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WHY IS RELATING PLANKTON COMMUNITY STRUCTURE TO PELAGIC PRODUCTION SO PROBLEMATIC?

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The conceptual framework for quantitative marine ecology is attributable to Victor Hensen (1887), who proposed that quantitative studies of plant and animal production in the sea would permit predictions of annual fish yields. Hensen was strongly influenced by concurrent conceptual developments in agriculture, in which crop production was being predicted from knowledge of physiology and its relationship to environmental variables. As fish were being "harvested" by man, it was argued that relationships similar to agriculture existed between primary production and fish yield. Thus was born the notion that pelagic ecosystems were structured from the "bottom-up", or resource-limited. Subsequent refinements argued that, from basic knowledge of how vertical mixing regulates primary production, and assuming certain features of food-chain length and efficiency, one can estimate fish yields. Fundamental to these arguments are assumptions concerning resource limitation which appear to be uncertain as generic marine pelagic characteristics, primarily that trophic levels are nutrient/food limited and respond to increased resource availability by elevated standing stocks. Whereas this conceptual model explains certain features of energy flow, it fails to describe how marine pelagic foodwebs are structured and why they function as they do. Rather, it appears that certain taxa are better than others at integrating their environments and regulating the flux of materials through the foodweb, and that predation is as important as resource limitation. There appears to be a distinct need in pelagic research to focus on predation, not as a rate process so much as a mechanism responsible for organism behaviour, morphology, life history and community structure.

Why is relating plankton community structure to pelagic production so problematic? It is an interesting question to attempt to answer. Certainly, the various components of plankton communities can be quantified. Further, many species properties, for example morphology, life history stage and certain aspects of physiology, can be determined in considerable detail, and there is promise of improved precision using tools such as molecular genetics. Nevertheless, although these general features have been identified, appreciation of the nature of the properties that gear a given species to a specific aquatic environment, and which are responsible for its occurrence, persistence or dominance in a given water mass, is poor at best. Knowledge of temporal and spatial distribution patterns of many species is now fairly sound, yet it is not known why they occur when and where they do. Therefore, efforts at prediction often fail.

Consider the terrestrial example: it is known how water supply regulates the extent and type of vegetation, e.g. forest v. grassland v. desert. Specific morphotypes, such as tree roots, trunk and crown, are recognized as adaptations to a combination of environment and competition. Within the primary morphotype "tree" can be distinguished those resistant to fire and those less susceptible to generalist herbivores (from insects to mammals) on the basis of bark, leaf type, presence or absence of secondary chemicals (ethereal oils, alkaloids). Also because such properties are conspicuous, it is possible to predict the mechanisms of adaptation to specific environmental factors. Indeed, on the basis of community structure alone, habitats can be defined and boundaries recognized that are in reality dictated by the abiotic environment. The same applies to terrestrial animal populations, because their patterns are regulated more by the composition of the plant cover than by abiotic factors. Thus, ecosystems in the African savannah or the Drakensberg Mountains can be visualized, described and understood.

It is further possible intuitively to quantify energy flow in terrestrial ecosystems using simple relations. For example, productivity of the grass prairies is highly correlated with seasonal rainfall patterns, which exhibit considerable interannual and mesoscale variability. The size, abundance, fertility and migration routes of the large ungulates are strongly linked to spatial and temporal patterns of primary production (Coe *et al.* 1976). Whereas prairie grazers consume a greater fraction of primary production than in other terrestrial ecosystems (references in Hairston and Hairston 1993), fire and detritivores remove even more (Sinclair 1975). As a result, it is apparently predation, primarily by the large cats, and not food limitation which regulates herbivore density (Sinclair 1985). This dependency is evidenced in the ratio of muscle to body mass

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in felines and their prey. Predation avoidance strategies, whether by flight or fight, select for investment in speed and/or strength, and therefore lots of muscle roams the savannah (Hildebrand 1959, Schaller 1972). However, the relationship is complex: seasonal shortages of grass attributable to inadequate rainfall result in herbivores too weak from intraspecific competition to post lookouts within the herds or to escape the cats, who then proliferate. In contrast, seasonal rains and ensuing grasses support sufficient nutrition for speed and good judgement by herbivores, such that the cats decline and their litters become smaller. These seasonal or short interannual patterns may differ from longer term effects, e.g. increases in rainfall in the dry season are associated with more abundant populations of herbivores and carnivores (Sinclair and Norton-Griffiths 1979).

Is there, however, comparable knowledge for the marine pelagic biome? The view espoused here is that aquatic ecosystems generally, and marine pelagic ecosystems specifically, are comparatively opaque. While they may function according to similar principles (discussed below), pelagic ecosystems cannot be observed and studied at the same fundamental level as the terrestrial systems in which mankind evolved and that mankind intuitively understands. Rather, conclusions concerning the structure and function of marine pelagic biomes are invariably derived from inadequate information collected in limited temporal and spatial domains, interpreted within conceptual expectations derived from terrestrial experience. Those expectations find their origin in longstanding assumptions: first, that resource availability regulates stock size; second, that predation has little significant impact; and third, that marine foodwebs can be modelled effectively using linear agricultural perspectives. These assumptions may need re-evaluation, possibilities for which are examined below.

HISTORICAL CONTEXT

Victor Hensen (1887) is generally considered to be the father of quantitative marine ecology. Hensen began with the assumption that food supply regulated adult fish stocks, and then proposed that quantitative studies of phyto- and zooplankton production would permit predictions of fish yields. He expected simple linear relationships among hydrography, plankton and fish, and specifically reasoned that, because marine waters were homogeneous compared to terrestrial systems, relationships among trophic levels measured in small samples could be extrapolated to larger scales. Conceptual developments in agriculture at that time significantly influenced his reasoning, because agricultural scientists were predicting crop yields from plant physiology and controlling environmental variables. As fish were being "harvested" by man, Hensen (1887) proposed that similar relationships likely existed in the sea. From these assumptions and deductions was born the notion that pelagic ecosystems were structured from the "bottom-up", or resource-limited (see Smetacek and Pollehne [1986] for further details).

This perception that resource availability was responsible for patterns and processes in the marine pelagial influenced thinking for the next century. During this time the notion was continuously reinforced that phytoplankton dynamics reflected regulation only by environmental variables, e.g. light, temperature and nutrients. Early development of quantitative analytical methods to measure nutrient chemistry supported the perception, by documenting direct relationships between nutrient availability and phytoplankton growth.

Production losses were considered minor, and the occurrence of phytoplankton blooms was put forward as sufficient evidence that zooplankton grazing could be ignored. Concurrently, zooplankton studies were inadequate to debate this view because, even though quantitative nets were available, the amount of work necessary to enumerate organisms resulted in inadequate datasets. Moreover, mesh sizes were too large so, even though Lohmann (1908) documented the abundance of small colourless single-celled zooplankton and quantitatively estimated their potential role as herbivores, his penetrating observation fell upon deaf ears. Accordingly, the combination of perceptual biases, nets of coarse mesh, strong preservatives inadequate to delineate plant from animal cells, and low magnification objectives, led to several generations of reinforced interpretation that large resource-limited organisms in a linear food chain led predictably to fish yields (see Banse [1992] for additional discussion).

MICROBIAL FOODWEBS, DETRITUS AND MIXOTROPHY

Beginning in the 1970s, several major conceptual revelations revised this paradigm of a linear food chain composed of relatively large multicellular organisms which were resource-limited. Pomeroy (1974) proposed that aquatic bacteria functioned very differently from terrestrial bacteria. In addition to decomposing non-living POC, aquatic bacteria also utilized the dissolved organic matter leaching from phytoplankton and excreted by zooplankton as carbon sources for growth. Apparent utilization was such that considerable bacterial biomass was available as the basis of an alternative "microbial" foodweb composed of protozoan grazers, the same organisms discovered by Lohmann (1908). Further research showed huge numbers of tiny phytoplankton also being eaten by protozoan zooplankton, and all contributing to the DOM pathway back to bacteria (Azam *et al.* 1983).

The technological basis for this conceptual revision was the adaptation of fluorescence microscopy from medicine into plankton ecology, which showed that bacteria were 100 times more numerous than plate counts suggested. Unfortunately, it was assumed but not documented that "fluorescently stained" bacteria were all living. It now appears that this assumed equality is incorrect (Zweifel and Hagström 1995, Choi *et al.* 1996). Rather, evidence is accumulating that perhaps only 10–40% of DAPI-stained bacterial cells are alive and metabolically active, a similar percentage are non-living, and the remainder, which constitutes a significant fraction, are metabolically inactive but not dead (Williams *et al.* in prep.). The implications of these findings for the relationship between primary production and fish yield are noteworthy: bacterial production is often considered to be a "tax" on primary production. When bacterial production is estimated from bacterial abundance or biomass, as often occurs in models, then the tax on phytoplankton in the past has been overestimated to the extent that many bacteria are inactive or dead; if so, more phytoplankton carbon is potentially available to pass up the traditional food chain to fish.

Another important distinction is the unique role of nonliving POC in marine pelagic foodwebs. Detritus is essential to the microbial foodweb as both a physical substrate and a carbon source (Angel 1984). Although its quantification was more an art than a science, detritus often appeared to be a larger carbon pool than that of living organic matter. This was not surprising for turbid coastal waters, but the same appeared to be true also of open ocean waters. In the absence of a technique to quantify detritus directly, early research elucidated sources and sinks, primarily biological ones such as faecal matter, degradation of dead organisms, sloppy feeding by zooplankton and microbial activities. Recent novel microscopic techniques may allow for quantitative determination of the volume, carbon and nitrogen contents of suspended detritus (Williams *et al.* 1995, Verity *et al.* 1996). Abiotic conversion, in which exopolymers excreted by bacteria and phytoplankton coalesce into larger microfibrils, colloids and eventually microscopically recognizable (>1 μm) particles, may also be significant (Khaylov and Finenko 1968, Decho 1990). Detrital carbon is significant to aquatic foodwebs because it can enhance survival and reproduction of zooplankton (Heinle and Flemer 1975, Roman 1984); this clearly has ramifications for predictive relationships between primary production and fish yield. Moreover, detritus can be a direct food source for planktivorous fish, and it also increases the filtering efficiency of fish on phytoplankton (Friedland *et al.* 1984). Detritus and detrivores may eventually prove to be as integral to the function of aquatic foodwebs as they are in terrestrial ecosystems.

Mixotrophy was another invaluable discovery associated with fluorescence microscopy. The presence or absence of chloroplasts in numerous taxonomic groups of nanoplankton provided insights into the potential extent of facultative or obligatory autotrophy or heterotrophy. Phytoplankton cultures incubated with fluorescently labelled cells of smaller organisms also showed that some apparent plants could ingest other plants, bacteria, or even heterotrophs (Jones 1994). Some of these were also able to utilize organic substrates for nutrition, in either light or dark conditions. If recent studies, which indicate that 18–86% of small pigmented nanoplankton also ingest bacteria (Havskum and Riemann 1996), are generally applicable, considerable bacterial biomass may be recovered into the phytoplankton-zooplankton-fish food chain. Likewise, some protozoan zooplankton either carry their own functional chloroplasts or else derive them from ingested prey by digesting the prey cytoplasm but retaining the chloroplasts, which remain active for extended periods (Stoecker *et al.* 1988). Thus, the distinction between plants and animals has become blurred, with each group containing members which function in part like the other.

LIMITATION BY RESOURCES OR PREDATORS?

These are but a few examples of the potential complications in rigidly applying a resource-based agricultural model to pelagic ecosystems. This argument does not imply that aquatic ecosystems are always interpreted within conceptual models of terrestrial origin. For example, it is clear that the biological structure of the two environments scales differently with respect to size (Steele 1991). Whereas organisms in both ecosystems exhibit the classic size dependence of growth rates, only in aquatic systems do trophic levels also sort by size. These fundamental differences may well account for why the two environments are so dissimilar in many ways (see Verity and Smetacek [in press] and references therein).

Nevertheless, the conceptual model that marine trophic structure is ultimately regulated solely by resource availability remains established dogma transcribed faithfully (if blindly) across generations. However, the significant question is: how well does the model actually hold up? There is plenty of evidence that primary production is positively correlated with resource (nutrients, irradiance) availability. It also appears that herbivore production exhibits a linear positive relationship with primary production (Cyr and Pace 1993). Nixon (1988) convincingly demonstrated that fish yields are linearly and positively related to primary production. These correlations imply that fish yields and herbivore production are also positively related but, more importantly, that resource or food limitation is common. When taken together, these relationships also validate the original predictions of Hensen (1887), when making comparisons among ecosystems. Nevertheless, this resource-based conceptual model is less successful in predicting other features, e.g. why certain organisms occur where and when they do, or why sardine and not anchovy? It also does not explain patterns or relationships among trophic levels within a given ecosystem.

What if most organisms most of the time are not food-limited? For example, there are large areas of the world's oceans with excess nutrients but low phytoplankton stocks: the regions high in nutrients but low in chlorophyll, such as the Antarctic, subarctic Pacific and equatorial Pacific. In those waters, grazing (predation) is thought to be an important component of the explanation (Miller *et al.* 1991, de Baar *et al.* 1995, Landry *et al.* 1997). Another example: crustacean zooplankton are often considered not to be food-limited (Huntley and Boyd 1984, Huntley and Lopez 1992) because they typically ingest only a small portion of the daily primary production available to them, and detritus, microzooplankton and other resources represent additional food. If they are not food-limited, they must be limited by predation (Hairston *et al.* 1960). Alternatively, it can be argued that, whereas ecosystems are regulated by trophic interactions, the latter are mediated by environments which shift in time and space. However, while substantial evidence ties ocean physics to organism biology (Verity and Smetacek [1996] and citations therein), this environmental variability acts to shift limitation from food to predation and back again.

Although resource limitation has been examined thoroughly, surprisingly little evidence was available until recently to document the occurrence of predation regulation of community structure. Provocatively, most of the examples come from aquatic communities, almost exclusively freshwater (Strong [1992], but see McLaren and Peterson [1994] for a recent terrestrial example). Verity and Smetacek (1996) discuss why trophic cascades, in which changes in composition or stock sizes of higher trophic levels cascade down to affect lower levels, may be more prevalent in aquatic than in terrestrial habitats, and present evidence for their occurrence in marine pelagic ecosystems. In the Benguela upwelling system, there are considerable qualitative and quantitative indications that trophic cascades are responsible for patterns in plankton communities. In regional surveys from the Cunene River south to the Cape Peninsula, waters with high biomass of chlorophyll *a* typically coincided with low euphausiid biomass (Pillar *et al.* 1992). A precedent for such inverse relationships between predator (grazer) and prey was reported by Cushing (1971), who documented that high biomass of anchovy off Peru invariably coincided with low biomass of meso- and macrozooplankton. On the Agulhas Bank in November/December of 1988 and 1989, inverse correlations were found between copepod and anchovy biomass (Peterson *et al.* 1992). In 1988, large stocks of anchovy were associated with very low copepod biomass and high phytoplankton biomass. In 1989, the anchovy stocks were about half those of 1988, whereas copepod biomass was some twice as high and phytoplankton biomass was about 30% lower than the year before (Peterson *et al.* 1992). Those data imply a strong trophic cascade operating in 1988, whereas the weaker year-class of anchovy in 1989 released copepods from strong control and thus phytoplankton stocks were grazed to lower levels.

CONCLUSIONS

Data such as these support the notion that the Hensen (1887) resource-based agricultural model is not the only one applicable to or helpful in interpreting patterns in community structure and carbon flow in marine pelagic environments. Predation is responsible for patterns in the ocean, as it is on land. Copepod body morphotype is designed to avoid predation as much or more than to capture food. The streamlined shape of dominant epipelagic fish enhances escape more than prey capture. In contrast, jellyfish do not need to avoid fast-attacking predators; hence their diverse morphologies (Verity and Smetacek 1996). While energy flows from phytoplankton to fish, whether in a simple linear (Ryther 1969) or more complex (Moloney 1992) foodweb, predation shapes natural communities and should receive equal attention as scientists strive to understand events occurring in a world where intuition serves them poorly. Verity and Smetacek (1996) argued that it is not more studies of feeding rates and other simplistic aspects of autecology which are required, but a synthetic focus on the biology of key species, which are responsible for the bulk of, for example, biogenic cycling and recruitment success, to identify critical aspects of behaviour, morphology and life history. Less focus is needed on black box measurements, but rather more on inferring the significance of phenomena from the structures seen, and from the consequences of those structures.

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