TROPHIC CASCADES

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PREFACE

Since its origins in the early decades of the twentieth century, the science of ecology has emphasized physical processes to account for the structure and organization of ecosystems. Photosynthesis is the basic energy transduction process of life and the primary productivity derived from it underlies all other biotic fluxes. Photosynthesis is supported by light, warmth and minerals and nourished by CO_2. It is thus understandable that the early generations of ecologists found compelling links between these drivers of primary productivity and the structure of ecosystems (Lindeman 1942, Odum 1957, Walter 1964, 1968, Holdridge 1967, Rosenzweig 1973, Whittaker 1975). Biogeography has followed in a parallel tradition of seeking understanding through the analysis of physical variables and processes: e.g., area, degree of isolation, elevation, and vicariance (Wallace 1860, Walter 1964, 1968, MacArthur and Wilson 1967, Croizat et al. 1976). Productivity in the sea has seemed even more tightly coupled to physical processes than vegetation on land, and oceanographers have accordingly devoted great attention to such processes as nutrient fluxes, temperature shifts, currents, upwelling, vertical mixing and convergences.

Physical parameters of the environment are easy to measure and obviously correlate with major features of the biological world, so it is natural that they were emphasized first. A century of studying the relationships between the physical and biological worlds has yielded a powerful science, able to predict such fundamental attributes of ecosystems as the productivity of aquatic and terrestrial ecosystems, the geographical extent of major biomes, responses to gradients in rainfall and elevation, latitudinal diversity gradients and much more (Whittaker 1975, but see Bond, this volume, Rosenzweig 1996).

Coexisting with the bottom-up flow of productivity-driven phenomena, is a top-down countercurrent. Products of photosynthesis are harvested by consumers and these, in turn, are eaten by predators. Predators reign at the top of the food chain and prey on consumers such as grazers, browsers, frugivores, and in the sea, the myriad life forms that feed on phytoplankton. But do predators eat *enough* consumers to make a difference at the producer level? Ecologists have been debating this question for decades. The question seems so simple, yet the answer has been exasperatingly elusive. But in the answer lies the key to how nature works, so the answer matters enormously, both as a matter of scientific understanding and as a point of departure for how to ensure the survival of biodiversity on earth.

If predators limit consumers, then the plants that constitute the producer level at the bottom of the food chain can flourish. This is the famous "green world" hypothesis of Hairston, Smith and Slobodkin (HSS, 1960). But if predators are able only to catch the sick and the weak and the old in prey populations, the prey (here referring to consumers) must be regulated from the bottom-up by their principal resources. But the world is obviously green, so how can this be true? The retort of bottom-up advocates is that much of that which is green in the world around us is either toxic or so lacking in nutritional value that it is inedible to consumers. In short, the world is green because so much of it is inedible (Ehrlich and Raven 1964, Murdoch 1966).

A parallel line of debate extends to the ocean margins where kelps and seagrasses are often the dominating features of shallow seascapes. Farther out to sea, across the vast surface waters of open oceans where photosynthesis occurs solely through phytoplankton, and in the dark abyssal realm where organisms obtain their energy through detrital fallout and chemosynthesis, alternatives to bottom-up control seem barely to have been considered. Despite the fact that most phytoplankton species are edible to a wide range of zooplankton, bottom-up regulation remains an article of faith among the vast majority of biological oceanographers.

To those ascribing to the view that much vegetation is inedible, or that rates of consumption are intrinsically exceeded by rates of production, the capacity of top-down forces to structure ecosystems has often been viewed with skepticism (Strong 1992, Polis et al. 2000). According to this point of view, strong top-down regulation is a curiosity or aberration, present in some circumstances but not in others, and overall, in the big picture, relatively unimportant.

Predation and other types of top-down forces (e. g., herbivory, parasitism) have been relegated to secondary status for the simple reason that bottom-up forcing processes have held an assumed but poorly supported position of primacy in controlling the distribution and abundance of species. However, regulatory processes at this level of nature ate difficult to evaluate through controlled experiments on appropriate scales of space and time. The experimental application of changes in temperature, nutrients, water, plant quality and all other purported bottom-up drivers at such scales are either infeasible or would be so prohibitively costly that they have and probably never will be attempted. As a consequence, most inferences concerning the role of bottom-up control are based on correlative evidence. Ttop-down processes are similarly difficult to study. The laws of thermodynamics require that predators are rare relative to their prey and that they range over much larger areas, rendering exclusion experiments difficult and expensive to implement. Consequently, most such experiments are conducted at the scale of a few square meters or less (Schmitz et al. 2000). Are such experiments going to convince anyone that orcas, great white sharks, wolves, tigers and jaguars are important? At best, such inference requires a leap of faith (Carpenter and Kitchell 1988).

Acceptance by scientists of the simple logic of HSS has therefore lagged. In part, scientists have been held back by their own cultural baggage – institutionalized skepticism, the existence of alternative hypotheses that have not been definitively ruled out and standards of evidence that exceed achievable limits. The native skepticism of science is most readily dispelled via rigorously controlled experiments. Yet, experiments on the scale necessary to study the predator-prey dynamics of large vertebrates have been beyond the capacity and the means of the scientific establishment in the US or anywhere.

These scaling challenges have been hindrance enough on land, but in the sea they have been insurmountable. Large marine predators such as great sharks, tuna and toothed cetaceans routinely track prey over hundreds or thousands of kilometers of open ocean. No experiments are possible here. But the fact that appropriate experiments are beyond the reach of investigators does not mean that the large predators of the sea are unimportant or that they should be ignored by ecologists. They present a challenge to the ingenuity of the investigator who must search the world for places, events or special circumstances that create "natural experiments" that could not be done in a planned or replicated fashion. Perhaps the evidence to be derived from such "experiments" is not as

airtight or repeatable as it would be from rigorously controlled and replicated treatments, but it is all we have or are likely to have in the foreseeable future as the basis for inferring how the world's largest ecosystem operates.

Biologists have recognized the central importance of predation since the mid-nineteenth century (Bates 1862, Müller 1879). But, in retrospect, it is now obvious that the green world hypothesis of HSS and an even earlier articulation of it by Charles Elton (1927) were ahead of its time. Many ecologists were convinced by the logic of the green world argument and conceded that HSS might be right, but there was no obvious way to put the idea to rigorous tests. Hairston, Smith and Slobodkin earned a tip of the hat in textbooks but, in an era of increasing reductionism, their thesis was put aside as unsubstantiated speculation.

Inspired by the insights of such distinguished forerunners as Charles Elton, Aldo Leopold, and HSS, a relative handful of ecologists sought to overcome the methodological handicaps inherent in the study of predator-prey systems through intensive investigations of systems that offered special tractability. Paine, in 1966, was the pioneer with his *Pisaster* removal experiment. The experiment was free of confounding variables and the results were dramatic. The experiment was immediately hailed as a landmark and enshrined in textbooks. But skepticism remained. Perhaps the results were attributable to a particularly powerful "keystone" predator; targeting by the predator of the dominant competitor in the prey community might have been a lucky factor that would not pertain to other systems; perhaps the space-limited system of the rocky intertidal zone created special conditions that did not apply to open systems; perhaps the results depended in some unknown way on the multi-stage life cycles of most of the organisms involved; and so on. Such lingering doubts caused many scientists to regard Paine's results as an isolated example without far-reaching relevance to how biological systems work in general.

A building consensus

Despite methodological handicaps, evidence corroborating key features of Paine's findings began to accumulate from carefully constructed case studies. Certainly the most dramatic and quotable of the early studies was the startling discovery by Estes and Palmisano (1974) of how Pacific kelp forests owe their existence to sea otters. Exuberant accounts of this signal breakthrough reverberated through the scientific and popular press, creating public awareness that biological interactions are important. Appearing in parallel with these early empirical investigations were seminal ideas that began to build a theoretical foundation under the concept of top-down regulation (Rosenzweig 1973, Fretwell 1977, Paine 1980, Okasanen et al. 1981). On the empirical side, Paine (1980) showed that food web dynamics were largely attributable to strong interactors, often referred to as "keystone" species, the starfish *Pisaster* being the prime example. The following year, Oksanen and his colleagues confirmed the existence of predicted abrupt state shifts driven by herbivory and predation on arctic productivity gradients (Oksanen et al. 1981). Soon after that, Schoener and Toft (1983) and Pacala and Roughgarden (1984) demonstrated that *Anolis* lizards could exert strong top-down control on spiders and herbivorous insects, respectively, on small West Indian islands. Close on the heels of these meso-scale terrestrial studies came the remarkable "whole ecosystem experiments" of Carpenter and Kitchell (1988, 1993). Predicted dramatic consequences to the

experimental removal or addition of the top trophic level from small lakes, again stirred the popular (and scientific) imagination.

Similar narratives now began to come in a rush from all types of ecosystems, from unbounded marine situations to fresh water streams and lakes, and from terrestrial systems from the arctic to the tropics. Here are some of the better-known examples.

- In the absence of top carnivores, white-tailed deer irruptions occurred over large portions of the eastern US with consequent suppression of hemlock recruitment in northern forests and oak recruitment in mid-latitude forests plus selective depletion of favored herbaceous plants (Alverson et al. 1988, McShea et al. 1997, Rooney et al. 2004).
- Cage experiments in tropical and temperate streams confirmed the structuring effects of top-down forcing and the importance of food chain length in determining whether autotrophs are enhanced or reduced by apex predators (Power 1990, Flecker 1992).
- Severe degradation of the vegetation of an oceanic island followed the reintroduction of a long-absent native herbivore (Campbell et al. 1991).
- The growth of balsam fir, as indicated by growth rings, is indirectly regulated by wolf predation on moose on Isle Royale (McLaren and Peterson 1994).
- Overharvest of fishes and invertebrates led to algal overgrowth of Jamacan coral reefs (Hughes 1994).
- Partial predator exclosures at a 1 km^2 scale in Yukon, Canada, resulted in a surge in snowshoe hare densities (Krebs et al. 1995).
- Mesopredator" release in coyote-free canyons of San Diego County, California, had strongly negative consequences for bird populations (Crooks and Soulé 1999).
- Decimation of the cod fishery on Newfoundland's Grand Bank was succeeded by an outbreak of sea urchins, dogfish, skates and lobsters (Worm and Myers 2003, Steneck et al. 2004, Frank et al. 2005).
- Parallel decimation of great sharks in US Mid-Atlantic coastal waters preceded an outbreak of mollusk-eating cow-nosed rays and the resulting collapse of estuarine shellfisheries (Myers et al. 2007).
- Aspen stands and riparian thickets in Yellowstone National Park declined after wolf extirpation (Ripple and Larsen 2000, Beschta 2005) and are recovering since wolf restoration (Ripple and Beschta 2007).
- Woody plant recruitment was suppressed by hyperabundant herbivores on predator-free islets in tropical Lago Guri, Venezuela (Terborgh et al. 2001).
- Vegetation was released on a remote oceanic island following local extirpation of a dominant herbivore (O'Dowd et al. 2003).
- Introduction of arctic foxes to islands in the Aleutian archipelago resulted in an ecosystem phase shift from grasslands to tundra (Croll et al. 2005).

As the number and variety of these case studies suggests, top-down forcing and its effects on lower trophic levels has not been overlooked by the scientific community, but it has been overshadowed by a dominant current of opinion that more was to be gained by investigating bottom-up forcing. A clear example of the secondary status afforded to top-down processes by funding agencies was the IBP (International

Biological Program?) of 1964-1974, a large US National Science Foundation-sponsored program of comparative research on ecosystems that emphasized measurements of climate, productivity, nutrient cycling, and other bottom-up processes. The current incarnations of big science programs in terrestrial ecology in the US are the Long-term Ecological Research (LTER) program. In marine science, the counterpart of these programs is GLOBEC (Global Ocean Ecosystem Dynamics). "The aim of GLOBEC is to advance our understanding of the structure and functioning of the global ocean ecosystem, its major subsystems, and its response to physical forcing, as the empirical foundation to be used in forecasting responses of the marine ecosystem to global change" (http://www.globec.org). In all these heavily funded programs, investigations of top-down processes have been relegated to a distant second place.

Single-minded focus on the role of bottom-up drivers has directed the flow of funding away from investigations of top-down processes, precluding even the most obvious experiments. For example, to date the US National Science Foundation has not sponsored any large-scale experiments designed to investigate the effect of predator removal on terrestrial ecosystems. The only US effort of which we are aware to control a mammalian predator on an ecologically significant scale was a coyote removal experiment, funded by a combination of state and private agencies, that used a 5 km^2 block design with replicates (Henke and Bryant 1999). The results demonstrated a powerful "Paine effect," as a 6-member rodent community collapsed to one dominant species, *Dipodomys ordii*. Deer irruptions in the eastern US motivated the U. S. Forest Service to install a series of 1 km^2 exclosures in Pennsylvania (Tilghman 1989). Neither of these experiments is well known to ecologists because both efforts were conducted by wildlife managers and published in the literature of that field. John Maron has a large-scale large-vertebrate experiment underway in western Montana but findings from that effort are as yet unpublished. We know of no other ≥kilometer scale experiments in the US, although a partial predator exclusion experiment conducted on a 1 km^2 block design has been implemented in Yukon, Canada (Krebs et al. 1995). These facts provide unequivocal testimony that top-down forcing has been systematically neglected by the agencies that fund basic science in the US.Lack of recognition and acceptance of the top-down countercurrent as a ubiquitous and fundamental structuring force in nature was felt by us to be retarding progress in ecological science at a crucial time when the stability of ecosystems all over he world is being threatened by multiple human interventions, not the least of which is the systematic elimination of top predators. If disrupting the trophic cascade were to lead to the dire consequences predicted by theory and anticipated by empirical studies (those cited above being but a sample), then many of the world's ecosystems would already be in serious trouble. Our deep anxiety at this prospect inspired us to organize a conference that was held at the White Oak Plantation in Yulee, Florida (USA) on February 7-10, 2008. For making our stay at the Plantation a memorable and pleasurable experience, we are most grateful to Tom Galligher, Troy Miller and the rest of the unfailingly friendly and helpful White Oak staff.   For sponsoring our stay at the Plantation, we express our deep gratitude to the Howard T. Gilman Foundation.

Our purpose in organizing this book was to elevate biotic forcing in ecology to what we believe is its proper place as coequal with physical forcing. The time for a synthesis is right. Evidence for top-down trophic cascades has been mounting, as indicated above, and has lately begun to snowball. The accumulated weight of this evidence has become overwhelming, as we shall demonstrate in the ensuing chapters. We hope that this book will be read by doubters and skeptics as well as the convinced, because we are confident that the theory, evidence, arguments and interpretations presented in it will open a new era in ecology.

We shall demonstrate that top-down forces interact with bottom-up forces through a dynamic balance and that this balance confers structure on ecosystems and ultimately regulates their species composition and diversity. Because of the huge historical disparity in funding and, consequently, scientific attention given to investigating bottom-up vs. top-down processes, understanding of how top-down forces operate via all their myriad and intricate pathways lags far behind. Temperature, moisture, production potential, and the serendipitous constraints of history set broad limits to the distribution and abundance of species. Yet beyond these rather obvious macroscale agents of physiological tolerance, as we shall stress, it is the operation of top-down forces that regulates and sustains biodiversity on our planet.   For this reason alone, the scientific community should focus much greater attention on top-down processes and their stabilizing effects on natural ecosystems.

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