

## Caught in the food web: complexity made simple?\*

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**SUMMARY:** Several historically separate lines of food-web research are merging into a unified approach. Connections between microbial and metazoan food webs are significant. Interactions of control by predators, defenses against predation, and availability of organic and inorganic nutrition, not any one of these, shape food webs. The same principles of population ecology apply to metazoans and microorganisms, but microorganisms dominate the flux of energy in both marine and terrestrial systems. Microbial biomass often is a major fraction of total biomass, and very small organisms have a very large ratio of production and respiration to biomass. Assimilation efficiency of bacteria in natural systems is often not as high as in experimental systems, so more primary production is lost to microbial respiration than had been thought. Simulation has been a highly useful adjunct to experiments in both population theory and in studies of biogeochemical mass balance, but it does not fully encompass the complexity of real systems. A major challenge for the future is to find better ways to deal with the real complexity of food webs, both in modeling and in empirical observations, and to do a better job of bringing together conceptually the dynamics of population processes and biogeochemistry.

*Key words:* food web, microbial food web, energy flux, community structure.

### INTRODUCTION

*“The classic marine food chain –algae, zooplankton, fish– can now be considered as a variable phenomenon in a sea of microbes (Karl 1999).”*

The food web is one of the earliest and most fundamental concepts in ecology. Darwin (1845) recognized the existence of a pelagic food chain. Elton is credited with first appreciating the importance of food chain and food web concepts (Lawton 1989), but major antecedents include Petersen’s (1918) quantitative conceptual model of the food web that is supported by eel grass, and Hardy’s (1924) conceptual model of the herring food web. Elton, and later Hutchinson and his students, developed both population and mate-

rials-flux approaches to food webs (Hagen 1992), but the two approaches quickly diverged. Paine (1980) showed that population interactions do not equate with energy flux, and asserted that energy flux was unimportant and “has generated few insights into ecological processes.” This put studies of population biology and energy-flux on separate paths that only recently have shown signs of beginning to merge into a unified paradigm (e. g. McQueen, *et al.*, 1986; Hunter and Price 1992; Polis and Winemiller 1996). Ecologists recognize that energy input matters, although they agree less on when and how it matters. What clearly matters is formulating tractable hypotheses about ecosystem structure and function. Repeated attempts to simplify the inherent complexity of food webs have led to Sisyphus-like progress in which investigators have made generalizations and then have been forced to qualify them.

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A step not yet firmly taken is the assimilation of microorganisms into conceptual food webs and food web models in spite of evidence that the ocean's food web, like most others, is primarily microbial (e. g. Fuhrman *et al.*, 1989; Li *et al.*, 1992; Sommer 1993; Karl, 1999). This review views microbial food webs and metazoan food webs as a single, continuous entity and examines evidence that energy flux can influence community structure. Of 113 food web descriptions compiled by Cohen *et al.*, (1990), 20 include bacteria, 9 protozoa, and 8 fungi. Virtually every one of those fails to include 2 or more microbial links. It is equally true that studies of microbial food webs have rarely included interactions with metazoans except as donors of organic matter, sometimes on grounds that the large metazoans constitute such a small fraction of energy flux.

## FOOD WEB STRUCTURE

### Recognizing microbial food webs

A very early suggestion of the significance of microorganisms in the sea came from Lohmann (1911), whose observations were imaginatively extrapolated by Vernadskii (1926). At that time, microbiology lacked the technology to enumerate bacteria or to estimate their production. During most of the 20th Century, microorganisms were thought to be significant in regenerating nitrogen and phosphorus but not to be significant components of the flux of carbon in the marine food web (e. g. Steele, 1974; Cohen *et al.*, 1982). Because their size is similar to the wavelengths of visible light, most marine bacterioplankton are invisible to conventional microscopy and could not be counted directly until the development of epifluorescence microscopy (Francisco *et al.*, 1973; Hobbie *et al.*, 1977). Their metabolic impact on ecosystems was underestimated until the development of tracer methods (Azam and Hodson 1977; Fuhrman and Azam 1980). The view that the ocean is a microbial system has not been shared by many fisheries scientists (e. g. Steele 1974; Cohen *et al.*, 1982; Boudreau and Dickie 1992; Cury *et al.*, 2000). They acknowledge the existence of the microbial food web but dismiss its significance to the food webs of fishes. A different view has been proposed by oceanographers, based on the work of Moloney and Field (1990) and Painting, *et al.*, (1993) which will be discussed in section 4.

Significant differences exist between terrestrial and aquatic food webs (e. g. Cohen 1994; Fenchel 1994) but there is not complete agreement on what the differences are. It is probably important that, unlike single-celled phytoplankton, entire terrestrial plants are rarely consumed completely by grazers, and the standing biomass of terrestrial plants is rarely depleted by them (Hairston *et al.*, 1960), while in the sea only transient phytoplankton blooms temporarily outrun consumption. What is sometimes overlooked is that in terrestrial ecosystems most of the microbial food web is situated in soils, which are not treated as a part of the system in most population models or analyses of terrestrial food webs, but are modeled separately by different investigators. Connections from microbes to consumer populations exist through soil invertebrates and their predators. A significant connection of microbes to higher organisms is through symbiotic mycorrhizae that sequester inorganic nutrients for trees while receiving organic nutrients. Mycorrhizae are consumed by the metazoan food web in the soil, and their sporocarps are eaten copiously by vertebrates, including *H. sapiens*. Much of the biodiversity and many physically small organisms in terrestrial systems are in the soil, so terrestrial systems may not be as depauperate in those respects as Cohen (1994) suggests.

### Size versus biomass

The total amount of prokaryotic carbon in the biosphere is at least 60% of that in plants and probably exceeds their metabolically active tissue (Whitman *et al.*, 1998). In terrestrial soils, 94-97% of the non-root biomass is bacteria and fungi, present in quantities of tons/ha (Coleman, 1994), similar in magnitude to root biomass (Schlesinger, 1991). In abyssal benthic systems, 87% of the biomass consists of bacteria, present in quantities of kg/ha (Tietjen 1992). In oligotrophic temperate lakes, bacteria comprise up to 58% of the biomass (Biddanda in press). In the oligotrophic Sargasso Sea, bacterioplankton constitute 70-80% of the biomass, and protozoa constitute 7-17% (Fuhrman *et al.*, 1989; Li *et al.*, 1992). In the North Atlantic spring bloom (Table 1), bacterioplankton constitute 15-50% of total biomass and 64-75% of heterotrophic biomass, with mesozooplankton being 0.5-2% (Harrison *et al.*, 1993; Li *et al.*, 1993). The distribution of biomass among different decades of size is not as regular as some earlier work suggested (e. g. Sheldon *et al.*,

TABLE 1. – Comparison of the biomass, mg C m<sup>-3</sup>, in a coastal marine system, an oceanic central gyre, and oceanic frontal region. Integrated to 100 m off New Zealand (Bradford-Grieve *et al.*, 1999), and to 200 m in the Sargasso Sea (Fishes: Angel, 1989; Net zooplankton: Ortner *et al.*, 1980 and Ashjian *et al.*, 1994; Protozoa: Caron *et al.*, 1995; autotrophs and bacterioplankton: Li *et al.*, 1992). English Channel sampled only at 10 m (Rodríguez *et al.*, 2000, except fishes Cohen *et al.*, 1982).

Season	English Channel off Plymouth				Sargasso Sea spring	Waters East of New Zealand						
	spring	summer	autumn	winter		Subtropical spring	Subtropical winter	Subtropical front spring	Subtropical front winter	Subantarctic spring	Subantarctic winter	
Fishes and squid	770	770	770	770	1							
Zooplankton	500	1200	1200	300	1.3	1.2	29	1.9	5.5	3.1	3.9	
Protozoa	50	150	25	15	4.3	1.2	10.1	1.3	4.7	1	5.9	
Bacterioplankton	10	20	20	15	5.6	5.1	22.4	5.7	14.2	7.9	11.5	
Autotrophs	45	160	28	10	5	11.2	9.7	22.2	43.5	3.4	10.8	

1972). Bacterial biomass in the ocean varies much less than the biomass of phytoplankton and other microorganisms (Table 1), and bacteria tend to be the dominant biomass in extremely oligotrophic environments, such as the central ocean gyres (Fuhrman *et al.*, 1989; Li *et al.*, 1992). Where seasonal studies have been performed, they tend to show major changes in biomass of other components (Donali *et al.*, 1999; Rodríguez *et al.*, 2000).

### Chain length and web complexity

Although not everyone agrees (e. g. Morin, 1999), probably neither the amount of primary production nor the assimilation efficiency of consumers is a major determinant of the length of food chains or diversity of most food webs. Fretwell (1977), while observing terrestrial metazoan food chains, proposed that high productivity produced longer food chains, although Ryther (1969), observing the sea, proposed that the high fish production of coastal upwellings was the result of high primary productivity and a short food chain. We now know that the food web of coastal upwellings contains most of the links present in the food webs of central gyres (Vinogradov and Shushkina, 1978; Moloney and Field, 1990; Painting *et al.*, 1993; Carr, 1998). The emergence of short chains in blooms and upwellings may, nevertheless, be significant for terminal-consumer fishes, as Ryther (1969) suggested (Legendre, 1990).

The number of trophic transfers is limited ultimately by dissipation of energy, but simple conclusions may be confounded by re-utilization of organic matter (Strayer, 1988) and by variable effects of scales of time and space. The scales on which system productivity affects system function and structure may be different from those of predator-prey effects (Menge, 2000), and empirical evidence from lakes indicates that food chain length correlates with

system size, but not system productivity (Post *et al.*, 2000). To make matters worse for investigators, a large fraction of the micro- and picoplankton is composed of mixotrophic organisms and internalized mutualistic associations (Safi and Hall, 1999; Caron, 2000; Dolan and Pérez, 2000). Also, chemolithotrophic bacteria have evolved associations with organisms in many phyla (Cavanaugh, 1994; Polz *et al.*, 2000).

### Predator or donor control of structure?

The proposition of Hairston *et al.*, (1960) that “the world is green,” because terrestrial predators control the size of grazer populations, instigated a cascade of research and theory which has trickled down to the ocean over four decades. Fretwell (1977) refined the proposition that the number of links in food chains determines whether primary producers were controlled by grazers. In systems with an even number of links, primary producers were grazer-controlled while in systems with an odd number of links primary producers were resource controlled. As Fretwell pointed out, this was most likely to happen in simple food chains with little or no branching. Under the rubric, exploitation ecosystems, this was formalized in models (Oksanen *et al.*, 1981). Based primarily on terrestrial examples, the principles found useful application in lakes (Carpenter and Kitchell, 1993). Further research in fresh water (McQueen *et al.*, 1986), in terrestrial systems (Hunter and Price, 1992), and in microbial microcosms (Lawler, 1998) has revealed a complex interplay of top-down (predator) and bottom-up (resource) effects. A general theory of food web dynamics has to take both into account, as well as other factors. The terrestrial world is green as much because plants have evolved defenses as because predators control herbivores (Polis and Strong,

1996). Most of the examples of predominant control by predators are from simple webs, such as rocky intertidal communities, or even more sparse experimental ones. More complex systems reveal more complex interactions (Polis, 1991; Polis and Strong, 1996; Polis and Winemiller, 1996). Wiegert and Owen (1971) pointed out that organic matter does not accumulate in ecosystems, despite the low utilization of plant resources, because it is being utilized along detrital-microbial pathways.

We are approaching a level of understanding where controls from top and bottom can be seen interacting. A modeling study suggests that the ability of copepods to control phytoplankton abundance may be limited by nitrogen-limited phytoplankton cells (Roelke, 2000). Also, Thingstad (2000) developed a marine planktonic food web model incorporating both resource limitation and grazer-predator controls. The model suggests that the control of relative population sizes is top-down but that the total amount of limiting element (C, N, P) in the entire food web mediates changes in the size of each population.

While empirical evidence in the ocean indicates that bacteria are partially resource-limited (Ducklow, 1992), their nearly constant abundance also suggests limitation by predators. Marine bacterioplankton approach the minimum size possible for an organism, having even reduced their water content to a minimum (Simon and Azam, 1989), possibly as a result of grazer selection of the largest prey. However, some of those very small bacteria transform into larger rods in the presence of added C, N, and P. Heterotrophic bacteria attached to detritus, where presumably there is a more favorable microenvironment, are large (2  $\mu\text{m}$ ) rods (Boenigk and Arndt, 2000). Their transformation from 0.3  $\mu\text{m}$  spheres to rods and back again has been documented (Wiebe and Pomeroy, 1972; Novitsky and Morita, 1976; Jacobsen and Azam, 1984). These hypotheses of strong control on marine bacterioplankton by both resources and predators have been difficult to test, but some progress has been made in lakes (Pace and Cole, 1996; Langenheder and Jürgens, 2001).

### **Stability: an hierarchical mismatch?**

Much theoretical work on food web stability has relied upon models, microcosms, and simple, accessible communities, such as the rocky intertidal or upon food chains condensed into trophic levels. Theory, thus derived, has often been extrapolated to

the larger world, although the problems inherent in doing this have been pointed out (Allen and Starr, 1982; Lawton, 1989; Polis and Strong, 1996). Models of food webs are necessarily structurally simple and lack complexity, redundancy, and much of the reticulate nature of real food webs (Polis, 1991; Polis and Strong, 1996). The empirical food web descriptions assembled by Cohen *et al.*, (1990) frequently contain “trophic species,” which are condensations of a guild of species or sometimes much more. Such caricatures of real food webs have been criticized as lacking reality (Lawton, 1989). Cohen *et al.*, (1990) wisely label these simplifying abstractions “spherical horses.”

Sometimes, as Cohen *et al.*, say, you can ride a spherical horse, but don't count on doing so. How effective condensation may be will depend on how similar the combined species are and what questions we ask about them. Suppose, for example, that in a model of an upwelling system we create a trophic species called dinoflagellates, a lesser condensation than the typical trophic species. Dinoflagellates are important in the diet of newly-hatched anchovy larvae (Lasker, 1979). If the dominant dinoflagellate is *Gymnodinium*, the larvae eat them and grow. If the dominant dinoflagellate is *Gonyaulax*, the larvae eat them, but cannot digest them, and die. Similar food-source problems have been demonstrated for oysters (Ryther, 1954a) and for *Daphnia* (Ryther, 1954b). Communities are filled with this sort of minute complexity. The obvious danger is in too casually transferring to the rain forest, or marine plankton, principles shown to work in three-level, five species models. Caswell (1988) quotes Lewontin: “It is not the function of theory to describe what has happened in a particular instance.” But investigators sometimes do that, even though the real world is more complex.

Lawton (1989) pointed out the lack of ecological studies encompassing both population structure and energy flux. Pickett *et al.*, (1994) say, “...unboxing organism features and behaviors and examining the reciprocal effects of organisms and ecosystems is a frontier for integration.” An inherent difficulty in this is that populations, communities, and ecosystems are on hierarchically different levels of organization (Allen, 1987) and have different return times (Slobodkin, 1961). A scheme of population structure and energy flux interactions was described for marine planktonic systems by Legendre and Rassoulzadegan (1995) who classified planktonic communities based on relative

fluxes of energy and nutrients. In the most impoverished central regions of oceans, a microbial-loop dominates biomass and energy flux. All community components are present, including large fishes and cetaceans, but the latter are rare. In upwelling systems, eukaryotic autotrophs and consumers are more abundant, but the microbial components are present and their abundance and energy flux is greater in absolute terms than it is in the central gyres (Carr, 1998).

The importance of species redundancy for ecosystem function continues to be debated (Hart *et al.*, 2001). By creating “trophic species,” modelers implicitly acknowledge species redundancy, although Polis and Strong (1996), among others, question the realism and usefulness of both trophic species and trophic levels. Systems that appear stable energetically over time may experience catastrophic changes in species interactions. Yet, experiments suggest interaction between biodiversity and system function, although most such experiments are small in scale and may not be representative of larger-scale processes (Moore and Keddy, 1989). In comparing the stability of different systems, it is also essential to consider the generation times of the dominant organisms. Forests appear to be more stable than phytoplankton until we normalize for generation time (Allen 1987).

## FOOD WEB FUNCTION

### Size versus metabolic rate

We have seen that microorganisms—especially bacteria—constitute a major fraction of the biomass in both marine and terrestrial ecosystems. While this alone should indicate a major role in energy flux for microorganisms, the case is made stronger by the relation of production per unit biomass (P/B) to body size. Both metabolic rate and P/B increase by a factor of approximately 1.75 with each order of magnitude decrease in body weight, although this is variable, with a normally distributed range having SD = 0.11 (Peters, 1983). Most compendia of allometric relationships do not include bacteria. Including them extends the range of P/B upward by an order of magnitude while extending the biomass range downward several orders of magnitude (Fig. 1). Bacterial production and bacterial respiration are the dominant processes in ocean waters (Sherr and Sherr, 1996) and in

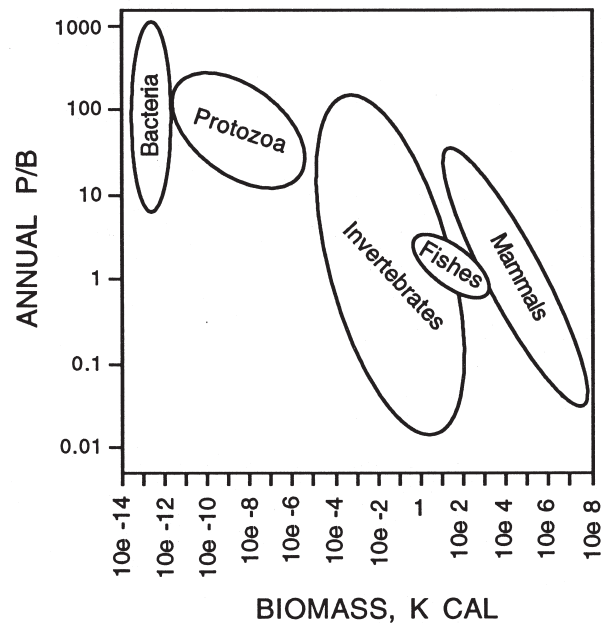


FIG. 1. – Ranges of annual production per unit biomass (P/B) for organisms of various sizes and taxa. Data from Banse and Mosher (1980) and Ducklow (1992).

most soils and sediments (Coleman and Crossley, 1996). Combining the ranges of bacterial production reported by Ducklow (1992) and the ranges of bacterial growth efficiencies reported by Jahnke and Craven (1995) and del Giorgio and Cole (2000), it is evident that most marine primary production is utilized in the microbial loop.

Because analyses of food webs that omit bacterial processes are usually missing most of the flux of energy or carbon, most theoretical population ecology involves a small fraction of the flux of materials. Microbial processes that dissipate large amounts of the energy sequestered by autotrophs have major, quantitative consequences for the production of biomass by terminal consumers (Pomeroy, 2000). While differences in energy flux may not change the length of food chains in predictable ways, they will affect the amount of biomass at the terminal levels, i. e. the rarity of large, terminal consumers such as fishes. To the above, Lenz (1992) adds temperature, pointing out that as temperature increases with the usual  $Q_{10}$  of 2-3, small organisms will have a greater increment in production than large ones. While this is true, we should note that temperature effects are relative and regional. The optimum temperature ranges of both bacteria and phytoplankton vary with latitude, and just because water is “cold” in polar regions does not imply that organisms are growing more slowly than in low latitudes, where water is “warm” (Pomeroy and Wiebe, 2001).

## Assimilation efficiency

Only recently has assimilation efficiency received the attention it deserves (del Giorgio and Cole, 2000). Early assumptions of a 10% “ecological efficiency” of each “trophic level” and later assumptions of a generally high growth efficiency of heterotrophic bacteria of around 50%, have been shown to be poor generalizations (Jahnke and Craven, 1995). Modelers conventionally put a constant in their equations to correct for energy losses owing to assimilation efficiency, but they rarely explore the sensitivity to variations in that constant. The efficiency of poikilotherms is generally assumed to be higher than that of homeotherms, with bacteria highest of all. However, these assumptions come largely from laboratory experiments that do not always duplicate natural conditions. In the real world, parasitized, starving beasts and bacteria often are shown to have low assimilation efficiency. Indeed, organisms sometimes subsist on stored materials, including structural proteins, but this is not usually captured in models, although simple sensitivity tests can show the importance of assimilation efficiency (Pomeroy, 2000).

An example of the importance of assimilation efficiency can be seen in the study of a *Phaeocystis* bloom in the North Sea. Rousseau *et al.*, (2000) found that 75% of the carbon sources of the mesozooplankton were diatoms, although diatoms were responsible for only 30% of primary production. Mesozooplankton obtained the other 25% of organic carbon from a microbial food web which originated from the 70% of primary production by *Phaeocystis*. Trophic efficiency of the food chain from diatoms to mesozooplankton was estimated to be 34%, while that from *Phaeocystis* via a detritus food chain was estimated to be 1.5%. A detritus food web, such as that originating from *Phaeocystis*, involves branching and looping food chains in which the passage of materials through bacteria, in particular, may be very inefficient (del Giorgio and Cole, 2000). If, however, as is the case in most oligotrophic waters, the primary producers are not diatoms but primarily a mixture of microflagellates and autotrophic bacteria being eaten by protozoans, the trophic efficiency of the microbial food web can be significantly higher. In both cases, the connections between the microbial chain and the metazoan chain are an integral part of a coherent food web that is the principal support of larger metazoans.

Although the length of food chains does not correlate well with primary productivity, variable assimilation efficiency can conspire with primary production to render chains beyond a given length energetically small and the terminal consumers rare. This would seem to work against the effectiveness of detritus food chains which tend to be long and to involve food sources of low quality (e. g. high C:N or C:P and a preponderance of aromatic rather than aliphatic organic compounds). But efficiency is not everything in life (Odum and Pinkerton, 1955). Abundant, low-quality food can be as satisfactory as rare, high quality food –ask any ruminant. Although early food web theory suggested that detritus food webs should be unstable and therefore rare in nature (Cohen *et al.*, 1990), empirical work suggests the reverse. Detritus food webs, and their internalized siblings, ruminant food webs, are everywhere (Polis and Strong, 1996), contributing to the reticulation and complexity of food webs, to the intermingling of microbial and metazoan consumers, and to blurring of trophic levels. Efficiency considerations suggest that detritus food webs support high trophic levels best where rumen-like short cuts have evolved. Rumens or rumen-like processes facilitate the transfer of energy from low-quality food sources to consumers (Pomeroy, 2000).

## Simulation and theory

The complex redundancy of most natural food webs is an important attribute. But as Polis and Strong (1996) point out, every species has a different range of food sources. Grazers and predators switch prey, and even “trophic levels,” as necessity dictates. Many terrestrial predators also eat fruit (Polis and Strong, 1996), owls can subsist on earthworms (Elton 1966), and alligators may subsist on snails (T. Jacobsen, pers. com.). The same is true of marine plankton. The detail of food webs only rarely appears in the literature, one of the better examples coming from the Coachella desert (Polis 1991). It is currently impossible to model detail on such a level not only because of the complexity of simulation but because the natural history is not that well known, especially for the microorganisms. Thus, a gap remains between ecological theory, as developed in simple food-web models, and real food webs in real communities (Polis, 1991; Polis and Strong, 1996; Polis and Winemiller, 1996). This leads to questions about the general applicability of simplistic theoretical approaches, and, for fisheries research, this cre-

ates a practical problem. Can one distinguish the effects of overfishing from natural, long-term trends of species abundance resulting from a movement between two or more poorly defined attractors (*sensu* (Lewontin, 1969) or within the influence of a strange attractor (Sugihara and May, 1990)? While it is necessary that scientists try to do only what is possible and simulate tractable systems, the inherent danger lies in extrapolating the results to more complex natural ecosystems. When overcome by the temptation to do that, we should seek ways to test our conclusions in the real world. At the same time, it should always be remembered that scale is important, and what dominates a microcosm may disappear at the landscape scale (Allen, 1987; Moore and Reddy, 1989)

### **Continuity of microbial and metazoan webs**

The connectivity between microbial food webs and metazoans has been addressed by several investigators (Petipa *et al.*, 1975; Vinogradov and Shushkina, 1978; Sherr and Sherr, 1987; Painting *et al.*, 1993; Sommer, 1993; Coleman and Crossley, 1996). Whether or not there is a significant flux of energy from a microbial web to metazoans may depend on the assimilation efficiency of the microorganisms (Pomeroy, 2000), which can be highly variable (Jahnke and Craven, 1995; del Giorgio and Cole, 2000). Legendre and Rassoulzadegan (1995) conceptualized a continuum of planktonic food web structure in which connectivity of the microbial loop with metazoans is maximum near the center of the continuum, which they term a multivorous food web. An inevitable consequence of the presence of a microbial food web is that it consumes much of the available organic matter, more in impoverished systems dominated by a 'microbial loop,' and less in systems like coastal upwellings that are more dominated by metazoans (Legendre and Rassoulzadegan, 1995). But even in upwellings, microorganisms play quantitatively major roles Painting *et al.*, 1993; Carr, 1998). Coastal upwelling systems have been viewed traditionally as short food chains of metazoans (Ryther, 1969) and are still viewed that way by fisheries scientists (Boudreau and Dickie, 1992; Jarre-Teichmann, 1998; Cury *et al.*, 2000). Upwelling systems are notoriously variable, depending upon the strength and frequency of upwelling, which regulates primary production, and on more subtle population interactions which may precipitate a shift from anchovy dominance to sardine dominance.

According to the models of Moloney and Field (1990) and Carr (1998), the early stages of a bolus of upwelled water are dominated by picoautotrophs, suitable food for small salps or ciliates but not for adult crustacean zooplankton. Copepod nauplii in recently upwelled water may be feeding on ciliates and may even prefer them to diatoms (Paffenhöfer, 1998). Picoautotrophs continue to grow at their maximum rate throughout the lifetime of the bolus and will still be growing and supporting a microbial food web after newly upwelled nitrate has been depleted and diatoms are no longer growing rapidly. However, diatoms will utilize upwelled nitrate and become the main food available for copepods. If copepods have not completed their life cycle when upwelled nitrogen is depleted, they return to eating ciliates (Painting *et al.*, 1993). Much of the primary production in coastal upwellings is shunted through a reticulated microbial food web, as Petipa *et al.*, (1975) told us, and the microorganisms may be a critical link for parts of the metazoan food web. The famous phytoplankton-zooplankton-fish food chain is not the whole story even in upwellings. While what are probably the most complete models of upwelling systems suggest that the phytoplankton-zooplankton-fish chain is energetically dominant (Baird *et al.*, 1991), Carr's (1998) model suggests that more than half the fixed carbon and energy flux is through picoplankton.

Another example of the differences between microbial loop systems and multivorous systems (the terms of Legendre and Rassoulzadegan, 1995), may be provided by a contrast between the continental shelves of Georgia-South Carolina (GASC) and Louisiana-Texas (LATX). The GASC shelf is one of the least productive of fisheries in North America while the LATX shelf is one of the most productive (Pomeroy *et al.*, 2000). The two shelves have similar areas and similar annual inputs of nitrate. The Mississippi River provides the LATX shelf six times as much fresh water as the GASC shelf receives from rivers, together with most of its nitrate, producing a seasonally nitrate-rich, stratified water column and a multivorous food web of diatoms and copepods. The GASC shelf receives a similar amount of nitrate from upwellings along the shelf break which produce local pulses of high primary production offshore. Most of the GASC shelf, most of the time, however, is unstratified and low in nutrients, with a microbial-loop food web. These differences in structure and in trophic efficiency, not the absolute amount of available nitrogen, may make the difference for the production of fishes.

## Future directions: Dealing with complexity

Ecology has the disadvantage of being largely a study of middle-numbers systems (Allen and Starr, 1982). Neither simulation models nor mesocosms capture the complexity of even relatively simple communities. Investigators of population dynamics and of the flux of materials are equally guilty of excessive condensation in attempting to simplify interactions within communities. Also, forcing nature into artificial and arbitrary concepts of trophic levels can do as much to obscure community processes as to explain them. Failure to consider differential responses of individual species (Sommer, 1993) and indirect, secondary effects (Leibold and Wilbur, 1992), as well as ignoring the microbial loop (Simon *et al.*, 1992; Sommer, 1993), all lead to oversimplified conclusions about system structure and function. Specialization is an enemy of synthesis in ecology. Studies involving input from both microbiologists and fisheries scientists, plus all that lies in between, are rare.

A more powerful solution of ecologists' dilemma of middle numbers and complex interactions has not yet been discovered. Krebs (1985) has compared the present state of ecology to that of chemistry in the Eighteenth Century. We continue to apply brute force, designing better instrumentation to give us more replication, automated measurements delivered from satellites, and computer programs to process data. It is no secret that we need data sets much larger in size and longer in duration than we now possess to deal with ecosystem complexity (Schaffer and Kot, 1985). This helps to test hypotheses derived from small-scale experiments. It is increasingly possible to test hypotheses by measurements of net changes in large systems. Such tests often tell us that complex interactions cannot be ignored. At present, the best way to integrate all ecosystem processes is with empirical measurements of natural, complex systems.

History suggests that we progress by making simplistic generalizations based on fragments of the real world and later define the limits of each generalization and how it fits into a more complex whole. To move beyond this, we need radical departures from the present mindset and approaches. One of the immediate challenges we face is assimilation. We have increasingly strong data sets in population ecology, biogeochemistry, and energetics, which are essentially the top-down and bottom-up approaches to community and ecosys-

tem structure and function. Neither approach alone provides a full explanation of the events we observe. Combining these approaches will involve bringing together quite separate academic communities for the examination of ecosystems and their function on several hierarchical levels and several scales of space and time.

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