BIOLOGY REPORTS

Published: 24 March 2009

Toward understanding the effect of top predators on ecosystems

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F1000 Biology Reports 2009,**1**:26 (doi: 10.3410/B1-26)

Abstract

To what extent top predators - carnivores at the top of food chains - drive or just respond to ecosystem dynamics is a central, but partially unresolved, question in ecology. In this report, we highlight how different research approaches employed in aquatic and terrestrial ecology may have a bearing on how the role of top predators in ecosystems is perceived.

Introduction and context

Population declines of top predators (TPs), such as sharks, whales, wolves, and raptors [1,2], are among some of the most obvious human impacts on biodiversity of the last few centuries [3–5]. Recent advances in food web modelling emphasize the role of TPs in the maintenance of biodiversity at several trophic levels, with the loss of TPs driving secondary extinctions faster than the loss of species at lower trophic levels [6,7].

Besides the immediate risk of TP extinctions, more general implications may be due to the different functions of TPs in ecosystems. Whereas removal of TPs may have relatively little ecosystem impact when the food webs are bottom-up (or donor) controlled, much stronger impacts are due to instances in which TPs exert strong top-down control on lower trophic levels. Where this occurs, declining TP populations may induce a trophic cascade, which in the worst case could result in a permanent regime shift, in the sense that the structure and functioning of the ecosystem could become irreversibly altered [8–10]. This outcome appears to be likely in models of food webs with few strong trophic interactions [11]. Yet, in other cases, TPs can be involved in reversible transition between alternative ecosystem states (Figure 1).

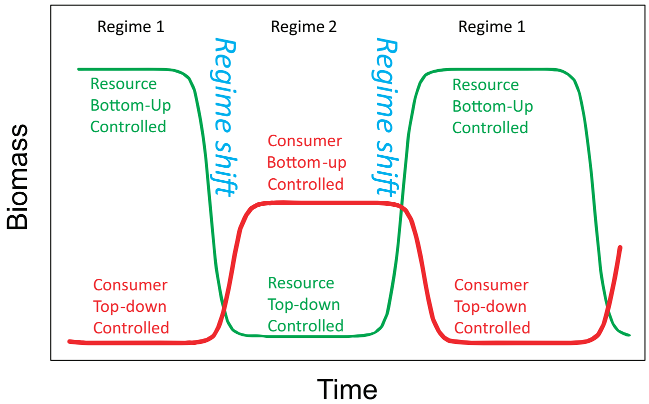
There has been a long-lasting debate about the role of TPs, and the relative impact of bottom-up and top-down forces in ecosystems (for example [12]). Fundamentally different environmental contexts (in particular, aquatic and terrestrial ecosystems) have been proposed to underlie context dependencies of TP ecosystem functioning. In this report, by insight gained from recent studies, we exemplify how the different approaches favored by terrestrial and aquatic ecologists may affect what we know about the role of TPs in ecosystems.

Major recent advances

Behavioral food web ecology

The role of behavior has been an important topic in studies focusing on predator-prey interactions and was first investigated in aquatic ecosystems [13,14], although much research was biased toward emphasizing risk-aversive prey behavior (reviewed in [15,16]). However, Lima's plea [15] to 'put back predators in the predator-prey interactions' has been realized recently through studies highlighting how TP hunting mode can contribute to trophic cascades [17]. Further advances in 'behavioral food web ecology' are likely to be brought about by studies that simultaneously consider behavioral interactions between predator and prey [3,18] as well as between multiple predators [19]. Although the role of non-consumptive effects of TPs currently appears to be less emphasized for aquatic food webs than for terrestrial food webs, we are not aware of any reasons why they should be less important [3]. Technical innovations that make behavioral studies more feasible under water are likely to change this state of affairs [20].

Figure 1. Dynamic model of an ecosystem shifting between alternative states (regimes 1 and 2)



In regime 1, the consumer is controlled by a top predator (top-down control) and the resource is controlled by nutrient availability (bottom-up), whereas in regime 2, the resource is controlled by the consumer (top-down) and the consumer is controlled by resource availability (bottom-up). The model is redrawn from [22] based on a marine ecosystem with four trophic levels, although this could be applied to ecosystems with a different number of trophic levels, in both terrestrial and marine environments.

Mesopredator release

An increasing abundance of smaller predators (mesopredators) when TPs disappear has been documented in both aquatic and terrestrial ecosystems. Such mesopredator releases have major consequences for prey species and primary producers. For instance, the collapse of cod stocks in the north-western Atlantic led to significant changes at several trophic levels, resulting in a transition to an alternative community state [21]. Elmhagen and Rushton [22] demonstrated in a terrestrial ecosystem how the decline in TPs (here, wolf and lynx) favored the increase in abundance of red fox populations, which, in turn, seemed limited by ecosystem productivity. Such joint action of bottom-up and top-down forces means that the concept of mesopredator release needs to be expanded toward an ecosystem-based perspective. In a similar way, Daskalov *et al.* [23] demonstrated how mesopredator populations can switch between top-down and bottom-up control in alternating regimes in the Black Sea ecosystem. Despite clear similarities across ecosystems in the reactions of mesopredator populations to changes in the abundance of TPs, the flexible size and stage structure in fish populations exacerbate the propensity for shifting trophic structure and dynamic in aquatic ecosystems, as compared with terrestrial ecosystems [21,24].

Predator feedbacks in pulse-driven ecosystems

Resource pulses (i.e. infrequent, short-term, and large-magnitude booms in productivity at low trophic levels that cascade upward in the trophic system) traditionally have been discussed with reference to terrestrial ecosystems. Although such resource pulses are among the best examples of bottom-up-dominated ecosystem dynamics, recent research has shown how impacts from mobile TPs tracking an asynchronously pulsed resource can dampen pulse amplitude through spatial averaging [25,26]. Moreover, diet-switching of generalist TPs is another mechanism driving community dynamics in many pulsed systems, especially through the process of apparent competition between prey sharing the same TP [25]. Despite an initial focus on terrestrial food webs, recent reviews highlight that resource pulses do occur in freshwater and marine ecosystems as well, and that comparative analysis may lead to a novel understanding of this area [26,27].

Data and methods

Statistical analyses of time series have played a key role in elucidating changes in TP abundance [3], the likely causes of these changes (in particular, the impact of harvesting versus climatic variability [28]) and finally the strength of trophic interactions [29]. Time series of TPs have also played a significant role in the development of statistical time series analysis in general (for example, Canadian lynx). However, in most terrestrial ecosystems, we usually lack information on trophic level dynamics besides TPs; for example, time series of plant and/or herbivore dynamics are nonexistent (except for certain pulse systems for which data on insects or seeds do exist [27]), whereas studies on marine ecosystems can rely on data from many trophic levels, sometimes from phytoplankton all the way to TPs [9,23]. The lack of information on other trophic levels obviously limits the inference we can draw regarding the importance of top-down versus bottom-up effects.

Further methodological developments have led to the detection of regime shifts [9]. Examples of such shifts emphasize the role of bottom-up processes and, in particular, climatic control [8,30]. On the other hand, interactions between environmental forcing and harvesting of TPs have also been described in marine ecosystems [9,28]. Most of the recent evidence for such shifts comes from aquatic ecosystems, although shifts of vegetation states in terrestrial ecosystems do occur (such as the biome shift from steppe to tundra [31] or through desertification [32]), yet remain contentious.

Future directions

As evidence accumulates, the simple distinction between bottom-up versus top-down control gets increasingly blurred, such that the same system can even alternate between these two states (Figure 1) [22]. The extent to which marine, freshwater, and terrestrial ecosystems differ with respect to such controls, and which structural parameters determine their strengths, will be reassessed repeatedly as evidence accumulates and valid statistical comparisons accounting for sampling biases are developed. Furthermore, we believe that much more can be learned by comparing these ecosystems within the same theoretical framework [4]. Indeed, although limnic, marine, and terrestrial ecology are often treated as different disciplines, they contribute to a common theory of food web and ecosystem function. Finally, the fact that TPs can link different ecosystems (for example, marine and terrestrial) through migration or subsidies [33,34] testifies for the importance of adopting a broad perspective when studying the role of TPs in ecosystems.

Abbreviation

TP, top predator.

Competing interests

The authors declare that they have no competing interests.

Acknowledgements

This report was funded by the Research Council of Norway through the International Polar Year project 'Arctic Predators' (http://www.arctic-predators.uit.no).

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