *We are but one thread in it.*
> *Whatever we do to the web, we do to ourselves. All things are bound together. All things connect.*"

We humans generally fail to acknowledge or appreciate this interconnectedness of all things in nature when we tinker with it and undertake activities that upset its delicate ecological balance, often with unforeseen consequences. Here are a couple of dramatic recorded cases. In the 1950s, the deliberate introduction (apparently with good intentions) of Nile perch[1] into Lake Victoria by a Ugandan governmental agency, proved to be a monumental ecological disaster. Within a short period after this introduction, nearly 200 species of cichlid fish endemic to the lake became extinct. Similarly, in the Pacific Island of Guam, naturally free of vertebrate predators, inadvertent introduction of brown tree snakes (which probably hitchhiked to the island in cargo boats), spelt doom for many indigenous fauna, causing the extinction of 12 species of birds and 6 species of reptiles.

[1] A species of freshwater fish.

Major changes, natural or man-made, occurring at one trophic level are known to affect other trophic levels in the food web of an ecosystem in a cascading fashion. Although Ripple *et al*. [1] define trophic cascades as "the indirect species interactions that originate with the predators and spread downward through food webs", trophic cascades may operate both ways – 'top-down'[2] as well as 'bottom-up'[3]. For instance, addition of essential nutrients such as phosphorus and nitrogen to an oligotrophic[4] lake may have a cascading effect on the herbivore and carnivore levels above. Recent studies show that in many ecosystems, both top-down and bottom-up factors might be operating simultaneously. Nevertheless, as we will see in the examples below, top-down cascades tend to be more dramatic and far-reaching than bottom-up cascades, particularly in aquatic ecosystems[5].

[2] Effects cascading down from apex consumer level.

[3] Effects cascading up from autotrophs to higher trophic levels.

[4] Nutrient- impoverished.

[5] See Vidyadhar Atkore and Jagdish Krishnaswamy, Exploring Freshwater Science, *Resonance*, Vol.21, No.11, pp.997–1006.

Top-down trophic cascades may not be readily discernable in an ecosystem; they are detected when existing top predators are excluded from a system or when they are introduced into a system naturally lacking them. Predator exclusion or inclusion may be a natural process (brought about by some sudden ecological change) or a deliberate human activity.

It may be noted here that the vital role of apex consumers in nature has not escaped the attention of Charles Darwin, the quintessential naturalist. In his celebrated book *On the Origin of Species*, Darwin cites a classic example of a trophic cascade – cats influencing the pollination success of red clover in rural England.

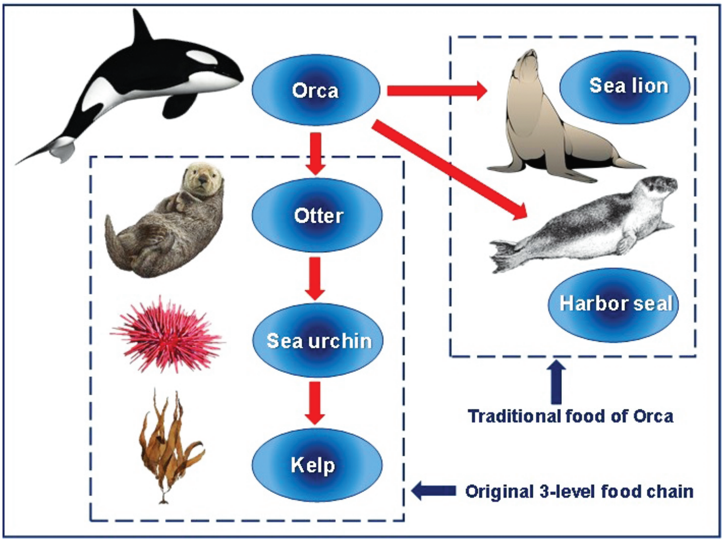

Figure 1. Orca (killer whale) which traditionally feeds on harbor seals and sea lions, enters the original 3-level food chain of a Pacific kelp forest and starts feeding on otters, causing a top-down trophic cascade.

It was observed that in villages with large cat populations, red clover pollination was far more successful than in villages with only a few cats. What links cats to flower pollination? It happens that cats kept the field mice (their natural food) population under control, which otherwise would destroy bumblebee nests for their food, causing a scarcity of pollinators.

2. Case Studies

2.1 *Otter–Sea urchin–Kelp Ecosystem*

In the coastal waters of the Pacific Ocean (importantly in Alaska), flourish a type of giant floating brown algae called kelp. With individual fronds growing up to 20 m, kelp grows so dense in some areas that they literally form kelp forests under the sea and support a diverse community of fishes and invertebrates. Dominant in this unique ecosystem is a three-level food chain (*Figure* 1) formed by kelp, sea urchins and otters. Otters feed on the sea urchins that graze on the kelp. Otter predation keeps the sea urchin population in check which otherwise could graze away the kelp. Now, what happened in the 1990s to this delicately balanced

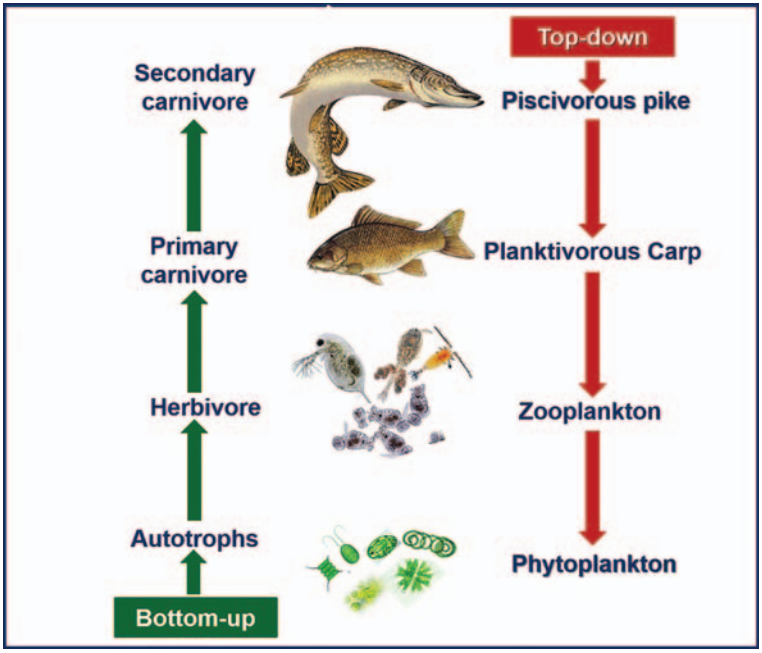

Figure 2. Top-down and bottom-up trophic cascades in a shallow lake ecosystem. Introduction of a top-level predatory fish causes downward-cascading effects along the food chain, ultimately resulting in a reduction of autotroph biomass. Enrichment of a nutrient-impoverished lake may initiate a bottom-up trophic cascade, where the effects of increased autotroph biomass cascade upwards to higher trophic levels.

ecosystem is a classic example of trophic cascade in which effects of a change at the higher trophic level cascaded down to the lower trophic levels. During this period, an extra trophic level was appended to the otter–sea urchin–kelp chain. Orcas (killer whales) which traditionally fed on sea lions and harbor seals elsewhere, entered the kelp ecosystem. During this period harbor seals and sea lions simply vanished, forcing orcas to switch to otters as their main diet. According to one hypothesis, increasing ocean temperatures caused sea lions and harbor seals to move away to more profitable feeding grounds. Now, the cascading effects started manifesting dramatically in the orca–otter–sea urchin–kelp food chain; increased predation on otters by orcas led to otter population declines, which in turn relieved pressure on their prey, the sea urchins. Their populations unchecked, the sea urchins grazed away the kelp in the ecosystem. Thus, the 1990s witnessed an alarming loss of kelp with an attendant decline in fish and invertebrate diversity in the ecosystem.

2.2 *Algae–Zooplankton–Fish Ecosystem*

A three trophic-level[6] system formed by algae, zooplankton and fish is characteristic of many lakes and other shallow water bodies around the world (*Figure* 2). The algae are grazed upon by zooplankton which in turn form the food of planktivorous[7] fish. Introduction of a piscivorous[8] fish into this simple food chain of a freshwater ecosystem often has a cascading effect on the lower trophic levels, similar to that of orcas on the kelp–sea urchin–otter food chain in the sea. In North American stream food webs with a 4-level food chain, it is ultimately the presence or absence of the top predator, the steelhead trout, that determines the autotroph biomass in the stream.

[6]Autotrophic producer–herbivore–primary carnivore.

[7]Plankton-eating.

[8]Fish-eating.

3. Biomanipulation

The biomanipulation method used by Dutch scientists to improve water quality in shallow lakes is based on the concept of trophic cascade.

Trophic cascade is the ecological process that underlies a unique biomanipulation experiment conducted by Dutch scientists to improve the water quality of the extensive network of shallow lakes in their country (Netherlands). Anthropogenic addition of organic effluents by diffuse sources makes excess amounts of plant nutrients – nitrates and phosphates – available to phytoplankton (algae and cyanobacteria), which results in massive algal blooms. Unless grazed down by zooplankton, the phytoplankton accumulates and starts forming rotting and unsightly mats, bringing down the overall water quality. Evidently, there wasn't enough zooplankton biomass to check the algal bloom which was in turn due to their predation by the planktivorous fish (bream). When efforts to remedy the problem by controlling the release of organic effluents from diffuse sources proved to be only marginally effective, scientists wanted to try 'biomanipulation'. They introduced into the degraded freshwater systems sufficient numbers of pike, a piscivorous fish known to feed on bream, and soon the cascading effects started becoming apparent. Pike fed upon the bream and brought down their biomass significantly. Relieved of the predation pressure from bream, zooplankton biomass increased, which in turn, through their grazing brought down the algal biomass, resulting in a significant improvement in water quality. Now, Dutch governmental agencies supplement their chemical control methods with biomanipulation to maintain the water quality of the country's shallow lakes and other important waterways [2].

4. Trophic Cascades: Aquatic *vs*. Terrestrial Ecosystems

Trophic cascades are stronger in aquatic ecosystems than in terrestrial ecosystems. Why is it so? Theoretical explorations on this question have led to research papers with catchy titles like 'Are all trophic cascades wet?' and 'Trophic cascades and trophic trickles'.

To answer this question, we will examine a simple theoretical model [3].

Consider a simple 2-trophic level food chain comprising Resource (R) and Herbivore (C) and a 3-trophic level food chain comprising Resource (R), Herbivore (C) and Predator (P) (*Figure* 3).

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In order to assess the impact of a trophic level on the one below it, we generally use as a measure their relative abundances (biomass or numbers) achieved at equilibrium, that is, the abundance when the population death rates and birth rates are equal (net population growth is zero). In *Figure* 3 these equilibrium abundances are shown as appropriate letters with a hat (e.g., $\hat{R}$).

Trophic cascade (TC) is the ratio of the equilibrium abundance of the basal resource (R) when occurring with its consumer (C) and predator (P), i.e., $\hat{R}_3$, to the equilibrium abundance of the resource when occurring with its consumer (C) only, i.e., $\hat{R}_2$.

$$TC = \frac{\hat{R}_3}{\hat{R}_2}.$$

For example, if the food chain is of phytoplankton (R)–zooplankton (C)–planktivorous fish (P) as in *Figure* 2, then TC is the ratio of the equilibrium abundance of phytoplankton reached with both zooplankton and planktivorous fish present to that reached when only zooplankton is present.

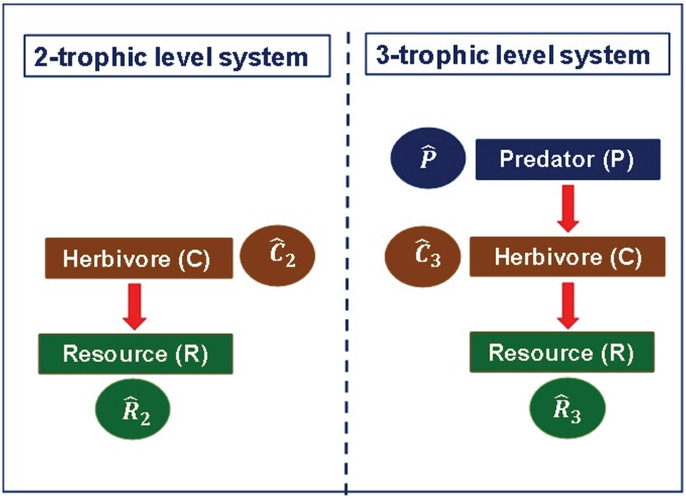

Figure 3. Equilibrium abundances (or biomass) (accented alphabets) achieved at different trophic levels in a two-level (Resource–Herbivore) system and in a three-level (Resource–Herbivore–Predator) system. The ratio $\frac{\hat{R}_3}{\hat{R}_2}$ is a measure of the strength of a trophic cascade.

TC is a measure of the strength of the trophic cascade.

Delong's model [3] further shows that the strength of interaction between the two trophic levels – Resource (R) and Consumer (C) – is the major determinant of the trophic cascade. Again, interaction strength can be expressed as a ratio of the equilibrium abundances of any two trophic levels. The ratio $\frac{\hat{C}_2}{\hat{R}_2}$ gives the interaction strength between the consumer and the resource in a two-level trophic system. The more efficient a consumer is at suppressing its resource biomass, the higher will be this ratio, and hence stronger the cascade is likely to be.

In the terrestrial ecosystem, body sizes (mass) of herbivores are much smaller relative to the plants they eat while in the aquatic ecosystem it is the opposite and the herbivores are very large relative to the algae they feed on.

Now, how does all this explain the differences between aquatic and terrestrial ecosystems? Interaction strengths can be related, through a set of physiological parameters, to the average body sizes of the resource and the consumer. In the terrestrial ecosystem, body sizes (mass) of herbivores (deer, rabbit, phytophagous insects) are much smaller relative to the plants they eat (low $\frac{\bar{M}_{\text{consumer}}}{\bar{M}_{\text{resource}}}$ ratio) while in the aquatic ecosystem it is the opposite and the herbivores are very large relative to the algae they feed on (high $\frac{\bar{M}_{\text{consumer}}}{\bar{M}_{\text{resource}}}$ ratio). For instance, the average weight of algal-feeding water flea *Daphnia* would be >3 million times the mass of an algal cell. Furthermore, aquatic autotrophs (phytoplankton) are better assimilated than terrestrial autotrophs (plants) by their con-

Terrestrial food webs are generally complex networks of interactions, forming 'trophic tangles' rather than the linear 'trophic chains' typical of aquatic food webs.

sumers. Therefore, aquatic consumers are more efficient and effective in suppressing the resource populations and thus facilitate a stronger trophic cascade.

There is also another explanation for the observed differences in the trophic cascade strength between terrestrial and aquatic food webs. Terrestrial food webs are generally complex networks of interactions, forming 'trophic tangles' rather than the linear 'trophic chains' typical of aquatic food webs. So, unlike the cascade-like propagation of top predator effects through the food chain in a lake, the top-down effects in terrestrial food webs tend to dissipate through the trophic network, making it difficult to detect readily. Recent studies, however, indicate that trophic cascades in terrestrial ecosystems are not as rare as they were thought to be earlier. In fact, there are now many documented cases of trophic cascades in all the major biomes of the world. Ripple and Beschta [4] discovered, by reconstructing historical data, a trophic cascade that started in the early 1900s in the Yosemite Valley (California). It involved a top carnivore, the cougar, its food (the mule deer), and the black oak, whose saplings formed the major food for the deer. Increased human activities in the Yosemite National Park during the 90s caused a decline in the cougar population. The reduced predation pressure soon led to an irruption of the deer population. The deer then browsed away all the oak saplings significantly diminishing tree regeneration in the valley.

5. Trophic Downgrading

Starting with the late Pleistocene, our planet has been experiencing large-scale extinction of species – a phase called the 'Sixth Extinction'[9] – which is still in progress. There is overwhelming evidence pointing to humans as the major driver of these mass extinctions in modern times. One prominent and alarming feature of this phase is the progressive loss of larger-bodied animals, especially apex consumers. Loss of apex consumers results in a reduction of food chain length, a process that Estes *et al.* [5]

[9]Also see Book Review, Prasanna Venkhatesh V, The Age of Extinction, *Resonance*, Vol.21, No.8, pp.748–750.

call the 'trophic downgrading'. In many cases, the impacts of trophic downgrading may not be readily evident since system responses to loss or addition of apex consumers occur only on large temporal and spatial scales. In addition to their direct top-down effects on primary producers, trophic cascades also generate 'knock-on' effects[10] with strong effects on ecosystem dynamics. Together, they indirectly influence diverse ecosystem processes such as wildfires, diseases, carbon sequestration and biodiversity. For this reason, ecologists emphasize the need to monitor and assess trophic downgrading impacts in managing wildlife, fisheries and other natural resources.

[10]Effects arising out of spin-off from the main interaction chain.

Suggested Reading

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Address for Correspondence
Prof. T R Rao
19 Shakti Apartments
Phase-III, Ashok Vihar
Delhi-110 052, India.
Email: trrao39@gmail.com