



University
of Victoria

Distinguished Women Scholars Lecture

The Distinguished Women Scholars Lecture series was established by the Vice-President Academic and Provost to bring distinguished women scholars to the University of Victoria.



Dr. Ruth Gates

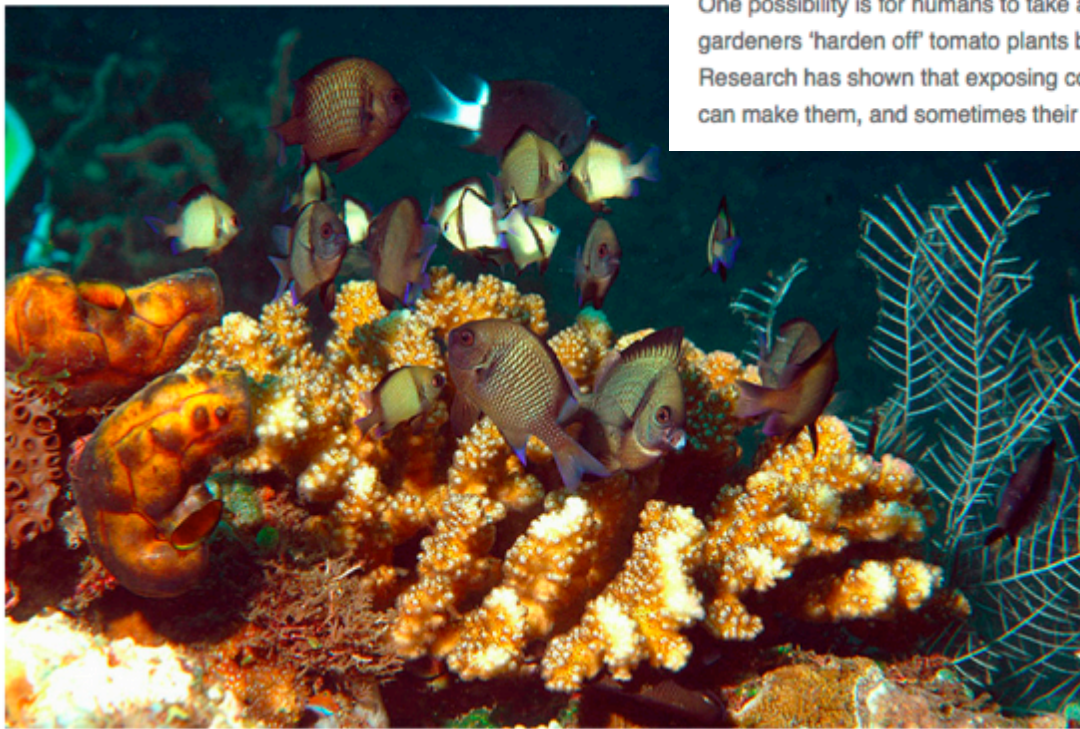
Gates Lab, Hawaii Institute
of Marine Biology
University of Hawaii at Manoa

The Wonderful World of Corals: Harnessing Basic Science to Address an Ecological Crisis

Wednesday, 25 February, 7:00 p.m.
Bob Wright Centre, Room B150

Sponsored by the **Department of Biology**

Coral Reefs in Hawaii and across the globe continue to decline in health due to intensifying climate change, resource extraction, and pollution. Although the future looks bleak, some corals and reefs are not only surviving but also thriving in conditions that kill others. Dr. Gates, a world renowned coral expert, unveils the complex biology that underpins this natural variation in response. She then discusses how this knowledge can be harnessed to develop tools that build resilience on reefs and arrest and improve the prognosis for coral reefs.



One possibility is for humans to take a more active role in acclimatizing corals to warmer waters, much as gardeners 'harden off' tomato plants by moving them outside for gradually longer periods in the spring. Research has shown that exposing corals to stressful but not lethal conditions such as heat or bright light can make them, and sometimes their offspring, better able to tolerate such stresses in the future.

TO ENSURE REEF SURVIVAL, HACK THE CORALS?

February 17, 2015 | Conservation This Week | 0 Comments

The past several decades have been tough on the world's coral reefs. Warming waters, ocean acidification, invasive predators, and toxic runoff have hammered these iconic hotspots of underwater biodiversity.

In response, conservationists have developed coral 'gardens' where young corals are reared to help rebuild damaged reefs. But some scientists worry that existing restoration strategies won't match the pace and magnitude of the threats these animals face.

In a paper published February 2 in the *Proceedings of the National Academy of Sciences*, biologists from the Australian Institute of Marine Science and the Hawaii Institute of Marine biology propose a more radical approach, which they call assisted evolution.

<http://conservationmagazine.org/2015/02/to-ensure-reef-survival-hack-the-corals/>

Week 7:

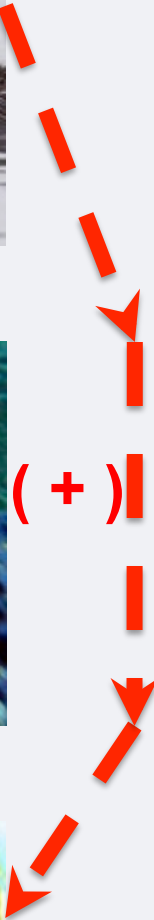
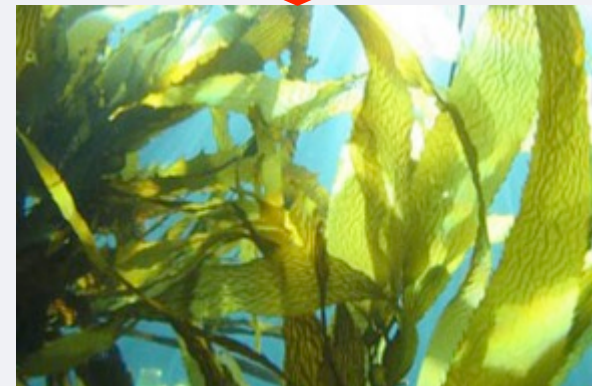
Food Chains and Food Webs



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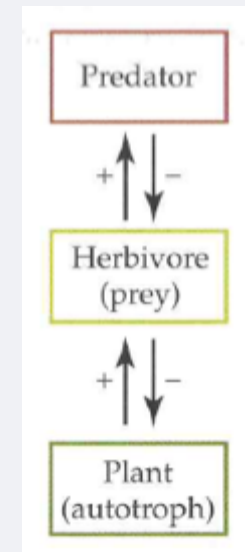
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Recommended Reading for this Week:

Mittelbach 2012 Community Ecology – Ch. 11

The “World is Green Hypothesis”

- (1) In the absence of higher level predation, carnivores should be limited by competition for their food (herbivores)
 - (2) Herbivore populations should be held below their carrying capacity and have little impacts on their food (plants)
 - (3) In the absence of control by herbivores, plants should be dense and limited by competition
- Conclusion: ‘Populations in different trophic levels are expected to differ in their methods of control’*



-HSS (Hairston, Smith, Slobodkin) 1960
Community structure, population, control, and competition. *American Naturalist*.

What determines abundances at different trophic levels?

EXPLOITATION ECOSYSTEMS IN GRADIENTS OF PRIMARY PRODUCTIVITY

LAURI OKSANEN,* STEPHEN D. FRETWELL,† JOSEPH ARRUDA,† AND PEKKA NIEMELÄ*

*Kevo Subarctic Research Institute, University of Turku, SF-20500 Turku 50, Finland; †Division of Biology, Kansas State University, Manhattan, Kansas 66506

Submitted October 17, 1978; Revised November 5, 1979; Final Revision December 9, 1980; Accepted January 12, 1981

Formal studies on trophic exploitation can be traced back to the Lotka-Volterra predation models summarized by Gause (1934). Since Rosenzweig and MacArthur (1963) included the resource-determined carrying capacity of prey in predation models, the development of these models has been rapid. Holling's (1965) study showed how the saturation of predators can be included and Rosenzweig (1969, 1971) related the shape of the prey-predator curve to the productivity and other changes

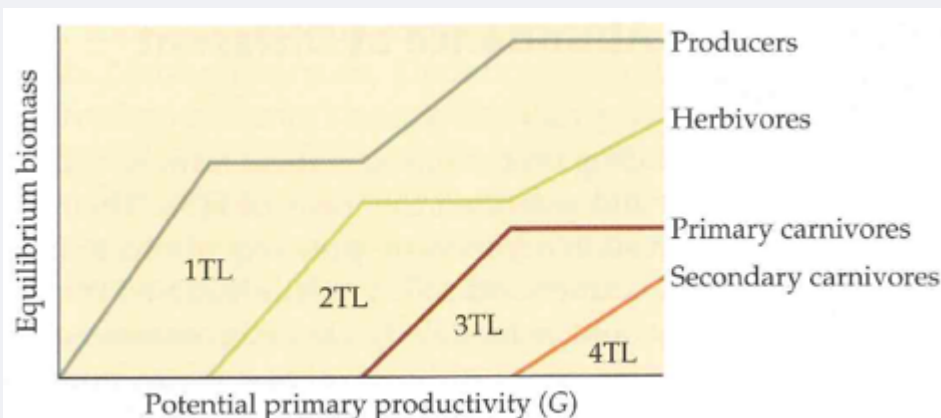


Figure 11.2 The predicted change in equilibrium biomass of different trophic levels in response to a change in potential primary productivity (G). These predicted responses are based on the model of Oksanen et al. (1981), which assumes that increases in potential productivity permit the addition of higher trophic levels (TLs). Complexities arising due to unstable consumer-resource interactions are ignored in this simplified treatment. (After Mittelbach et al. 1988 and Leibold 1989.)

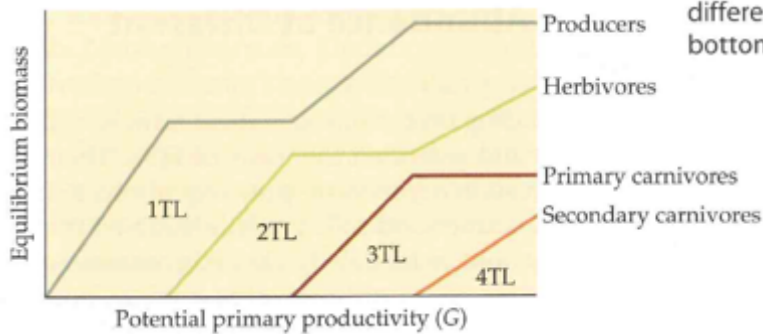
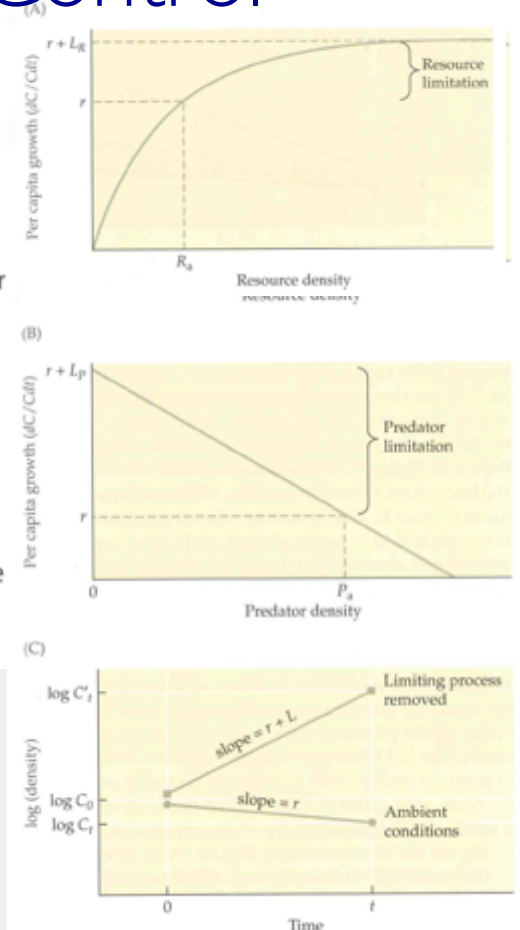
Oksanen et al. applied consumer-resource equations to interacting trophic levels. They modeled food chains as linked consumer-resource interactions.

1. Model predicts: positive correlation between potential primary productivity and # of trophic levels
2. Model predicts: that whether a trophic level responds to an increase in potential productivity depends on the number of trophic levels in the system, and that adjacent trophic levels will show an alternating pattern of response (ODD vs EVEN).
3. Appears to support HSS's argument of different control by trophic level, but in fact the equilibrium biomass at each level below the top trophic level reflects the balance between the effects of predation and competition....

Effects of Predator and Resource (competition) Limitation

Top-down and Bottom-up Control

Figure 11.3 Graphic representation of the concepts of (A) resource limitation, (B) predator limitation, and (C) the assessment of limitation. (A) Per capita growth of the consumer population increases with resource density and is equal to r under ambient conditions (i.e., when $R = R_a$) and to $r + L_R$ in the absence of resource limitation (L_R). The difference between per capita consumer growth rates r and $r + L_R$ is a measure of resource limitation. (B) Per capita growth of the consumer population declines as predator density increases. The difference between per capita consumer growth rate in the absence of predators ($r + L_P$) and per capita consumer growth rate at ambient predator density (P_a) is a measure of predator limitation. (C) Limitation can be estimated with short-term field experiments as the difference between per capita growth under natural conditions (r) and under the conditions in which the focal (limiting) process has been removed ($r + L$)—that is, the difference between the slopes of the two lines in the bottom panel. (After Osenberg and Mittelbach 1996.)



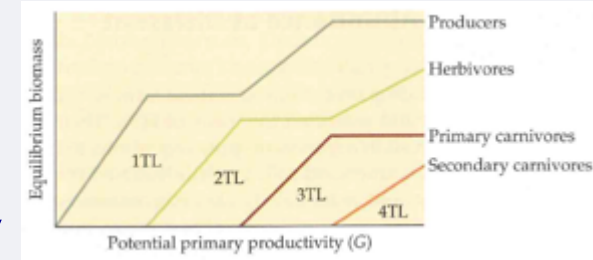
Although Oksanen et al.'s stepped response pattern appears to support HSS's hypothesis that competition and predation alternate in importance in controlling trophic levels, a more accurate assessment is that each trophic level below the top one is simultaneously limited by competition and predation.

Initial attempts to characterize regulation as top-down versus bottom-up presented a false dichotomy; the relative strengths of predator limitation and resource exploitation may vary with trophic level and ecosystem productivity.

Testing Model Predictions

I. Effects of productivity on trophic level abundances:

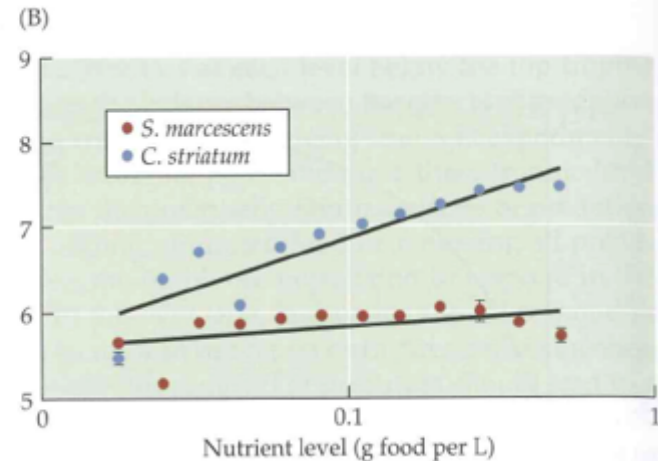
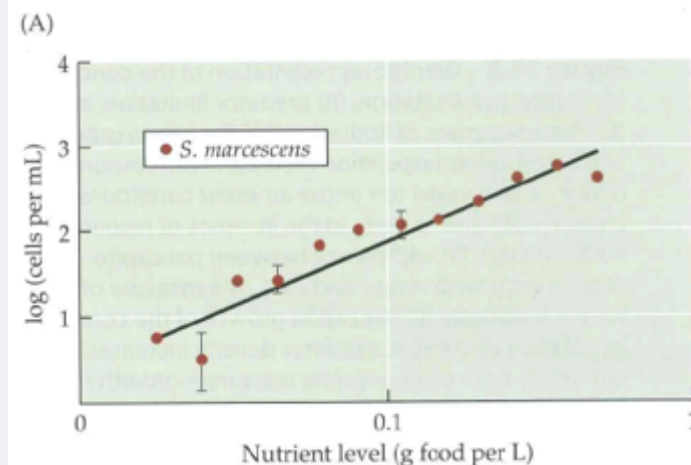
An increase in primary productivity will increase abundance of the top trophic level and at alternating trophic levels below the top level



A Laboratory Microcosm Test:

- microbial Communities w. 1 and 2 trophic levels

Figure 11.4 One- and two-trophic-level food chains respond differently to an increase in resources in a laboratory microbial community. (A) In the absence of predators, the abundance of the bacterium *Serratia marcescens* increases directly with an increase in the amount of resources. (B) In a two-trophic-level system, an increase in resources leads to an increase in the abundance of the bacterium's predator (the ciliate protozoan *Colpidium striatum*), but no change in the abundance of *S. marcescens*. (After Kaunzinger and Morin 1998.)



Testing Model Predictions

I. Effects of productivity on trophic level abundances:

An increase in primary productivity will increase abundance of the top trophic level and at alternating trophic levels below the top level

A Field Test:

- experimental enclosures in Eel River, California
- predators (small fish, dragonflies) – herbivores (mayfly nymphs, snails) – basal resource (algae)
- trophic level biomass in enclosures responded as predicted:

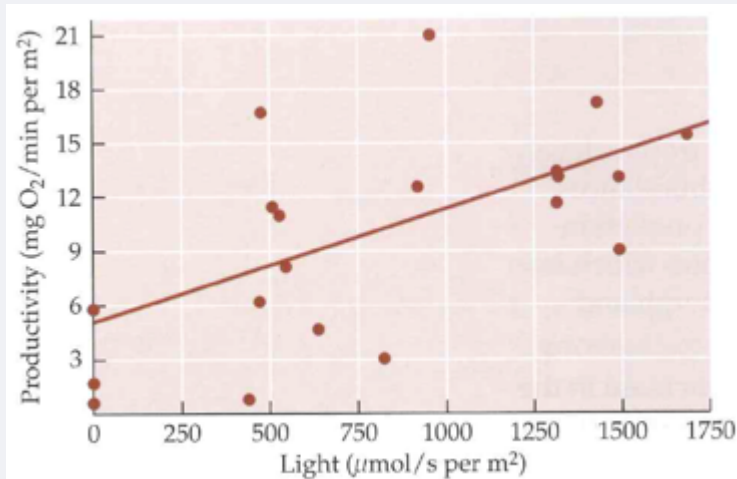


Figure 11.5 Shading of experimental enclosures in northern California's Eel River limited the productivity of algae on the stream bottom. Primary productivity in these systems was directly related to the amount of light transmitted to the stream. (After Wootton and Power 1993.)

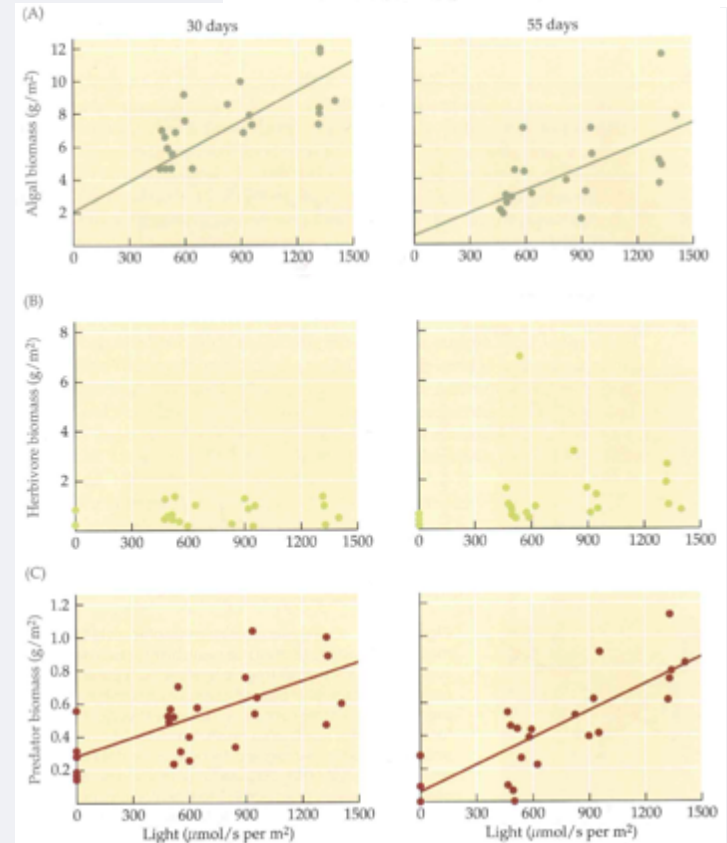
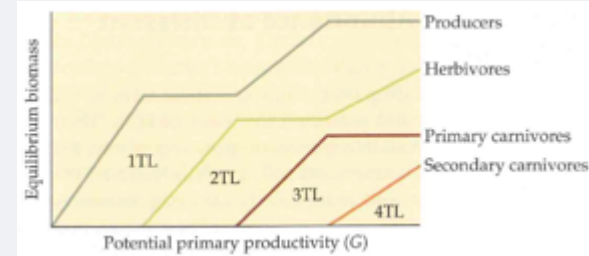


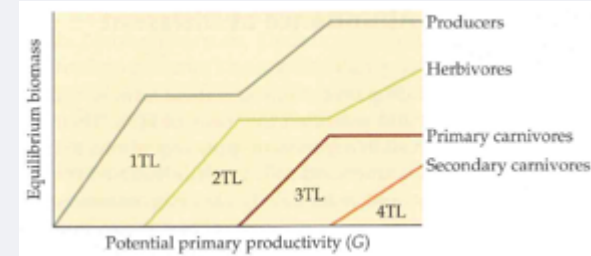
Figure 11.6 Trophic levels in a three-trophic-level food chain in the Eel River responded differently to increased primary productivity brought about by changes in resource (light) availability. The biomass of the bottom and top trophic levels (algae and predators, respectively; A and C) increased with increasing light availability, but the abundance of the middle trophic level (herbivores; B) did not change. This differential trophic level response is consistent with predictions of Oksanen et al.'s 1981 model (see Figure 11.2). The stability of the patterns after 30 and 55 days indicates that the system is in steady-state, although there is a suggestion of an increase in herbivore abundance with increasing resources after 55 days. Regression lines show significant relationships. (After Wootton and Power 1993.)

Testing Model Predictions

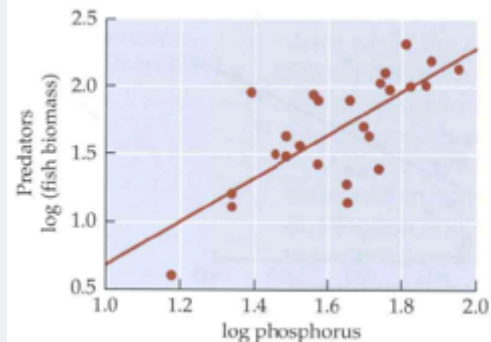
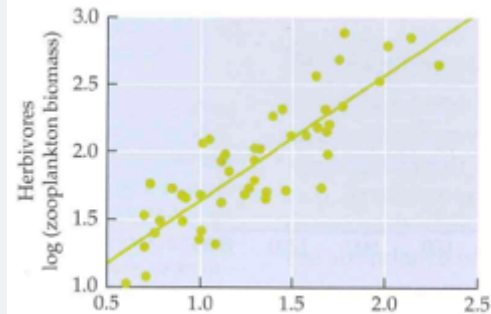
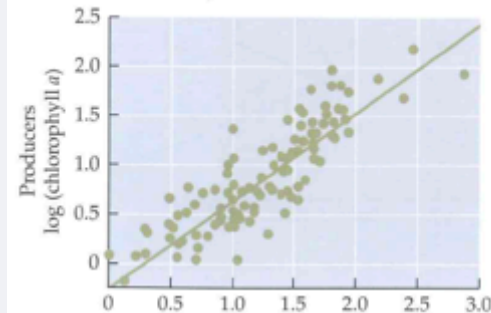
I. Effects of productivity on trophic level abundances:

An increase in primary productivity will increase abundance of the top trophic level and at alternating trophic levels below the top level

Many empirical results do NOT match the model predictions



(A) Three trophic levels



(B) Two trophic levels

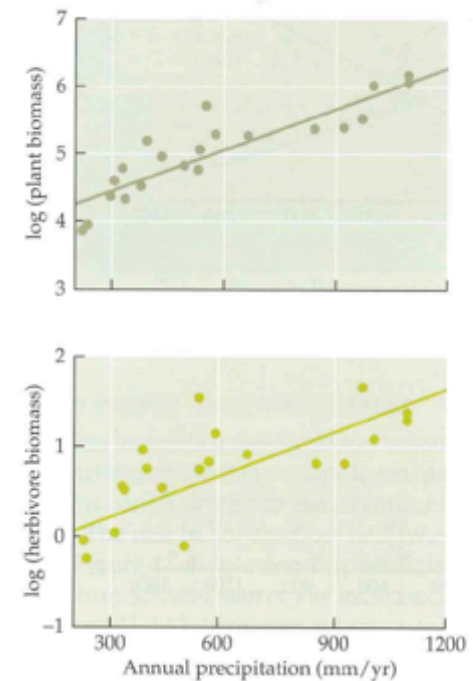
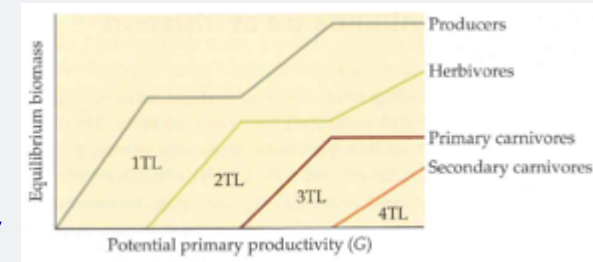


Figure 11.7 Correlations between trophic-level biomass and measures of resource availability in two natural systems indicate that all trophic levels show a pattern of positive response to increased resources, in contrast to the predictions of simple consumer–resource theory. (A) Data for three trophic levels from North American lakes in which phosphorus limits primary productivity. Each data point represents a single lake. (B) Data for plants and herbivores on North American grasslands where annual precipitation limits primary productivity. Each data point represents a grassland. (A after Ginzburg and Akçakaya 1992; B after Chase et al. 2000.)

Testing Model Predictions

I. Effects of productivity on trophic level abundances:

An increase in primary productivity will increase abundance of the top trophic level and at alternating trophic levels below the top level



Why? Examine which types of species respond to increases in productivity and which do not:

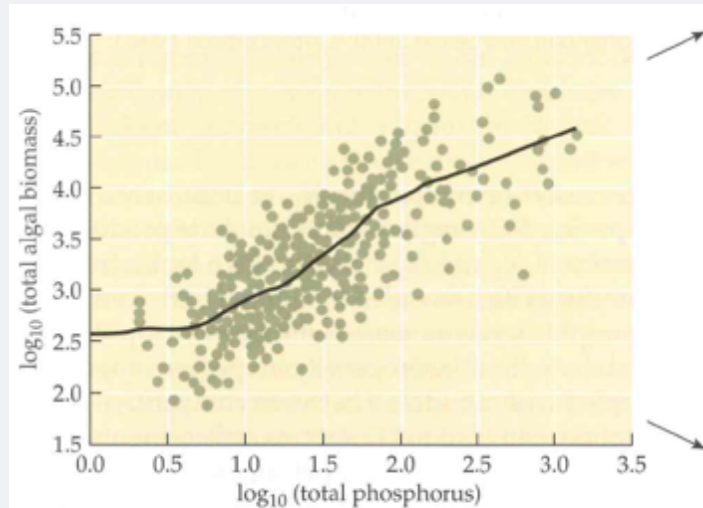
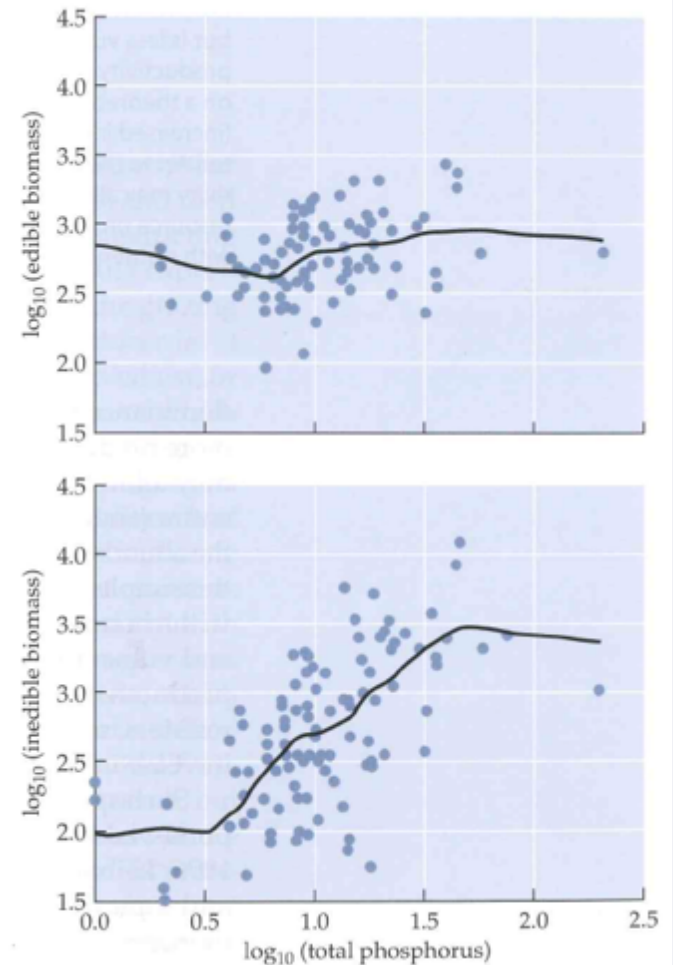


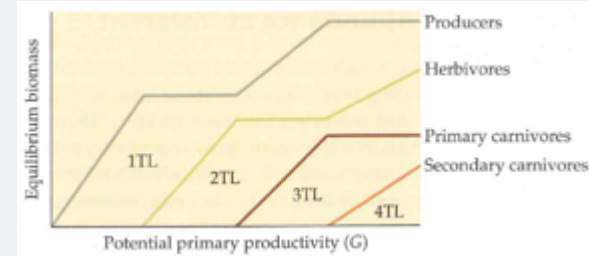
Figure 11.8 The overall positive relationship between phosphorus availability and total algal biomass in lakes (left-hand graph) has two separate components. Algal species small enough to be consumed by herbivores ("edible biomass"; above right) show no increase in abundance with increasing phosphorus input, whereas large, grazer-resistant algae ("inedible biomass"; below right) increase in abundance as phosphorus levels increase. All units are $\mu\text{g/L}$; the curve is fitted by LOWESS ("locally weighted smoothing") regression algorithms. (After Watson et al. 1992.)



Testing Model Predictions

1. Effects of productivity on trophic level abundances:

An increase in primary productivity will increase abundance of the top trophic level and at alternating trophic levels below the top level



Diamond Shaped Food Web:

Implication: Heterogeneity in species composition within a trophic level coupled with a trade-off between competitive ability and vulnerability to predation can lead to:

- 1) Species replacements along productivity gradients (from good competitors to good predator resistors)
- 2) Increases in Ns of all trophic levels with increases in primary productivity

Evidence of such species turnover from ponds, lakes, streams, grasslands – more predator-resistant species predominate in more productive systems.

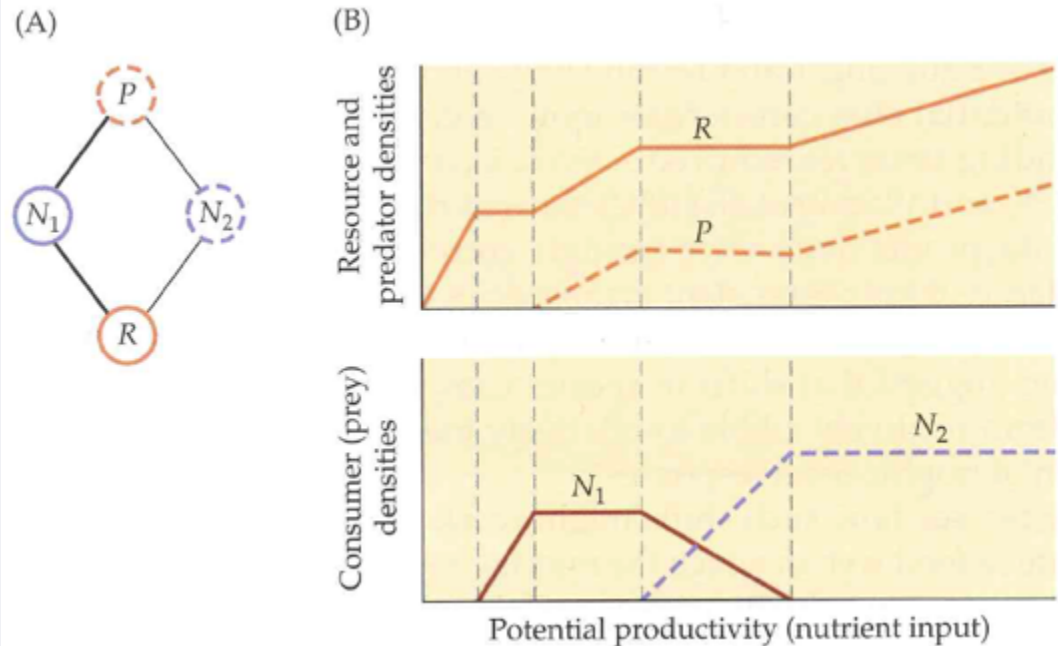


Figure 11.9 (A) An example of keystone predation, in which two prey types (N_1 and N_2) share a resource (R) and a predator (P) and there is a trade-off in the prey species' competitive ability and vulnerability to predation. The thick lines linking N_1 to R and P indicate that N_1 is a better competitor for resources and is more vulnerable to predation, whereas the thin lines linking N_2 to R and P indicate that N_2 is a poorer competitor but is less vulnerable to predation. (B) The predicted effect of an increase in potential productivity on the abundances of resources (R), prey (N_1 , N_2), and predators (P), based on a theoretical model of the diamond-shaped food web. An increase in productivity (increased input of resource R) leads to a shift in dominance from the better competitor, N_1 , to the more predator-resistant species, N_2 . A region of intermediate productivity may allow for the coexistence of N_1 and N_2 . Looking across the entire range of resource productivities, we see that the abundance of all three trophic levels increases with nutrient input. (A after Bohannan and Lenski 2000; B after Leibold 1996.)

Testing Model Predictions

1. Effects of productivity on trophic level abundances:

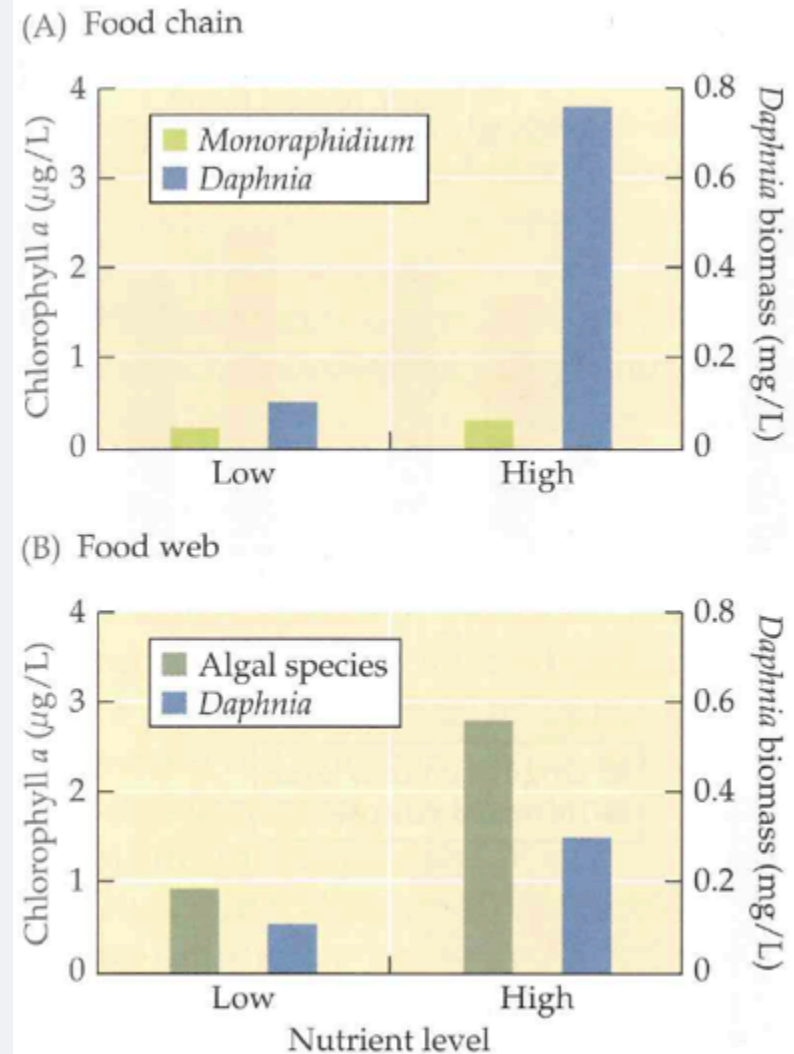
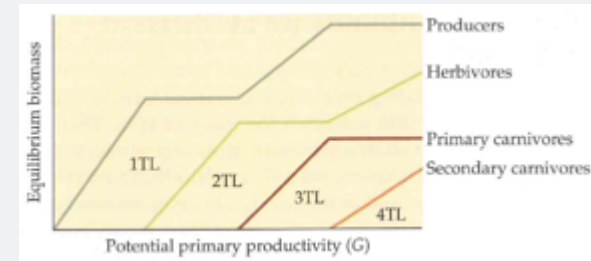
An increase in primary productivity will increase abundance of the top trophic level and at alternating trophic levels below the top level

A laboratory test of whether food chains (single algal species) and food webs (multiple algal species) respond differently to increases in productivity:

Figure 11.10 Trophic-level biomass responds differently to nutrient inputs in food chains and in food webs. In Steiner's laboratory microcosms, food chains included only a single species of algae (*Monoraphidium*) and a single species of herbivorous zooplankton (*Daphnia*), whereas a food web comprised *Daphnia* and a mixture of multiple algal species, some edible and some relatively inedible. (A) The food chain system responded as predicted by Oksanen et al.'s (1981) model: nutrient addition had little effect on average algal biomass at the end of the experiment, but resulted in a dramatic increase in average herbivore biomass. (B) In the food web, both the algae and the herbivore increased in average biomass with increased nutrient input. Note that the size of *Daphnia*'s response to nutrient addition was less in the food web than in the food chain, which is expected if the composition of the producer trophic level is shifted towards less edible species at high nutrient concentrations (After Steiner 2001.)

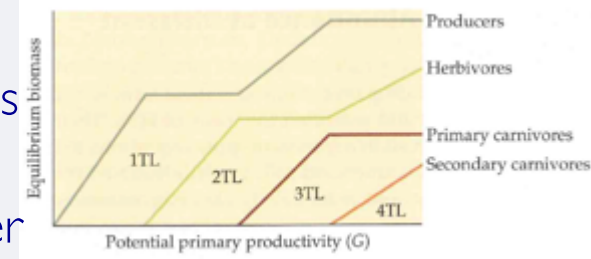
Overall conclusion: Shifting species composition within a trophic level* can prevent predator control and maintain the importance of resource limitation, even in high-nutrient systems.

*or other mechanisms: invulnerable life stages, adaptive foraging, omnivory...



Testing Model Predictions

2. Trophic Cascades: A reduction in abundances of populations at the top trophic level will lead to an alternating increase and decrease in the abundances of population at sequentially lower trophic levels.



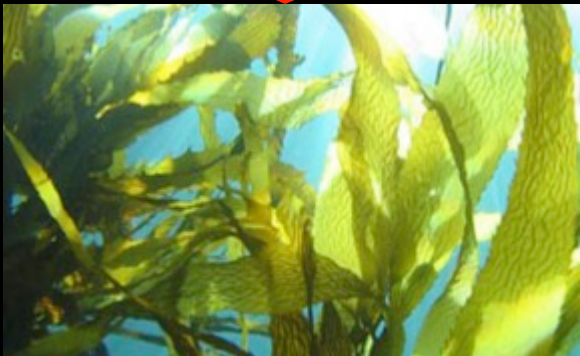
Trophic Cascade



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Estes & Palmisano 1974;
Estes *et al.* 1998

Testing Model Predictions

2. Trophic Cascades: A reduction in abundances of populations at the top trophic level will lead to an alternating increase and decrease in the abundances of population at sequentially lower trophic levels.

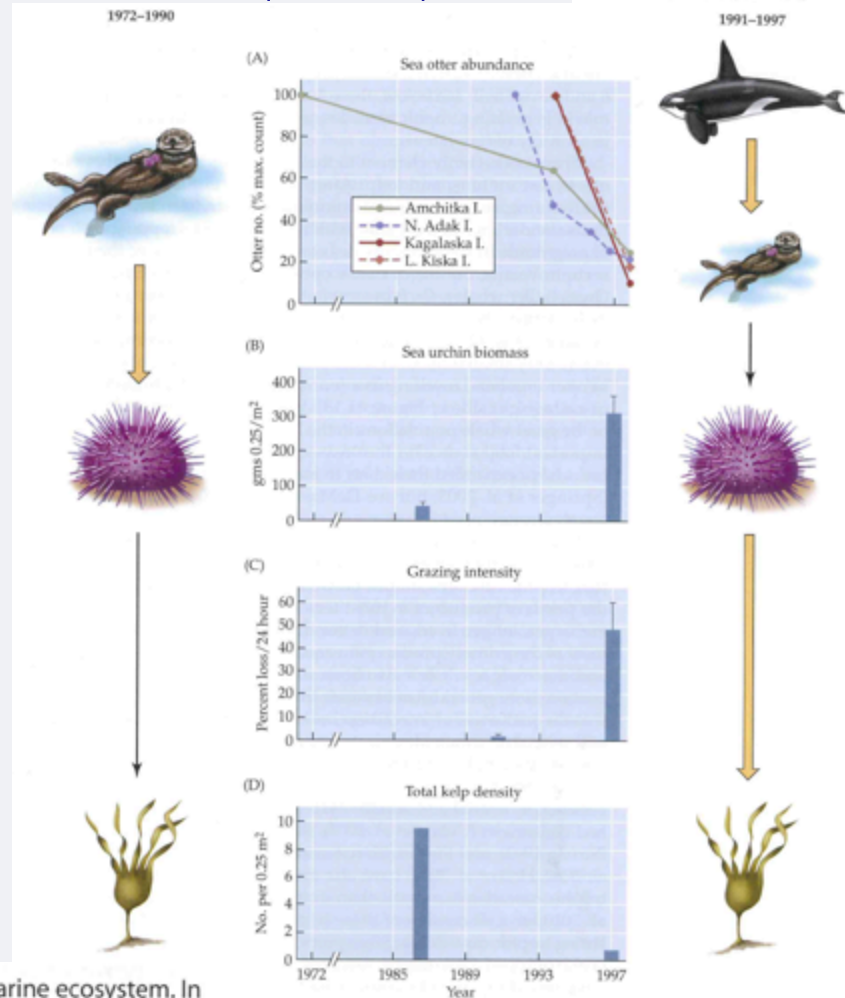
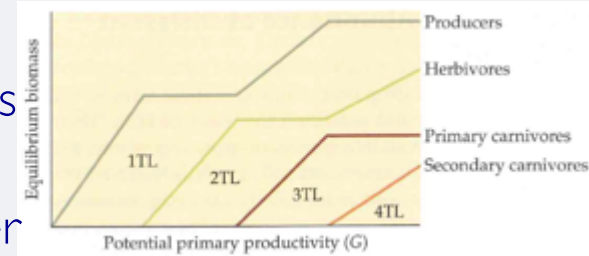


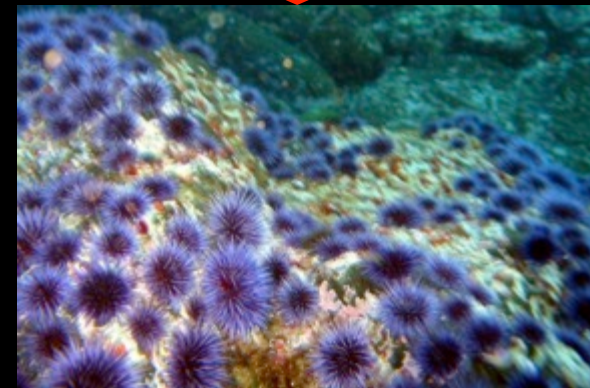
Figure 11.13 Examples of strong trophic cascades in a nearshore marine ecosystem. In the 1970s, abundant sea otter populations along the Aleutian Islands limited the numbers of sea urchins, reducing urchin grazing intensity and promoting dense stands of kelp (left). However, what appears to be a shift in the foraging behavior of a small number of orcas (killer whales) in the 1990s led to a dramatic decline in sea otter numbers, an increase in urchin biomass and urchin grazing, and a decline in kelp (right). (After Estes et al. 1998.)

Trophic Cascade

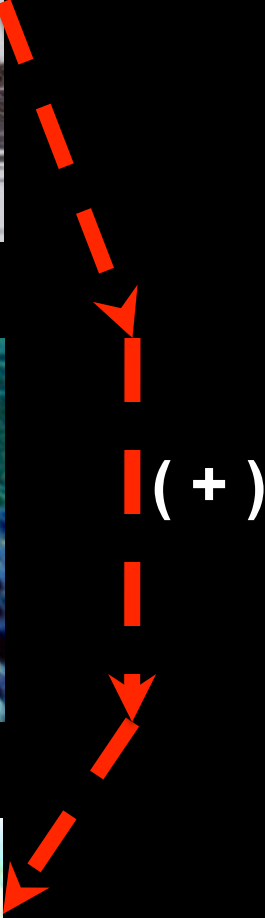
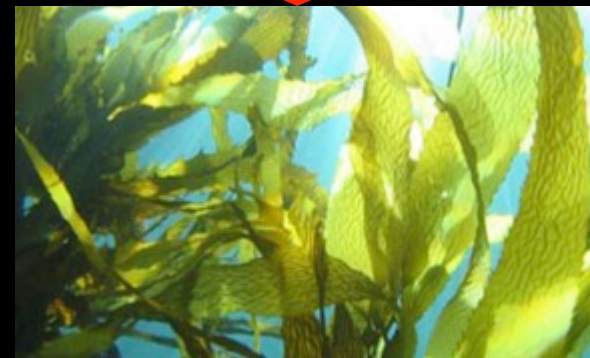
Mesopredator Release



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Crooks & Soulé 1999

Estes & Palmisano 1974;
Estes *et al.* 1998

Testing Model Predictions

2. Trophic Cascades: A reduction in abundances of populations at the top trophic level will lead to an alternating increase and decrease in the abundances of population at sequentially lower trophic levels.

Ecology, 73(3), 1992, pp. 747–754
© 1992 by the Ecological Society of America

ARE TROPHIC CASCADES ALL WET? I DONOR-CONTROL IN SPECIOS

DONALD R. STRONG

Are there real differences among aquatic and terrestrial food webs?

Jonathan

REPORT

Ecologists have long recognized the importance of predators in structuring both aquatic and terrestrial ecosystems^{1,2}. However, since the inception of these hypotheses, there has also been considerable controversy surrounding the importance of predators relative to other limiting factors (e.g. resources and abiotic stresses). To disentangle these effects, modern ecologists rely on manipulative experiments³. Although experimental studies have facilitated insight into the detail and mechanisms that underlie the inner workings of a particular system, they have also meant that ecologists have inevitably specialized on studying a particular type of ecosystem (such as aquatic

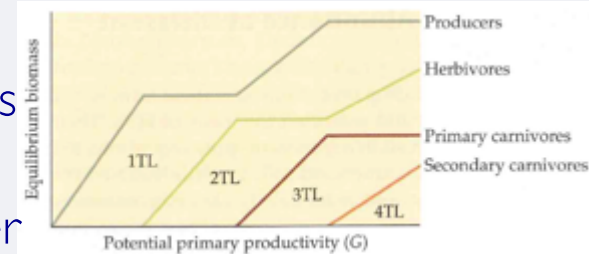
Recently, aquatic ar have put forward regarding similarit food-web structuri these ecosystem ty these hypotheses e: down effects and ti be less common aquatic ecosyst theoretical or empir to support or refu Many unanswered c potential differenc types: progress v studies designed wi that allows for moi

Jonathan Chase is at the and Pymatuning Laborat Pittsburgh, Pittsb

Jonathan B. Shurin^{1*}, Elizabeth T. Borer², Eric W. Seabloom¹, Kurt Anderson², Carol A. Blanchette², Bernardo Broitman², Scott D. Cooper² and Benjamin S. Halpern²

¹National Center for Ecological Analysis and Synthesis, University of California- Santa Barbara, 735 State St., Suite 300, Santa Barbara, CA 93101, USA

²Department of Ecology,



Trophic cascades revealed in diverse ecosystems

Michael L. Pace, Jonathan J. Cole, Stephen R. Carpenter and James F. Kitchell

ew studies are documenting trophic cascades in theoretically unlikely systems such as tropical forests and the open an. Together with increasing evidence

complexity, types tors or the trophic sumers. It is possib cascades are less

Ecology Letters, (2002) 5: 785–791

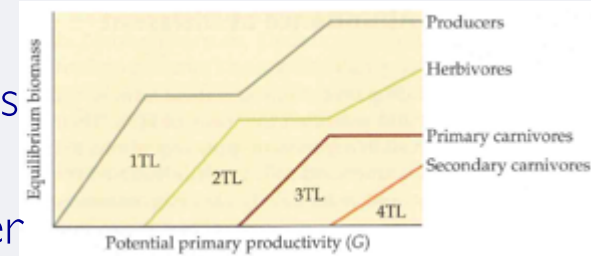
A cross-ecosystem comparison of the strength of trophic cascades

Abstract

Although trophic cascades (indirect effects of predators on plants via herbivores) occur in a wide variety of food webs, the magnitudes of their effects are often quite variable. We compared the responses of herbivore and plant communities to predator manipulations in 102 field experiments in six different ecosystems: lentic (lake and pond), marine, and stream benthos, lentic and marine plankton, and terrestrial (grasslands and agricultural fields). Predator effects varied considerably among systems and were strongest in lentic and marine benthos and weakest in marine plankton and terrestrial food webs. Predator effects on herbivores were generally larger and more variable than on plants, suggesting that cascades often become attenuated at the plant-herbivore interface. Top-down control of plant biomass was stronger in water than on land; however, the differences among the five aquatic food webs were as great as those

Testing Model Predictions

2. Trophic Cascades: A reduction in abundances of populations at the top trophic level will lead to an alternating increase and decrease in the abundances of population at sequentially lower trophic levels.



Although the weight of the evidence suggests top-down effects are more pronounced in aquatic than in terrestrial ecosystems, trophic cascades are commonly found in both habitats.

-Some of best terrestrial examples not included in the meta-analyses

Trophic cascades provide strong evidence for the importance of top-down processes, but the existence of a trophic cascade says little about the relative importance of predator limitation vs. resource limitation

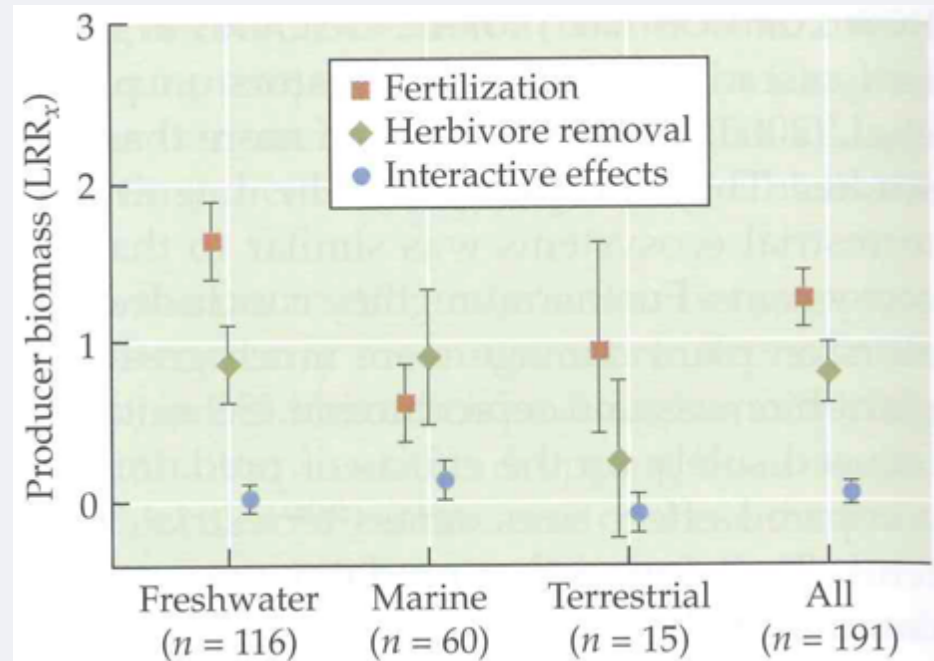
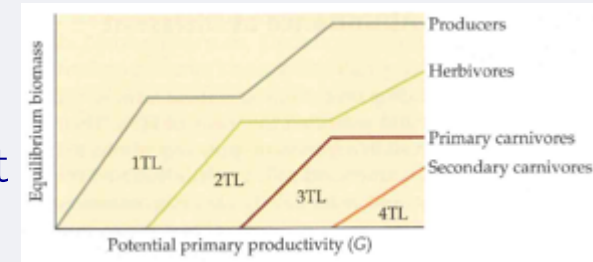


Figure 11.14 Results of a meta-analysis of 191 factorial manipulations (cross-classified for all possible combinations of fertilization and herbivore removal) show that herbivores and nutrients control plant community biomass to similar degrees across freshwater, marine, and terrestrial systems, and that these two processes act together in an additive fashion (i.e., interactive effects were minimal). LRR (natural log response ratio) measures effect size of fertilization or herbivore removal or their interaction on plant biomass. (After Gruner et al. 2008.)

Testing Model Predictions

3. Food Chain Length: An increase in potential productivity should lead to an increase in the number of trophic levels that can be supported in an ecosystem



What limits the length of food chains in nature?

1. ENERGY LIMITATION HYPOTHESIS: E lost in transfer between trophic levels, thus FCL should be ltd by available energy

Little evidence that resource availability and FCL are positively correlated in nature (minimum threshold)

2. DYNAMIC STABILITY HYPOTHESIS: based on prediction that longer food chains are less resilient to disturbance, thus disturbance should limit FCL

Minimal support for role of disturbance in determining FCL in natural systems.

3. ECOSYSTEM SIZE HYPOTHESIS: food chains longer in larger ecosystems (greater total area)

because these support more individuals and hence more species

Best Supported (lakes and streams, and on islands)

4. PRODUCTIVE SPACE HYPOTHESIS: ecosystem size \times productivity (per unit size)

Some support



What's Next:

Week 7 (February 23-27th) - Trophic interactions

M: Skills Tutorial 6 - Diversity indices in R

T: L - Food chains and food webs, top down vs. bottom up control

W: D - Top down control and trophic cascades - Led by Gillian & Owen

Required Reading:

- *Hairston et al. 1960 Community structure, population control, and competition. American Naturalist.*
- *Estes et al. 2011 Trophic downgrading of planet earth. Science.*

F: P - Mesopredator release - Led by Brynlee & Amanda

Required Reading:

- *Prugh et al. 2009 The rise of the mesopredator. Bioscience*



diversity_statistics.pdf
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hairston_etal_1960.pdf
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estes11topconsumerloss.pdf
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What determines abundances at different trophic levels?

Oksanen et al. applied consumer-resource equations to interacting trophic levels. They modeled food chains as linked consumer-resource interactions. This model predicts that whether a trophic level responds to an increase in potential productivity depends on the number of trophic levels in the system, and that adjacent trophic levels will show an alternating pattern of response.

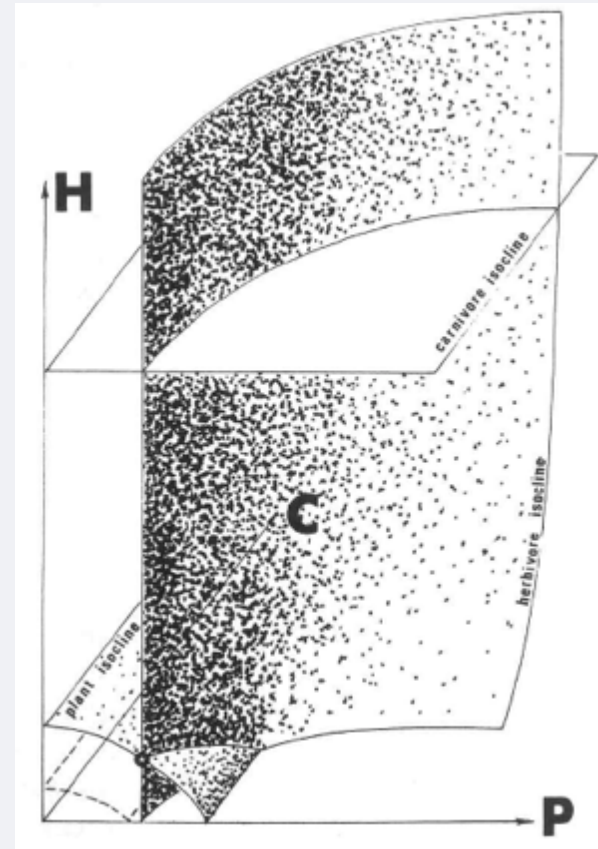
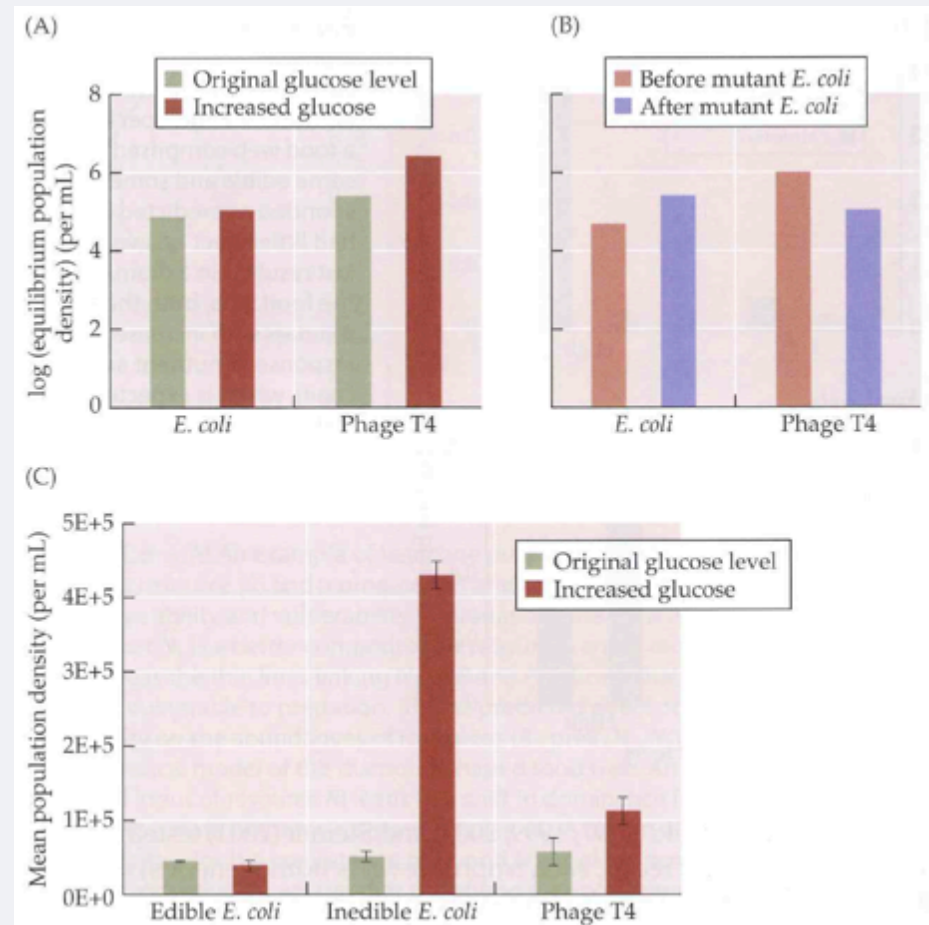


Figure 11.1 An example of a three-dimensional isocline plot showing the equilibrium biomass of three trophic levels (plant, herbivore, and carnivore abundances) in a system of linked consumer–resource populations. (From Oksanen et al. 1981.)

Species Composition and Nutrient Input

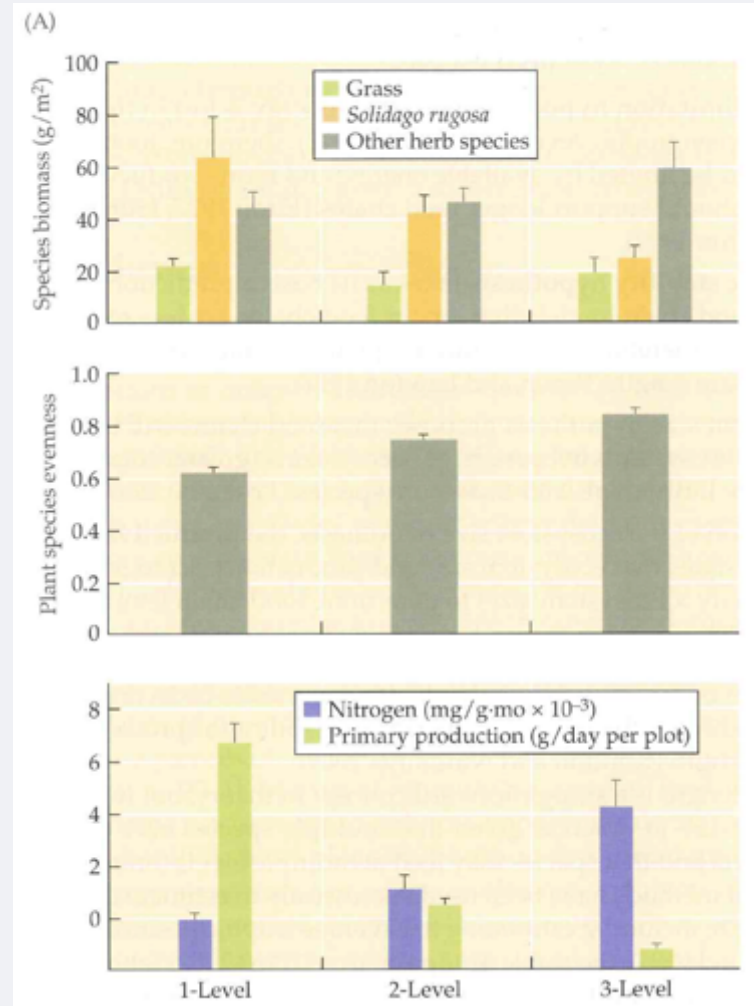
Shifting species composition within a trophic level can prevent predator control and maintain the importance of resource limitation, even in high-nutrient systems.

Figure 11.11 Bohannan et al. performed experiments with a simple microbial food chain maintained in continuous-culture chemostats, with glucose as the resource for the bacterium *E. coli* (the prey) and the bacteriophage T4 as the predator. (A) The experimental system responded to an increase in glucose as predicted by a two-link food chain model—that is, predator abundance increased while prey abundance remained nearly constant. (B) When phage-resistant mutants of *E. coli* arose spontaneously, bacterial abundance increased and phage abundance decreased. (C) Over time, phage-resistant *E. coli* came to dominate the bacterial population, at which point *both* trophic levels responded positively to increased glucose. The invasion of the phage-resistant bacteria thus changed the dynamics of the system from that of a food chain to that of a food web. (After Bohannan and Lenski 1997, 1999.)



Trophic Cascades and Nonconsumptive (trait-mediated) Effects

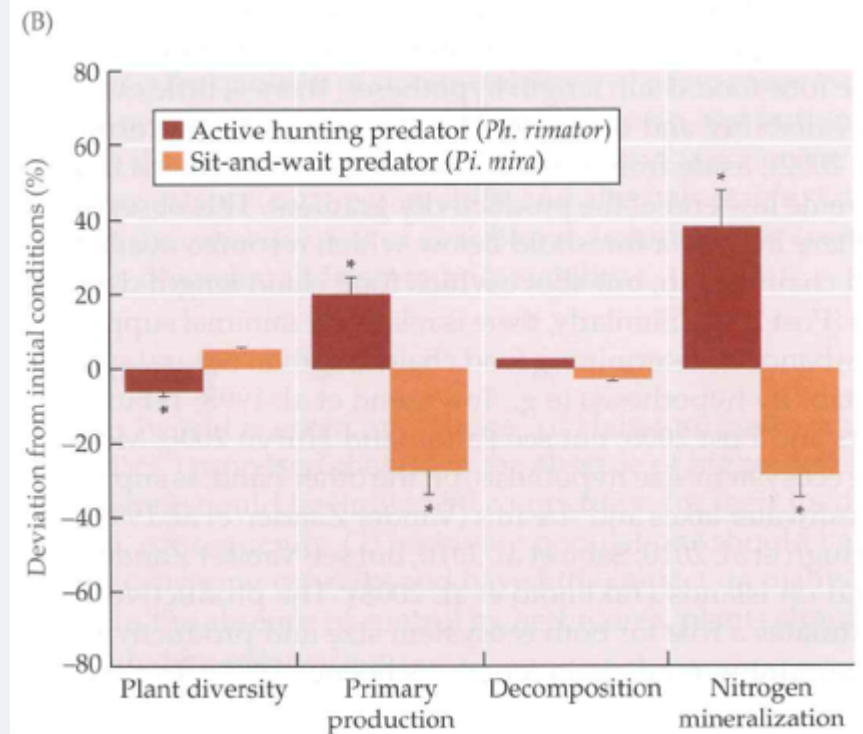
Figure 11.15 Behavioral responses to predators can lead to strong cascading effects. The spider *Pisaurina mira* is a sit-and-wait predator whose presence causes grasshoppers to switch from feeding on their preferred plant species (a grass, *Poa pratensis*) to feeding on goldenrod (*Solidago rugosa*). Because *S. rugosa* is competitively dominant, the net result of the predator-induced shift in herbivore foraging behavior is a change in plant diversity and productivity. (A) In the absence of *P. mira* (a two-trophic-level system), *S. rugosa* is abundant in the plant community. But in the presence of the spider (a three-level system), grasshoppers suppress the growth of *S. rugosa*, reducing its competitive effect on other plant species, and thus increasing plant diversity (measured as species evenness), but decreasing the overall productivity of the plant community. (B) This trait-mediated trophic cascade depends on the hunting mode of the predator. When an actively roaming spider (*Phidippus rimator*) was substituted for the sit-and-wait spider *P. mira*, grasshoppers did not switch to feeding on *Solidago*; instead, they fed on *P. pratensis*. As a result, there was a 14% reduction in plant diversity in the actively hunting predator treatments compared with the sit-and-wait predator treatments; a 163% increase in above-ground productivity in the active predator treatments compared with the sit-and-wait treatments; no difference in plant matter decomposition rates between treatments; and a 33% increase in nitrogen mineralization in the active as opposed to the sit-and-wait predator treatments. Values are mean \pm 1 SD. Asterisks indicate significant treatment effects ($p < 0.05$) by t-test. (After Schmitz 2008, 2010.)



Strong cascading effects result from both the consumptive (density-mediated) and nonconsumptive (trait-mediated) effects of predators.

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Marine Food Webs

