

Organism life cycles, predation, and the structure of marine pelagic ecosystems

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ABSTRACT: This paper explores the notion that the theoretical basis for contemporary research concerning the structure and function of marine pelagic ecosystems is self-limiting. While some findings such as the microbial food web have extended our knowledge of the biological components of the upper water column and their relationships to fluxes of materials and energy, they have not advanced our understanding of why specific pelagic forms occur in time and space, and why only some attain dominant status and contribute the bulk of biogenic fluxes emanating from the mixed layer. It is argued here that a major impediment to improved conceptual models is the historic focus on resource-driven or 'bottom-up' factors as being the dominant variables structuring planktonic ecosystems. Evidence is presented that predation or 'top-down' trophic effects may be equally important in specifying the occurrence of particular taxa, the biomass within adjacent trophic levels, and the morphology of dominant herbivores and carnivores. It is suggested that key species, because of unique combinations of life history strategies, metabolic demands, and physiological performance, may exert a dominant role in the extent to which predatory interactions cascade through pelagic food webs. There is considerable evidence of evolution of predation avoidance strategies among phytoplankton and zooplankton. It is proposed that future research might profitably be directed toward the question of how the pelagic environment selects for life histories and morphologies of organisms under conditions when resource availability and predation are both significant structural buttresses. Methodological approaches should include detailed studies of dominant key taxa from different environments, with the goal of identifying the critical aspects of life history, behavior, or morphology which account for their success.

KEY WORDS: Morphology · Life history · Plankton · Pelagic · Top-down · Trophic cascade · Predation · Ecosystem structure · Bottom-up

CONCEPTUAL OVERVIEW

Quantitative understanding of marine processes has increased rapidly in the past decades, driven by the development of new methods and tools enabling measurement, mapping and modelling of the fluxes and cycling of biogenic elements, at scales extending from molecular diffusion to global ocean circulation. However, these substantial advances in quantification and delineation of biogeochemical processes and provinces have not been accompanied by commensurate progress in understanding of the mechanisms

that structure pelagic ecosystems. Thus, the distribution patterns of dominant pelagic species are fairly well established, yet we do not know why they occur when and where they do. What is lacking is knowledge of the nature of properties that gear given species to specific environments, and which are responsible for their occurrence or persistence in given water masses.

For example, we do not clearly understand why only a few diatom genera dominate oceanic new production, or why calanoid copepods contribute the bulk of marine zooplankton biomass. These are important questions because the respective diatoms and copepods each impact the fate of organic matter produced or processed by them in unique ways: the silica frus-

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tules of diatoms and the compact fecal pellets of copepods both enhance vertical flux of organic matter. In contrast, the gelatinous colonies of *Phaeocystis*, which dominate new production in some environments, often contribute less to vertical flux than the equivalent biomass of diatoms (Wassmann 1994). Further, *Daphnia*, the dominant zooplankton in many lakes, produces loose fecal matter that disintegrates following release (Lampert 1987) and hence does not contribute to vertical flux. Thus, neither of these properties — silica frustules or fecal pellets — can presently be related to the dominant role diatoms and copepods play in the marine pelagial.

The above examples illustrate the extent to which biological properties of dominant organisms determine patterns of biogeochemical cycling in today's ocean, but they also demonstrate the substantial gaps that still exist in our understanding of marine ecological processes and seriously hamper further progress. The traditional approach to the study of marine pelagic ecology is biased toward factors regulating growth of organisms, i.e. resource acquisition (bottom-up force) is accorded more importance than predation (top-down force) in regulating the structure and functioning of marine pelagic systems. We argue that this approach is now self-limiting, as it has not provided an adequate framework to advance our understanding of how natural selection works in the marine pelagial.

We advocate here that predation and resource availability act through morphologies and life history strategies of organisms to structure pelagic ecosystems, and hence to drive biogeochemical cycles. The potential significance of the biological pump (organism-mediated incorporation of inorganic carbon into organic carbon, and its sequestration into the interior ocean via downward flux of biogenic particles), and our uncertainty in resolving that role (Longhurst & Harrison 1989), speaks volumes for the need of an improved mechanistic understanding of the linkages between cause and effect in plankton dynamics. For example, changes in food web structure have been associated with altered patterns of vertical flux in Lake Michigan, North America (Kitchell & Carpenter 1987), and in the North Atlantic Ocean (Sieracki et al. 1993). In other words, changes in structural components of the pump lead to changes in how the pump works. But what are the linkages, and how do the biological components direct one another? The ideas which follow are by no means designed to promote one architectural principle over another (e.g. resource limitation vs predation), but to emphasize that it may be more valuable to understand why carbon flows where it does, rather than merely how much.

THE ROLE OF ORGANISM LIFE CYCLES AND MORPHOLOGIES

The bulk of large-scale biogenic cycling and production of fish food is dependent on relatively few taxa and morphotypes. In the following sections, we discuss some examples of key species and their morphologies to illustrate how specific knowledge of individual biologies will greatly improve our understanding of the forces shaping ecosystem structure and driving biogeochemical fluxes. This information holds considerable promise for development of a predictive framework.

***Fragilariopsis (Nitzschia) kerguelensis*.** This is a medium-sized (15 to 30 μm long) pennate diatom that lives in ribbon-shaped chains of 20 to 100 cells and forms almost monospecific blooms in the Antarctic Polar Frontal Zone (Bathmann et al. 1994). Its global significance is bestowed by its inordinately robust siliceous cell walls, which contribute the bulk of the silica deposits in the underlying sediments (Burckle & Cirilli 1987). Indeed, deposition of its frustules has continued unabated through glacial and interglacial cycles. This siliceous girdle around the continent is reputed to accumulate fully 75% of the biogenic silica being deposited in today's ocean (Ledford-Hoffman et al. 1986), although only 20% of global biogenic silica production occurs in these waters (Treguer et al. 1995). It is tempting to speculate that the thick cell wall of *F. kerguelensis* is somehow selected for as a grazer deterrent in these waters, inducing blooms and mass sedimentation. It follows that these factors, be they sinking and seeding strategy (sensu Smetacek 1985), or grazer protection, or both, indirectly shape the ocean silica budget. But what are these factors?

***Emiliania huxleyi*.** This is a small (<10 μm) coccolithophorid that forms blooms in many different regions of the world oceans in both high and low latitudes (Brown & Yoder 1994) but also from oceanic to coastal regimes (Berge 1962). Its sedimentary record indicates that this amazing ability to grow to bloom proportions under such a wide variety of conditions has developed only since the Holocene. Prior to the last Ice Age, another small species (*Gephyrocapsa*), now of minor importance, dominated coccolithophorid blooms. Circumstantial evidence from mesocosm studies implicates viral attack rather than nutrient exhaustion in the demise of 2 *Emiliania* blooms studied in successive years (Bratbak et al. 1993). Indeed, Emiliani (1993) himself suggested that viral infections were a significant factor in driving species extinctions in marine plankton. Although biogeochemical fluxes (dimethyl sulfide or DMS, and carbonate) mediated by this species are only important on a regional scale (Brown & Yoder 1994), its extraordinary ecological flexibility cries out for elucidation.

tion. Molecular genetic studies indicate that open ocean and coastal forms belong to the same species (Barker et al. 1994); however, when clonal cultures from the same mesocosm experiment were compared with one another, a surprising degree of genetic variability within the bloom population came to light. *Emiliana* is indeed a tantalizing species.

***Phaeocystis*.** This is a polymorphic phytoplankton taxon whose life cycle includes, but may not be limited to, solitary flagellated cells of 3 to 8 μm and gelatinous colonies of non-flagellated cells up to 2 cm in diameter (Kornmann 1955, Verity et al. 1988, Rousseau et al. 1994). While some uncertainty remains about taxonomic identity, details of its life cycle, and transitions therein (Baumann et al. 1994, Cariou et al. 1994, Medlin et al. 1994), *Phaeocystis* is well known for prodigious blooms of the colonial phase. These occur primarily in boreal and polar waters of both hemispheres, but occasionally in temperate and tropical waters (Kashkin 1963, Baumann et al. 1994). These blooms are important regionally and seasonally to primary production, and their significance to global CO_2 sinks has also been promoted (Smith et al. 1991). There is evidence that changes in the size structure of *Phaeocystis* blooms can alter the zooplankton community (Hansen et al. 1994), and that omnivorous zooplankton in the presence of *Phaeocystis* prey instead on protozoans, thereby releasing *Phaeocystis* from herbivory (Hansen et al. 1993). In the absence of substantial grazing pressure, sedimentation of colonies occurs in some environments (Wassmann 1994), although emigration of cells out of the colonies might minimize vertical export of cellular carbon (Verity et al. 1988). *Phaeocystis* is also a copious producer of DMS and its precursor in seawater, DMSP (Stefels & van Boekel 1993), so that *Phaeocystis* may be important to global sulfur balances, acidification of atmospheric aerosols and rain, and climate change (see Liss et al. 1994 for review). Thus, factors influencing its productivity and fate may significantly and interactively affect biogeochemical cycling. However, the fate of *Phaeocystis* colony blooms seems intrinsically associated with its life cycle and the associated match or mismatch with herbivores.

***Euphausia superba*.** Antarctic krill is the key species of the Southern Ocean, as it maintains an enormous biomass (still in excess of *Homo sapiens*) in an area only twice the size of the USA. Its average density, using conservative stock estimates, is at least 10 to 30 ind. m^{-2} , equivalent to 1 to 3 g C m^{-2} . None of the other species of pelagic euphausiids are as prominent in their respective habitats as krill in the Southern Ocean; therefore, the unique status of krill has to be explained by unique features of its biology and/or its habitat.

Apart from its larger size, krill is very similar to other euphausiids, hence any unique ability is not reflected in its morphology. Productivity of the krill habitat — the region bounded by the winter extent of sea ice around Antarctica — is rather low and the composition and biomass of plankton, contrary to earlier belief, is similar to that of other high latitude oceans (Smetacek et al. 1990). Krill utilizes a wide range of food sources: phytoplankton, ice algae (Marschall 1988) and copepods (Huntley et al. 1994) and can easily survive long periods of starvation (Ikeda & Dixon 1982). Clearly, versatility is necessary if such a large portion of the annual primary production is to be sequestered in a single population, and Smetacek et al. (1990) argued that it is the way in which *Euphausia superba* has geared its life cycle to the seasonality of sea ice that enables it to maintain such large stocks. However, a notable feature of krill is its long life span, and consensus is now emerging that individuals live for at least 5 or 6 yr (Knox 1994), which is very unusual among pelagic crustacea and implies a slower turnover rate of the population than was previously believed. It follows that the exceptional stock size of krill when compared to euphausiid populations of other oceans cannot be explained by a faster growth rate but is more likely due to a lower mortality rate, as discussed below.

The unique feature of the krill habitat is the presence of the seasonal sea ice cover which is utilized by krill as a food source but which also offers protection, particularly during winter, from the air breathing, visual predators that are the chief predators of krill. Another unique feature of the krill habitat is the relative absence of clupeid type fish swarms. Although a clupeid morphotype has evolved in the Antarctic (*Pleurogramma antarcticus*), its predation pressure on local euphausiids is negligible compared to that of e.g. capelin, herring, or sardines in their respective habitats. We speculate that this is due to the stress that hypoosmotic teleosts would experience in continuous, close contact with sea ice. Whatever the reason, the fact remains that their relative absence reduces predation pressure not only on krill but also on their alternative food, copepods, which are hence available to krill. Indeed, the actively foraging krill swarms encountered in open water during summer are themselves reminiscent of clupeid fish. It follows that the presence of sea ice, by changing predation patterns, leads to a biomass bulge in the euphausiid group, which in turn has considerable ramifications for the structure and population dynamics of the predators. The implications of the krill example for our conceptual view of factors constraining marine zooplankton populations are discussed next.

The organisms described above represent but a few examples of species whose morphologies or life history strategies are sufficiently successful that they dominate their respective environments in time and space. *They may hold space because they sequester resources (bottom-up structuring) better than their rivals, or because they avoid or inhibit predators (top-down structuring).* The former strategy has generally attracted the most attention in marine plankton research. We consider in the following sections some conceptual arguments on why equal attention should be focussed upon the significance of predation, and the potential selective pressure of avoiding being eaten, in conceptual models of food web structure and biogeochemical fluxes in the marine pelagial.

PREDATION CONSTRAINTS ON ZOOPLANKTON MORPHOLOGY

Oceanic zooplankton are the most widespread form of animal life on earth with the longest history of evolutionary continuity. Yet the number of taxa is orders of magnitude smaller than that of the marine benthos. Furthermore, the bulk of the biomass is present within only a few morphotypes represented by dominant species of copepods, euphausiids, pteropods, and chaetognaths. Among holoplankton, the same basic body shape is maintained through 10 to 100× variation in body volume in many cases. The special case of gelatinous zooplankton is further discussed below. The perceived similarity within the groups just mentioned is all the more striking when compared with morphological variation within the major benthic groups. Here we discuss the respective roles of food acquisition and predator avoidance as constraints on morphology using the most ubiquitous form, the epipelagic copepods, as an example of a highly successful body shape.

The similar morphology of calanoid copepods which is retained through about 2 orders of magnitude range in length contrasts strikingly with the degree of genetic variation (Bucklin et al. 1995), suggesting strong environmental constraints on morphology. The constraints do not appear to be dictated by food acquisition strategies because copepods as a group are known to feed on a wide variety of foods ranging from small suspended particles to zooplankton of equal size. Indeed, gut contents and the actual process of feeding need to be examined if one is to find out what constitutes the major food sources of the various species (Paffenhöfer 1988, Turner 1991). It follows that food acquisition (bottom-up control) is not a major determinant of general body shape of epipelagic copepods.

Life history patterns also vary widely, ranging from an apparent absence of seasonality, even in polar waters, to presence of diapausing eggs in coastal species and diapausing sub-adults in many oceanic copepods (Smith & Schnack-Schiel 1990). Again, a particular life history does not select the morphology of the various life cycle stages that all copepods undergo, although geographical distribution of the various species is probably constrained by this factor. Differences in reproductive behavior are manifested in relatively minor details such as morphology of appendages involved in transfer of sperm, although females of some species carry conspicuous egg sacs while others release them as they are produced. We are left with predation as the major constraint on copepod morphology and several arguments can be broached in support of this.

Firstly, all copepods throughout their respective ranges share the same types of predators: active hunters such as chaetognaths and fish, and passive trappers such as jellies and foraminifera. Most copepod predators are too large to be deterred by defenses such as spines or thick carapaces formed in limnetic cladocerans and none of these have been developed by copepods. Camouflage from visual hunters is effected by small size and transparency but also by avoiding the epipelagial during the day, using diel vertical migration (DVM), and both of these properties are well developed in copepods. Hays et al. (1994), in a comprehensive study of DVM behavior in copepod species across the North Atlantic, found that large and pigmented species migrated more. They concluded that 'the risk of predation from visual predators [is] the most important factor influencing taxonomic differences in DVM'.

Upon detection, escape from attacking predators is by flight and, to our knowledge, all copepods can 'jump' considerable distances when threatened. Hardy (1956) stated 'if it (*Calanus*) makes a sudden spurt the first antennae fold back to offer the least resistance', propulsion being effected by the 'oar-like thoracic limbs'. The much shorter antennae of those copepods with well-developed eyes (e.g. *Corycaeus*) suggest a sensory (mechano-tactile) function of these appendages. Experimental studies indicate that the first antennae are environmental sensors (Gill & Crisp 1985, Bundy & Paffenhöfer 1993), which could function to perceive food (Paffenhöfer & Lewis 1990) or predators. Support for the latter comes from those species in which adult males cease feeding and reduce their mouth parts whereby the first antennae and the basic morphology are retained, although locating females by e.g. pheromones will also be an important function. Indeed, in some male copepods, one of the antennae is hinged and used to embrace the female during mating

(Hardy 1956). Apart from this minor modification, male and female antennae are so similar that one would expect the same function in both sexes. Escaping predation is, of course, equally as important in males as in females. Short-range predator recognition would be worthless were it not followed by an effective escape response, which is a common feature of copepods. Indeed, about two-thirds of the body is occupied by the segments carrying the thoracic limbs responsible for flight. Vertical migration and horizontal swimming is also effected by these limbs, although slower speeds require correspondingly less investment in muscle. In the absence of evidence to the contrary, we suggest that the characteristic shape of the cephalothorax of copepods is selected more by flight ability from predators (top-down) than by foraging efficiency (bottom up).

That genetic constraints on morphotype are not involved is amply demonstrated by the diverse grotesque morphologies of parasitic copepods that attach themselves to much larger hosts. These aberrant forms belong to the Poecilostomatoida and cyclopoid groups which in general exhibit much greater morphological plasticity than the more common calanoids. Steinberg et al. (1994) found that copepods were the most numerous animals living on discarded larvacean houses at midwater depths (100 to 500 m) and that many of these species 'possess benthic-like morphology and feeding strategy'. This example also indicates that morphology can well be modified to improve food acquisition. However, these species are only common below the depth where visual predation is efficient. The dominant cyclopoid genus in the epipelagial, *Oithona*, has a morphology remarkably similar to that of the common calanoids. Thus, a substantial case can be argued for predation as a major factor constraining copepod morphology. In the past, feeding behavior of marine copepods has received much more attention than mechanisms of predator avoidance (see Kerfoot & Sih 1987 for freshwater zooplankton). This imbalance now needs to be rectified. We dwell next on some implications for pelagic food web structure.

We have argued that the characteristic copepod morphology is an effective way of avoiding predation in their respective size class. Further up the size spectrum, the euphausiid morphology, also shared by mysids and decapod shrimps, appears to be a better way of avoiding predators and maintaining large stock size. In this morphological group, the large muscular abdomen is used for the typical tail-flip flight mode, which differs strikingly from the 'normal' swimming pattern. The large investment in body tissue solely for flight is very evident here. The streamlined form of chaetognaths and juvenile fish will be equally effective in capturing motile prey and escaping predators; how-

ever, each uses a different strategy. Both rely on transparency to disguise themselves from predator and prey. The typical motionless hunting behavior of chaetognaths, interrupted by short distance darts for prey capture, further contributes to their invisibility. However, while fish larvae are also comparatively transparent, their well-developed pigmented eyes are not; this undoubtedly increases both their detection of prey and their perception by predators. In contrast, chaetognaths have almost completely eliminated pigmented organs and instead rely upon sensory hairs to detect prey and predator (R. L. Hopcroft pers. comm.).

So far we have only considered the non-gelatinous zooplankton that provide the bulk of the food for commercially important fish stocks. The biomass of gelatinous zooplankton (hereafter called jellies), e.g. coelenterates, ctenophores, salps and doliolids, does not flow up the economically important food chain and, because they eat the same food as the other zooplankters, they have long been considered a trophic dead-end, perhaps unjustly, since over 100 fish species are reported to occasionally or regularly ingest jellies (G. R. Harbison pers. comm.). Perhaps freed from the need to escape from attacking predators, jellies exhibit a much wider range of shapes than their more muscular counterparts. For example, 3 ctenophore genera (*Pleurobrachia*, *Beroe*, and *Mnemiopsis*) have strikingly different morphologies, each associated with a specific food acquisition strategy. In coelenterates, too, the range in body shape is wider than e.g. among free-living copepods, and feeding behavior is more easily apparent. Furthermore, the barrel-shaped body plan of salps and doliolids can be readily explained solely on the basis of food acquisition.

The common feature of jellies is their high volume: plasma ratio, which is widely believed to deter predators because of its low nutritional value. However, the constraints on eating jellies must be more subtle, as there are enough examples of non-gelatinous predators of jellies (e.g. pelagic turtles, moon-fish, stromateoid fishes) to show that vertebrates can indeed make a living off jellies. But turtles and moon-fish are morphologically very different from the standard pelagic fish shape (exemplified by clupeids), and the stromateoid fish have a crop in their digestive system (Bühler 1930) presumably to facilitate feeding on jellies (G. R. Harbison pers. comm.). The question is, why are jellies not a principal dietary component of commercially important fish? The answer may reflect the sleek, streamlined form of the dominant epipelagic fish which, as in the case of the zooplankters, is maintained over several orders of magnitude (from anchovies to tuna). The bodies of these fish consist largely of flight muscle: 80 to 95% of the swimming musculature is white muscle which enables the high velocities neces-

sary to avoid predators or to capture prey, with a correspondingly lesser investment in red muscle dedicated to 'normal' swimming (Bone 1978, Driedzic & Hochachka 1978). As in the case of copepods, fish body form deviates, often grossly, from the streamlined form wherever the environment offers protection from visual predators. This is exemplified by the grotesque shapes of deep sea fish and by surface-living *Sargassum* fish that are models of effective camouflage. While streamlining may facilitate rapid motions to capture prey (Kils 1990), the above considerations imply that escape from predators may be equally or more important than resource acquisition in constraining morphotype of epipelagic fishes. (Among lizards, for example, speed is used for escape from predation rather than food capture; Hertz et al. 1988.) This streamlining may also be the selective factor primarily responsible for the development of gape limitation in pelagic systems (Hairston & Hairston 1993). In contrast, a diet composed solely of jellies inevitably requires large gut volume, and a 'belly full of jelly', by producing drag, will critically reduce escape speed. It follows that exclusive jelly feeders will not be able to maintain the body form and muscle necessary for survival in the epipelagic, and we suggest that this may be the underlying reason for the dichotomy between the muscular and the gelatinous food chains. As always in nature, exceptions do occur, such as in streamlined mackerel actively preying on small medusae in the laboratory (Runge et al. 1987) and on salps in nature (Konchina 1991); however, such events are unlikely to reflect the principal diets of these and similar-bodied fish, given the highly episodic nature of abundant distributions of gelatinous planktonic organisms. Conversely, perhaps the potential ability of a school of predatory fish to nearly exterminate a patch of jellies favored another life history strategy: the very high rates of population growth characteristic of smaller gelatinous forms, e.g. salps, doliolids.

PREDATION AVOIDANCE AND THE ARMS RACE

It is a delicate balance to find sufficient food while avoiding being eaten and there are several hypotheses describing the interdependent nature of organisms in evolution. It is generally recognized that terrestrial plants coevolve with their insect herbivores (Ehrlich & Raven 1964, Strong et al. 1984), with attendant costs, e.g. plant growth rates are inversely proportional to their chemical defenses (Coley et al. 1985). Another theory, recently termed escalation (Vermeij 1994), proposes that enemies are the primary agents of natural selection among organisms, and that predation-induced adaptations direct long-term behavioral and

morphological traits. This theory, described elsewhere as an 'arms race' (Dawkins 1987), proposes that as predators evolve more effective weapons systems, prey match these advances with equally successful antidotes. These arms races do not escalate out of control, or evolve into perfect capturing and escaping machines, because biological weaponry (e.g. speed to capture prey or to escape predators) must be bought at some other escalating cost (e.g. decreasing reproductive success).

Signor & Vermeij (1994) hypothesized that herbivorous and carnivorous plankton originally evolved as refuges from predation by marine benthic organisms. *The present paper argues that the concept of the arms race is currently applicable to the marine pelagic, where if predation is so important, selection for predator avoidance mechanisms should be evident.* Among plankton, predator avoidance strategies appear well developed, though perhaps not broadly distributed, and fall into 4 general categories: chemical, morphological, behavioral, and life history defenses. A few of these are described below; the reader is also directed towards detailed reviews elsewhere (Havel 1987, Sih 1987). Predation avoidance has also recently been evaluated as a selection pressure acting on bacteria (Jürgens & Güde 1994).

Chemical defenses. Several classes of phytoplankton are known to include taxa which are inhibitory or toxic to herbivores. Examples include the presumed raphidophyte *Olisthodiscus luteus*/*Heterosigma akashiwo* (Verity & Stoecker 1982, Van Alstyne 1986); several dinoflagellates (Huntley et al. 1986, Taniguchi & Takeda 1988); and the freshwater cyanophytes *Microcystis* and *Aphanizomenon* (Fulton & Paerl 1987, Jungmann et al. 1991). The active agents are generally unknown but presumed to be secondary metabolites sequestered within the cells (Faulkner 1984, Carmichael 1986). Some diatoms apparently contain or excrete chemical compounds which interfere or inhibit grazing by copepods (Malej & Harris 1993) and reduce egg production and hatching success (Poulet et al. 1994). While it cannot be certain that such compounds evolved in response to predation, i.e. allelochemical interactions within a trophic level may also be important (Lewis 1986), they are widely recognized for their role in deterring herbivory in terrestrial plants (Schultz 1988) and macroalgae (Hay & Fenical 1988). Lowered nutritional quality, independent of toxins or compounds which reduce digestibility, can also affect susceptibility to predation (Butler et al. 1989). Induction of chemical defenses in plankton are inadequately understood.

Morphological defenses. These include both fixed and inducible morphologies (Havel 1987). Among defensive changes in prey architecture that have been ex-

perimentally verified are: formation of colonies by previously single-celled *Scenedesmus* when exposed to herbivorous zooplankton (Hessen & Van Donk 1993, Lampert et al. 1994); growth of neck spines by *Daphnia* when exposed to kairomones of invertebrate predators, a process which is stage- and concentration-dependent (Tollrian 1993); development of extended wings and ridges by grazing ciliates when exposed to larger predatory ciliates (Kuhlmann & Heckmann 1985); and growth of spines by rotifers to deter predation by larger zooplankton (Stemberger & Gilbert 1987). In at least 2 of these cases, the prey apparently perceived the presence of the predator through polypeptides released by the predator. Several phytoplankton taxa with fixed morphological protuberances have been speculated to function as anti-predation devices, e.g. *Ceratium* (Hargrave & Geen 1970, but see Nielsen 1991). Rigid chitan threads, extending from cells of the diatom family Thalassiosiraceae, were shown to reduce their susceptibility to grazing by proto- (Verity & Villareal 1986) and metazooplankton (Gifford et al. 1981). While effective, some morphologies may not have evolved in response to predation, e.g. mucous sheaths in rotifers (Stemberger & Gilbert 1987).

Behavioral defenses. Diel vertical migration, whereby zooplankton descend to depth during daylight hours and ascend again to feed during darkness, is often attributed to a behavioral response to predators which hunt by sight (Zaret & Suffern 1976, Ohman et al. 1983). Direct support for this notion comes from experiments in which the amplitude of migration varied in proportion to predator abundance (Gliwicz 1986) and predation pressure (Bollens & Frost 1989). The freshwater cladoceran *Daphnia* also avoids predatory invertebrates by migrating upwards in their presence (Dodson 1988, Ramcharan et al. 1992), while the invertebrates themselves remain at depth during daylight to avoid predation by visually feeding fish (Roth 1968). Provocatively, both marine and freshwater crustacean zooplankton can reverse their migrations in response to surface-feeding predators (Dodson 1988, Ohman 1990), indicating behavioral flexibility rather than strict genetic programming. As observed for the inducible morphological defenses, the behavioral responses appear to be triggered by chemical signals released by feeding predators (Dodson 1988, but see Bollens et al. 1994 for marine copepods). Such anti-predator defenses may have costs in terms of reduced nutrition when feeding and defense are both dependent upon motility (Werner & Hall 1988, Ramcharan et al. 1992). For example, among marine zooplankton, those taxa which are especially visible to fish predators feed primarily at night (Hobson & Chess 1976).

Behavior such as DVM apparently evolved to minimize encounters with potential predators. Copepods

(and presumably other metazooplankton) also have sensors which detect variations in mechanical stimuli, irradiance, and chemical gradients, and these provide defense mechanisms to reduce the probability of capture after encounter. Copepods, especially, are capable of rapid accelerations resulting in short-term swimming speeds of many body lengths per second (Strickler 1975). Their combined perceptive abilities and escape responses function to avoid potential predators which are stationary (Haury et al. 1980), drifting above (Buskey et al. 1986), in pursuit (Singarajah 1969), or are attempting to entrain prey in their flow fields (Trager et al. 1994). Developmental stages as well as adults are capable of escape responses (Yen & Fields 1992), although the vulnerability to capture varies with prey taxa (Drenner et al. 1978), size and morphology (Confer & Blades 1975), and developmental stage (Greene & Landry 1985). Likewise, fish vary in their ability to capture evasive and non-evasive zooplankton (McComas & Drenner 1982, Vinyard 1982), and some can learn to improve capture efficiency for more evasive prey (Coughlin & Strickler 1990). Fish and large zooplankton also exhibit complex behaviorally mediated predator avoidance mechanisms, e.g. swarm formation.

Life history strategies. In the enigmatic phytoplankton *Phaeocystis* (see above) cells form colonies, colonies can increase or decrease in size, and cells can emigrate from colonies (Verity et al. 1988, Cariou et al. 1994), altering the size of *Phaeocystis* by volume factors of 10^6 to 10^9 . While no direct evidence ties life cycle changes to grazing pressure, it is clear that the life history stages of *Phaeocystis* vary in their susceptibility to grazers and potentially structure the herbivore community (Hansen et al. 1994). Another approach is that of bioluminescent dinoflagellates, whose mechanically stimulated flashes reduce their consumption by copepods (White 1979) and increase predation by fish on the grazing copepods (Abrahams & Townsend 1993), irrespective of whether bioluminescence actually evolved as an anti-predatory device. A different anti-predation strategy is exhibited by the copepod *Diaptomus*, which switches from laying subitaneous eggs to diapause eggs coincident with seasonal peaks in predation pressure (Hairston 1987). A further example is the cladoceran *Daphnia*: in the presence of visually feeding planktivorous fish, which are especially effective at removing larger daphnids, *Daphnia* increases its intrinsic rate of population growth (Dodson 1989), reduces juvenile length increments, matures earlier, and lays larger clutches of smaller eggs (Machacek 1993); the latter responses are induced by chemicals associated with the predatory fish. In this regard, it may be that trophic cascades are more likely to occur in the freshwater pelagial because *Daphnia* is

so often the major herbivore: through parthenogenesis it can reproduce as rapidly as its prey and therefore control their stocks, but its swimming behavior leaves *Daphnia* particularly susceptible to population decimation by invertebrate and vertebrate predators (Allan 1976, Lynch 1980, Jürgens 1994).

PREDATION AND TROPHIC CASCADES AS STRUCTURAL PRINCIPLES

We argue that the morphologies and life history strategies of plankton have evolved in relation to their environments. Traditionally, that 'environment' has been considered to be a physical or chemical one, e.g. Margalef (1978) proposed that the functional morphology of phytoplankton is selected by the decay of mechanical energy of water, or turbulence. Kiørboe (1993) argued eloquently that pelagic food web structure is mediated by turbulence and phytoplankton cell size, and that general patterns of mesoscale plankton distributions are consistent with the theoretical bases for such arguments. However, this bottom-up or biogeochemical approach has not proven successful in predicting the timing, magnitude, or temporal dynamics of plankton communities. For example, considerations of fluid dynamics and cell physiology are consistent with the notion that small size is less advantageous to phytoplankton in turbulent waters, but they do not explain the comparative dominance of large cells in such environments, much less the typical dominance of large cells in blooms. Kiørboe (1993) proposed instead that large size provides a refuge from predation, for 2 reasons: the relative abundance of predator to prey decreases as size increases; and the generation times of predators increase more rapidly than those of their prey as size increases, yielding longer lags between phytoplankton growth and zooplankton response. Thus, the risk of being eaten is diminished for larger cells. Banse (1994), too, argued that food web structure cannot be fathomed without equal consideration being given to top-down control.

While the extent of predation between adjacent trophic levels has been the subject of considerable interest (e.g. Sih et al. 1985), here we explore whether the consequences of predation cascade into more distant trophic levels, and the characteristics of predators which are associated with such multi-trophic relationships. *This discussion also has implications for the historically different approaches to limnology and oceanography.* While biology in the marine pelagial has been pre-occupied with biogeochemical fluxes and stock exploitation, freshwater efforts have been quietly dedicated to deconvolving how lakes and streams work. Hence, the following discussion includes exam-

ples from both disciplines, and identifies both similarities and differences between them where evidence warrants.

Although it has been common knowledge among farmers and hunters that both resources and predation are important in structuring plant and animal communities, most ecologists prior to 1960 viewed populations as being entirely resource-driven. In that year, Hairston et al. (1960) published their famous 'the world is green' hypothesis. They began with the observation that excessive or widespread destruction of vegetation by grazers is rare, and thus there was an abundant food source available to herbivores. If the grazers were not food-limited, then their abundance must be restricted by predators, preventing the herbivores from depleting their plant resources. Furthermore, since grazers must be predator-limited, their predators must be food-limited. These ideas were developed for terrestrial ecosystems, while aquatic ecosystems were omitted because they are not always 'green' (N. G. Hairston Jr pers. comm.), but the concepts were later adapted to aquatic habitats (Hrbacek 1962, Brooks & Dodson 1965, Smith 1969, Persson et al. 1992).

The generic form of these hypotheses is that organisms at the top of the food chain are food-limited, and at successively lower levels they are alternately predator- and then food-limited. Changes in food chains with strong trophic links may then 'cascade' from top to bottom (McQueen et al. 1986, 1989, Carpenter et al. 1987). The trophic cascade model predicts that, by their presence or absence, higher trophic levels will determine whether or not conspicuous accumulations of plant biomass will occur at the base of the system. The largest body of evidence supporting the trophic cascade model derives from freshwater habitats (Strong 1992; see McLaren & Peterson 1994 for a recent terrestrial example). One reason why trophic cascades may be more likely to occur in aquatic than in terrestrial habitats is because water is so much denser than air that plants can be physically supported without having to put the vast majority of their primary production into relatively inedible structural components, as do terrestrial plants. Being small and of high nutritious quality, they can be eaten in their entirety by small grazers, for which prey capture is typically gape-limited (Zaret 1980), leading to a size-structured food chain. Thus, there is little cheating in plankton-based food webs, because predators have to be big enough to eat their prey in its entirety (Hambricht et al. 1991), unlike browsing herbivores in terrestrial ecosystems. Hairston & Hairston (1993) developed this idea further, suggesting that predator:prey size ratios in pelagic systems (where they may be size-dependent; Longhurst 1991) are likely to be substantially larger than those typical of terrestrial ecosystems.

In the marine pelagial, little attention was given for many years to the possibility that top-down forces might be important. In part, this reflected the biased view of phytoplankton ecologists that production of algal biomass was limited by availability of nutrients or irradiance, and that accumulation of biomass depended only upon the extent of production. This bottom-up or resource interpretation was indirectly supported by the traditional view of marine food chains as diatoms → copepods → fish (see Kleppel 1993 for origins), because estimates of grazing impact by copepods typically were ca 10 to 50% of primary production (e.g. Mullin 1969, Kiørboe 1991). This apparent inability to keep pace with algal growth implied that phytoplankton were not grazer-limited and that copepods were not food-limited (Huntley & Boyd 1984). Studies showing strong dependence of copepod growth upon temperature (Huntley & Lopez 1992) also implied that food was not limiting.

Since that time, contemporary thinking about plankton community structure has undergone a revolutionary reversal, a change too significant to be merely labelled a new paradigm. In one generation, the hundred year old view that diatoms were the pastures of the sea has been replaced with the notion that much smaller cells are the workhorses in the euphotic zone (Pomeroy 1974), with occasional diatom blooms superimposed on their productivity. It is this microbial food web that tracks changes in controlling physical and chemical processes; diatoms leave and enter the system according to their own unique biology (Smetacek et al. 1990, Lenz 1992). With the recognition of pico- and nano-sized autotrophs and mixotrophs came the understanding that small zooplankton were often the dominant herbivores (references in Pierce & Turner 1992), and estimates of their grazing plus that of larger zooplankton can equal or exceed that of primary production (e.g. Lenz et al. 1993, Verity et al. 1993). The possibility of predator (grazer) control of

prey became more distinct, especially given the capabilities for prey selection evidenced by both proto- and metazooplankton (Cowles et al. 1988, Verity 1991).

However, there are relatively few instances of actual trophic cascades in marine waters across 3 or more levels (Table 1). Of these, some are direct experimental manipulations, some are merely interpretations of gross patterns in field communities, and some include models of laboratory or field studies. The most compelling evidence suggests that certain plankton food webs may show coupled population oscillations with trophic levels limited alternately by predation and resource availability (e.g. Horsted et al. 1988, Dolan & Gallegos 1991). Provocatively, fully three-quarters of the cascades in Table 1 were initiated by gelatinous predators, which suggests that their ability to rapidly increase population biomass, their high weight-specific ingestion, and/or their large predator:prey size ratios, may be key characteristics in pelagic organisms involved in trophic cascades. It has been argued that trophic cascades are unlikely in the absence of keystone predators (Strong 1992). Alternatively, the common denominator may be moderate-to-strong predation pressure rather than a true keystone predator (Menge et al. 1994). For example, the occurrence of gelatinous carnivores is not always associated with obvious trophic cascades (Purcell et al. 1994).

Only 2 regional assessments of the potential importance of trophic cascades in marine pelagic ecosystems have apparently been published. In both the Baltic Sea and the Chesapeake Bay, USA (Verity 1987, Rudstam et al. 1994), limited evidence suggested that trophic cascades may be seasonally or historically important, but convincing documentation was not available. It has also been argued that trophic cascades may be responsible for patterns in plankton biomass in HNLC (high nutrient low chlorophyll) regimes such as the subarctic

Table 1. Examples of trophic cascades influencing the structure of marine pelagic communities. Mesoz.: mesozooplankton; microz.: microzooplankton; nanoz.: nanozooplankton; phytopl.: phytoplankton

Location	Cascade	Data source	Citation
Roskildefjord, Denmark	Sticklebacks → Mesoz. → Phytopl.	Enclosure	Horsted et al. (1988)
Limfjord, Denmark	Mussels → Mesoz./Microz. → Nanoz. → Bacteria	Enclosure	Riemann et al. (1990)
Loch Ewe, Scotland	Ctenophore → Mesoz. → Phytopl.	Enclosure	Gamble et al. (1977)
Narragansett Bay, RI, USA	Ctenophores → Mesoz. → Phytopl.	Enclosure/field	Deason & Smayda (1982a, b)
Rhode River, MD, USA	Rotifers → Nanoz. → Bacteria	Enclosure/model	Dolan & Gallegos (1991)
Vancouver Fjord, BC, Canada	Medusae → Mesoz. → Phytopl.	Field observation	Huntley & Hobson (1978)
Kiel Bight, Germany	Medusae → Mesoz. → Phytopl.	Field observation	Möller (1979)
North Sea	Euphausiids → Copepods → Phytopl.	Field observation	Roff et al. (1988)
Gullmar Fjord, Sweden	Medusae → Mesoz. → Phytopl.	Field observation	Lindahl & Hernroth (1983)
Helgoland Bight, Germany	Ctenophore → Ctenophore → Mesoz.	Field observation	Greve & Reinert (1980)
Chesapeake Bay, USA	Cteno/Medusae → Mesoz. → Phytopl.	Field/model	Baird & Ulanowicz (1989)

Pacific (Frost 1991), and that recent accidental introductions of ctenophores into the Black Sea have caused significant structural changes (Kideys 1994).

The apparent importance of gelatinous predators in the few reported marine trophic cascades may also reflect on the role of fish in this capacity. While density-dependent competition for food is a general feature of larval and juvenile fish (Valiela 1984), fishery ecologists generally hold that stocks of adult fish are not limited by their resources and thus cannot limit them (Cushing 1975). This conclusion is supported by several typical features of fish populations, including: the lack of a density-dependent stock-recruitment relationship, the occurrence of strong year classes developing from weak spawning events, and the huge variation in fish recruitment among years with no evidence of similar variance in prey production. All of these features support the notion that populations of adult fish in the oceans are seldom likely to control the abundance of their prey, in contrast to the evidence from freshwater systems. It has been speculated that fish in the oceans are 10 to 1000 times less abundant than their freshwater counterparts (Horn 1972), perhaps accounting for their apparent lack of predatory impact. If this comparative dilution of fish in the sea is correct, the mechanism would seem to be the huge mortality losses applied primarily during embryonic and larval development.

It may be instructive to consider why trophic cascades appear so well developed in freshwater compared to in marine pelagic ecosystems. An important distinction is that taxonomic diversity of the freshwater pelagial is simplified compared to that of marine waters (Valiela 1984). For example, a variety of herbi-/omnivores (Lehman 1988) and carnivores (Greene 1985) are missing, including the near-absence of planktonic ambush predators and clupeid-like fishes (Banse 1990). Moreover, feeding at more than one (lower) trophic level may be more extensive in saltwater because of the common importance of mixotrophic ciliates there (Stoecker et al. 1989, Putt 1990); mixotrophic flagellates are well developed in both fresh- and saltwater (Sanders 1991). In general, mixotrophy appears more important in oligotrophic vs eutrophic waters (Arenovski 1994). If omnivory and generalist feeding are common in marine waters, and if such trophic diversity reduces the likelihood that, e.g. a climatically induced, strong year class of predators would decimate only a single trophic level, then trophic cascades may be minimized there or difficult to validate unequivocally. However, although the success of trophic level manipulation experiments in freshwaters implies that omnivory there is not sufficient to obscure distinctions between trophic levels (Hairston & Hairston 1993), the converse (that extensive omnivory pre-

cludes trophic cascades) is not necessarily true. If cascades are less likely in oligotrophic environments, due to strong substrate control, then the better documentation of cascades in freshwater may reflect the generally more productive trophic status there compared to marine waters (Valiela 1984). Also relevant may be the life history of *Daphnia*, whose reproductive strategy is designed for rapid colonization and for export to new environments (e.g. by duck's feet), but whose motility behavior prevents it from holding space in the presence of visual planktivores. It is indeed intriguing that the predators most common in marine cascades (jellies) are essentially absent from freshwater, where cascades have been more commonly described, while the freshwater herbivore typically linked to cascades (cladocerans) are unimportant in marine waters.

ROLE OF PHYSICS AND IMPLICATIONS FOR DESIGN OF FUTURE STUDIES

Ecological communities and physical processes vary in time and space across a broad range of scales (Marine Zooplankton Colloquium 1 1989, Powell 1989). In the ocean, the space-time scales of biology and physics are nearly coincident, so it is likely that their interactions are closely coupled (Steele 1991a). If so, positive correlations might be expected between the variabilities in physical and biological processes (Walsh 1977), although correspondence does not establish cause and effect. Physics and biology are best integrated at mesoscales where biology can be budgeted, e.g. as energy or mass, analogous to the physical laws of conservation of energy, mass, and momentum (Denman & Powell 1984). At these scales there is good evidence for strong influences by the physics of ocean circulation on the biology of fish and plankton. One example is the close correlation between ocean currents and life cycles of fish such as herring, driven by climatic variations (Steele 1991b). At the population level, this is explained by links between mesoscale mixing and reproductive processes. However, changes at the community level, such as switching between dominance by pelagic versus benthic fish, have not been explained. On the other hand, there is also no indication that dramatic changes in fish stocks (abundance or composition) in such areas as Georges Bank or the North Sea have cascaded down to impact zooplankton (Koslow 1983, J. H. Steele pers. comm.).

The present paper addresses mechanisms whereby individual species, their characteristics, and their interactions contribute to ecosystem structure. Thus, the central question in the context of physics is at what spatial and temporal scales do community parameters become less significant than species attributes (behav-

ior, morphology, life cycles) in determining apparent success, i.e. standing stocks (Steele 1991a)? While the larger scale physical processes previously discussed also cascade down to the level of the individual, e.g. turbulence effects upon encounter rates (MacKenzie & Leggett 1991), 'conservation laws for mass, energy, and momentum ... are not sufficient to understand ... competition, predation, species succession and diversity, etc.' (Denman & Powell 1984, p. 127). Although at larger scales the 'concept of ecological succession ... does not seem appropriate to the changes in marine systems where we explain changing community patterns in a physical context' (Steele 1991a, p. 433), it can also be argued that organisms, especially successful key species, have evolved to take advantage of the higher frequency variability at smaller scales.

Other aspects of physics are relevant to evaluating the role of predation and key species in structuring pelagic ecosystems, and they are advection, dispersal, and patchiness. As discussed in the previous sections, there is sufficient theoretical and experimental evidence to show that predation, morphology, and key species are crucial in structuring marine pelagic communities. However, much of the experimental support derives from contained populations or from descriptive field data, so that the significance of predation-driven forces in open waters remains uncertain. Both supportive and dispositive data are available. The major weakness of descriptive data from open waters is that absence of evidence is not evidence of absence. The problem with containment, however, is that enclosures must be sufficiently large to mimic the real world. For example, if they offer no refuges or lack natural feeding guilds to utilize changing resources, then discrepancies will occur between theory and experimental results. Thus, perhaps the ideal environment in which to test these hypotheses is an enclosed body of water with naturally restricted exchange with adjacent waters, e.g. Landry (1978). The ctenophore-zooplankton-phytoplankton cascade observed in Narragansett Bay (Rhode Island, USA; Deason & Smayda 1982a, b), which has a turnover time of ca 26 d (Pilson 1985), is perhaps the best example to date.

A related issue is that patchiness, dispersal and advection cause significant sampling artifacts in marine ecosystems. The latter problems are minimized in small lakes, perhaps contributing to better documentation of trophic cascades there, or perhaps simply making cascades more likely to occur; large lakes are more complex (Schelske & Stoermer 1994). Thus, it is not so much whether predation or trophic cascades structure marine plankton communities, but whether we can provide definitive approaches and methodologies to test competing hypotheses. Top-down forces may not cascade in the pelagial because advective processes

act to separate predator and prey before cascades can be complete, i.e. disequilibria, or because seasonal weather patterns 'reset' the system, e.g. Landry (1977). Or perhaps top-down forces may be operating but cannot be confirmed because advection separates us in space from processes in different stages of temporal equilibrium. These sampling issues have long hindered pelagic science, whether chemistry or biology, but in trying to determine the forces structuring an ecosystem, there is an additional, formidable obstacle: trophic identifications for each major taxonomic group are also necessary. Some techniques have been developed to sample over large spatial and temporal scales, to minimize problems of sampling statistics. For example, acoustics can be used for fish stock assessment over large scales; but can the return echoes distinguish a planktivore from a primary carnivore from a secondary consumer? The crux of the problem is the extent to which we are comfortable trading realism for analytical accuracy: our conceptual models and scientific methods must necessarily be 'a judiciously chosen set of lies, or perhaps more accurately put, partial truths about reality, which have been chosen to permit us to reason more effectively about some issue than we otherwise could' (Baumol 1984).

Let us assume for the moment that one has carefully designed an experimental test, and sampling was spatially and temporally complete. Do complications exist which could impede interpretation of the data? Evidence from both freshwater and marine habitats suggests that several factors may obfuscate data analysis. For example, predator-induced effects may occur but may not be evident as changes in population abundance or as bulk removal. Rather, the affected populations may alter patterns in vertical distribution or migration (Rudstam et al. 1994), the taxonomic composition of a trophic level may change (McCauley & Briand 1979), or its size structure (Hrbacek 1962). As such, food webs may not collapse clearly into food chains. Moreover, 'tangles in trophic architecture' (Strong 1992) (i.e. omnivory, mixotrophy, substitutability of species, compensation among taxa for functions of others, inedibility, mobility and defenses) may prevent the occurrence of key species upon which sustained consumption can more clearly take its toll. Top-down and bottom-up regulation can be additive, for example, starving fish larvae may be more susceptible to predation, or both forces can be (differentially) influenced by the same abiotic factors, e.g. increased irradiance stimulates both primary production and visual predation (Aksnes & Giske 1993). Conversely, relationships between trophic levels may be non-linear (Dwyer & Perez 1983), non-additive (Stoecker & Evans 1985) or exhibit threshold dynamics: predation impact upon a prey population may be sustainable up to a cer-

tain point, beyond which drastic declines in prey abundance occur. If ontogenetic changes (e.g. dietary) or time lags between prey consumption and predator reproduction occur, top-down effects may be obscured (Power 1992). Finally, physical processes on long time scales may dominate shorter frequency biological interactions (Aebischer et al. 1990), so that any top-down effects are muted or invisible.

CLOSING THOUGHTS

Theory is rather explicit about the conditions under which resource availability and predation should dominate trophic interactions. On the other hand, the real world is seldom as simple as theoretical boundary conditions (Pimm 1992). Research during the past 50 yr has shown that not all plants are equally edible, not all herbivores are equally effective, not all predators are equally proficient, and not all environments are equally hospitable (Hunter & Price 1992). The considerations in this paper illustrate that it can be simpler to construct pragmatic post hoc explanations for observed patterns in trophic structure than it can be to devise sound theoretical underpinning.

We propose that biogeochemical fluxes are spearheaded by key taxa, perhaps even 'keystone species' (sensu Bond 1993) whose environmental adaptations, whether through behavior, morphology, physiology, or life history, are so strong that they direct trophic relations. Some specific examples were postulated in the section on life histories and morphologies. We have argued that dominant species in the marine pelagial attain their status as much by reducing mortality due to predation as by increasing growth or reproductive rates. While it can still be instructive to ask whether top-down or bottom-up forces regulate community structure, because the regulatory mechanisms are distinctly different, we suggest a new synthetic focus: *'How does the pelagic environment select for life histories, morphologies, and behaviors of organisms under conditions when food availability and predation both affect trophic interactions?'* In our rush to get into explanatory modelling, planktologists have trodden on the species and stuffed them into trophic boxes, pyramids or size fraction relationships. The underlying assumption has been that the categories comprise homogeneous units. Recent work is leading to differentiation and also to expansion of our knowledge of pelagic system structure and its shaping forces: picoplankton and protozoa of the 1980s are now extended into viruses and parasitoids. At the same time, group-specific differences in behavior are coming to light that make it necessary to discriminate smaller constituents within the tidy boxes: compare Longhurst's (1991) box

model with that of Steele (1974). We now advocate opening the boxes, taking out the dominant species and studying them at their relevant levels of selection (e.g. predator avoidance, life cycle strategy) and not just growth physiology (ICES 1994).

This proposal has implications for contemporary ocean science, which is being increasingly focused on large-scale, interdisciplinary programs. Some of these are designed to derive horizontal or vertical fluxes of elements which have anthropogenic or geochemical significance, e.g. the carbon-based Joint Global Ocean Flux Study (JGOFS). Others concentrate on establishing the linkages between predator and prey, and their relation to physics, in order to describe ecosystem function, e.g. Global Ocean Ecosystem Dynamics (GLOBEC). The paths are distinctly different, yet the long-term objectives are identical: an improved mechanistic understanding of ocean dynamics and the ability to predict future changes. *The inescapable conclusion from the present analysis is that attempts to identify the forces structuring the marine pelagial must be specifically designed to address that question, i.e. organism-organism and organism-environment interactions, and not to measure carbon fluxes.* This is simply because adaptation and selection operate at the species level. But the connection between organism- and element-driven oceanography is that the transfer of elements or energy through the system depends upon trophic structure and activity (Hairston & Hairston 1993): the composition of the biological pump determines its efficiency of operation. One can no more predict carbon fluxes without a mechanistic understanding of ecosystem structure than one can deconvolve the mechanisms from flux measurements alone: flux estimates cannot predict whether sardines vs anchovies, or herring vs mackerel, will dominate, but evidence *does* suggest that species determine fluxes. A study could be envisioned where both approaches are applied concurrently: thus, the thermodynamic constraints on the system (e.g. light field) could be derived from measurement of total community metabolism or throughput. The deviation of in situ instantaneous rates from theoretical maxima indicate the 'state' of the system and would be necessary to define the units in structural terms; i.e. how much of the energy is diverted to deterrents or flight muscle and how much to reproduction of DNA supporting living plasma. Only by combining the 2 approaches will we ever understand how pelagic environments select their inhabitants and how the inhabitants determine energy flow and material fluxes.

Banase (1994) argued insightfully that 'in regard to more realistic modeling of food webs .. we are short on explicit theory, not only for marine and freshwater systems, but also for ecology in general'. He, too, pro-

posed that research should focus on the biology of key species, but did not believe that scientists and funding agencies would support endless autecological investigations. The avenues we suggest here are not to concentrate so much on metabolic assessments or to search for minutiae, which are unlikely to differ much among species, but to identify critical aspects of life history, morphology, or behavior. These should be examined in the context of rigorous testing of explicit hypotheses. For too long we have shied from playing Pandora, that is, harnessing courage to curiosity. By studying individual species in greater detail, we will be able to understand the shaping forces of the abiotic environment on the one hand, and biotic interactions, including competition and predation, on the other. In answering this question we can truly integrate ecological concepts with predictive models, and make significant purchase in our climb toward understanding pelagic processes.

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