

## The continuity of living matter and the discontinuities of its constituents: do plankton and benthos really exist?

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**Plankton and benthos are popular concepts identifying two ways of life of aquatic organisms. Their spatial separation led to the development of different sampling techniques and to separate conceptualizations of the principles governing these subsets of the aquatic environment. Reciprocal connections between plankton and benthos, however, are very strong both from a functional (energy fluxes) and a structural (life cycle dynamics) point of view. A full appreciation of such links is forcing marine ecology towards a more integrated approach.**

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The marine environment is usually divided into benthos and pelagos. Pelagos is further fractionated into sub-components such as neuston, plankton and nekton, although these cannot always be treated as autonomous communities: nekton, for instance, includes no primary producers.

The abundance of plankton shows cyclic variation between high and low values, especially at polar, boreal and temperate latitudes. If plankton were a compact unit, that is, an individual, the variation could be explained by invoking its expansion and shrinkage. This is what is implied in the thermodynamic explanation of plankton dynamics, where nutrient availability is the main cause for phytoplankton growth, and phytoplankton availability is the main cause for zooplankton growth<sup>1</sup>. But plankton is not an individual; it represents a group, that is, a class, of individuals. If one splits the 'class' into its individual components (the species), discontinuities become apparent. Many coastal species are

represented by high numbers of individuals for a short time and then disappear from the water column or, in the case of benthos, from the bottom, to 'reappear' at the onset of the next favourable season. Pelagic communities and many benthic ones have discontinuities in the presence of species<sup>2</sup> that need to be explained if we are to understand the cycling of matter and energy through ecosystems.

The seasonal absence of many species is explained by periodic rarity – even though we do not catch specimens, some are present – or by their going 'somewhere else', to deep water, for example, but for other species there is another solution to the problem. Many seasonal organisms spend the adverse season as resting stages, the morphology of which is much different to that of the functional stages<sup>2,3</sup> (Fig. 1). In the sea, pelagic resting stages might remain suspended in the water column as cocoliths or as lecithotrophic larvae or, especially in coastal waters, sink to the bottom and become incorporated into the sediments as spores, cysts or resting eggs. The functional discontinuity in the presence of a species, especially of adults, is compensated for by a structural continuity: the same species is present in different forms (something else) at different times of the year (sometime else) and in different environments (somewhere else).

Resting stages can also explain the discontinuous presence of brackish water species or their cosmopolitan distribution (e.g. that of *Artemia*), or both. Although it is the active stages of species that are mainly responsible for plankton distribution, major geographical or ecological barriers can be crossed by resting stages, and sometimes only by resting stages<sup>4</sup>. For both marine and terrestrial species, the existence of resting stages offers the basis for a new interpretation of such complex phenomena as population and community dynamics, and the distribution and the evolution of species.

### The jellyfish paradigm

Most marine species are known only as adults. Some juveniles have been described, but little has been done to link benthic and planktonic stages, especially for species in which adults are conspicuous and other stages hard to find<sup>3</sup>. Jellyfish are paradigmatic because, like other com-

ponents of plankton, they have discontinuous presence in the water column; we know from their life cycles that when they are absent from the plankton they are present in the benthos in the form of polyps. The modular, polypoid colonies represent the continuity of the species, whereas the medusa is the 'discontinuous' stage that accomplishes sexual reproduction<sup>5</sup>. Such a pattern is likely to explain the sudden disappearance of many coastal planktonic forms. Instead of promoting a conceptual link between plankton and benthos, however, the two-phase life cycle of the jellyfish has resulted in the development by specialists in medusae and polyps of unnatural classifications, with separate taxonomic systems for the two stages. The division between 'plankton' and 'benthos' is so absolute that, even when it is known that an animal is represented by planktonic and benthic stages, each is studied by different people: benthologists and planktonologists. Unfortunately, they rarely communicate.

If this is bad for taxonomy, the harm done to ecology is even greater. For instance, the seasonal blooms of planktonic organisms depend on the availability of both nutrients and propagules (Box 1), but only nutrients are usually considered: the 'founding propagules' are often benthic, but planktonologists do not study benthos and benthologists usually disregard plankton.

### Towards a unified system

A single classification that includes both hydroids and medusae is desirable, not only on the grounds of phylogenetic soundness but also to indicate ecological relationships. Plankton and benthos are useful concepts that meet our psychological need to split topics for ease of analysis, but such analyses must be followed by a synthesis that identifies differences, similarities and links.

The need for synthesis is often taken for granted, but it is seldom carried out. It is surprising, for instance, that the US ecological community feels the need to emphasize the important part played by abiotic factors in conditioning the structure and organization of environmental communities<sup>6</sup>. It is even more surprising that, in supply-side ecology, the role of complex life cycles in structuring marine communities has only recently received proper attention<sup>7</sup>. The need to emphasize the roles of abiotic factors and life cycle dynamics arises because, even though their importance is 'obvious', they are seldom considered during research projects.

Because of the way their communities are studied, discussion of the dynamics of the main marine domains sees plankton as 'explained' mainly by abiotic factors (light,

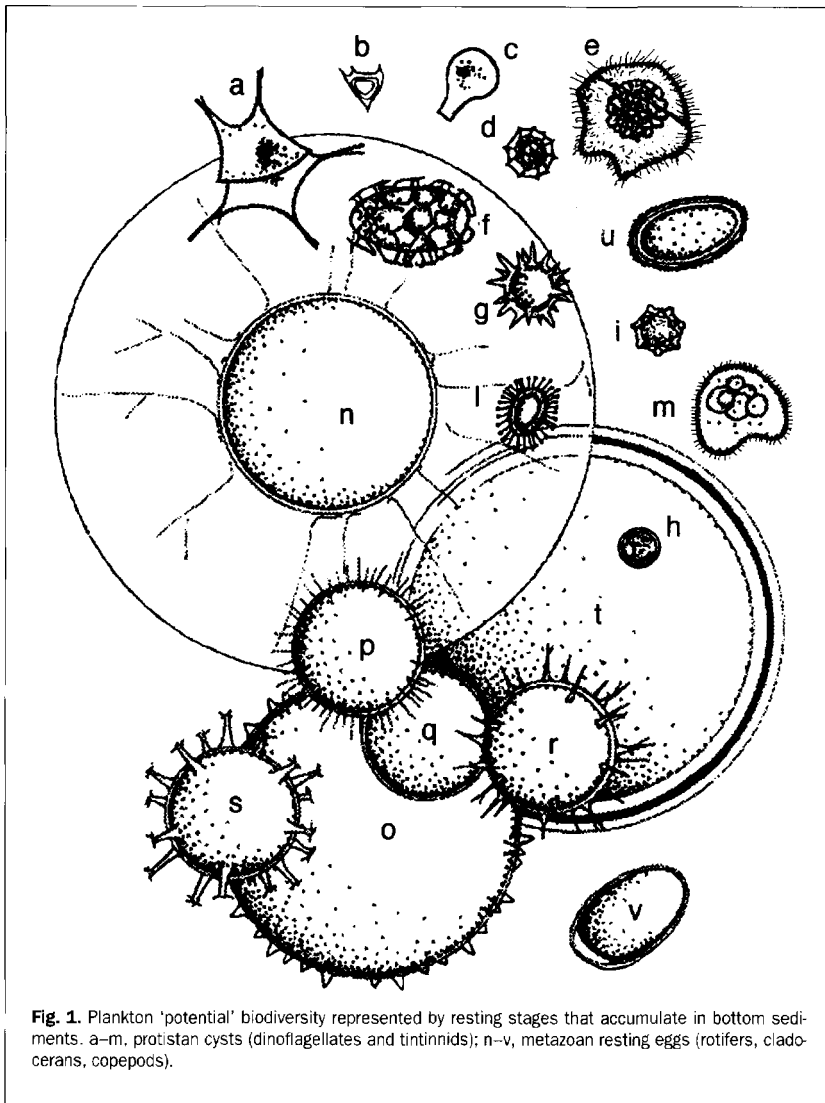


Fig. 1. Plankton 'potential' biodiversity represented by resting stages that accumulate in bottom sediments. a-m, protistan cysts (dinoflagellates and tintinnids); n-v, metazoan resting eggs (rotifers, cladocerans, copepods).

nutrients), nekton (and especially fisheries) by life-cycle dynamics, and benthos by biotic interactions. Benthic research is usually conducted either in the intertidal zone or, especially in coral reefs and hard-bottomed sea areas, by scuba diving so that the organisms can be observed directly in the field. Interactions are evident and persistent, as vagility is reduced even in non-sessile benthic organisms<sup>8</sup>. The small size of most plankters precludes their study *in situ*, and they have to be collected by surface-operated devices, as do soft-bottom benthic communities. The fine spatial and behavioural organization of the natural communities is lost, and because it cannot be observed it is simply neglected. The study of nekton, driven by economic pressures, focuses on life-cycle dynamics and emphasizes the renewal of the resource in terms of recruitment<sup>9</sup>. When observed patterns are correlated with the considered parameters, a cause-effect relationship is usually identified, in

spite of the fact that correlation does not necessarily imply causation. There are exceptions to these generalizations, but inspection of marine ecology textbooks and journals of oceanography and marine ecology will make such patterns evident. None of the main textbooks of ecology or even marine biology considers the role of resting stages in plankton dynamics!

The pattern of asexual reproduction of most subtidal organisms, furthermore, suggests a change of focus in supply-side ecology in the subtidal zone. As Jackson<sup>10</sup> pointed out, intertidal animals are mostly individual, whereas subtidal ones are mostly modular, and this difference has a great influence on their ecology. Individual animals, for instance, rarely reproduce asexually by fission, so that their 'continuity' mostly relies on sexual reproduction. Modular organisms can easily lose pieces<sup>11</sup> that can drift just above the bottom and settle far from their original site of attachment. Such propagules are not a substitute

for the sexually produced planktonic stage, but their role in species distribution has yet to be properly assessed. In the subtidal zone, propagules may comprise mainly fragments that are not sampled by plankton nets and are treated as 'detritus' by benthologists. The use of plankton traps placed on the bottom reveals a great abundance of both algal and animal fragments, some of which settle on experimental plates.

Plankters that feed on the larvae of benthic (and nektonic) organisms, and the plankton-based diet of benthic filter-feeders, represent further interactions between the three compartments. These trophic relations are not properly dealt with, and are referred to under the all-embracing concept of 'larval mortality'. For instance, jellyfish and ctenophores are the main predators of zooplankton, including fish larvae<sup>12</sup>, but their presence is underestimated (if not completely neglected) in most plankton studies. Gelatinous zooplankton clogs plankton nets and 'spoils the copepods', so it is often treated as a nuisance by planktonologists.

But trophic roles are often inferred from limited observation. Polis<sup>13</sup> warned against generalization when assigning functional roles to species or to broader taxonomic categories. 'Phytoplankton', for instance, can comprise protists that can alternately be auto- or heterotrophic. The study of gelatinous zooplankton by scuba or submersible diving<sup>14</sup> is starting to reveal complex interactions and behaviours, similar to those of both benthos and nekton, simply because it is carried out by people who 'look' at the object of their studies. For example, the feeding behaviours of hydroidomedusae vary widely. Some medusae are active filter-feeders on protists<sup>15</sup> rather than the cruising or ambush hunters that most are considered to be<sup>16</sup>. Many hydroids with minute polyps are active filter feeders on phytoplankton, regularly beating their tentacles to create water currents towards their mouth<sup>17</sup>; hydroid feeding specialization can be so extreme that species symbiotic with bryozoans will feed exclusively on the particles gathered by the lophophore of their host<sup>18</sup> or on its lophophore arms<sup>19</sup>. From a trophic point of view, hydroids are commonly considered to be carnivorous, passive, filter feeders!

Again, jellyfish can be a 'paradigm' for future research. They have complex life cycles, showing a stronger link between plankton and benthos than is usually considered to exist (the role of resting stages, having a similar function to that of hydroids, could become a new frontier of marine ecology, if we want to understand fully plankton-benthos dynamics and interactions; see Refs 2,3 for reviews).

### Box 1. Nutrient versus propagule (and especially resting-stage) availability in the causal explanation of plankton dynamics

- During the winter, water movements resuspend nutrients derived from the decomposition of biomass produced during the preceding favourable season.
- Increases in both day length and nutrient availability are required for phytoplankton blooms.
- The spring phytoplankton bloom cannot be started by the few algal cells that survived the winter in the water column. Not all species are represented by these 'survivors', and the drastic decrease in number of each species each year should lead to genetic drift and founder effects, with profound genetic consequences.
- An important contribution to the bloom of phytoplankton might be activation of resting stages floating in the water column or incorporated into the sediments: the 'marine seed bank'. In marine coastal areas, the density of resting stages can reach one hundred million potential individuals per square metre.
- The internal circannual clock of each species might regulate the timing of resting-stage activation (e.g. the diatom-dinophyte succession). Coincidence of activation timed by the circannual clock (a presumably rigid feature) with the onset of the favourable season (a widely varying feature) might account for the relative abundances of the various species in different years, leading to a dynamic equilibrium.
- The relative percentages of producers and consumers in marine seed banks roughly correspond to those in the water column.
- Activation of the 'cyst' of each primary consumer could be associated, or even correspond, with that of the primary producers it lives on. The relative quantities of resting producers and consumers are such as to permit a sudden start of community functioning.
- The time lag between phytoplankton and zooplankton peaks could also result from differential reproductive rates (e.g. 1–3 days for protists, 20–30 days for copepods).

Resting stages constitute a 'potential' biodiversity that is much higher than the 'realized' one formed by active organisms (Fig. 1). They allow continuity of a species when conditions are unfavourable and form a marine seed bank. Hatching of the resting stages starts plankton blooms, which are then sustained or limited by nutrient availability. Plankton and benthos are thus subsets of a single system through which the constituents of living matter flow in both an organized (resting and active stages) and disorganized (nutrients) form.

When resources in the plankton have been consumed, species go back to the benthos (or can remain suspended in the water column) as resting stages.

(Mainly derived from Refs 2 and 3 and references therein.)

Furthermore, jellyfish have complex behaviours (both in the hydroid and the medusa stage) and are a good indication of what is to be discovered by pursuing behavioural ecology of marine organisms.

### Epilogue

It is evident from the picture sketched above that, in coastal areas particularly, plankton and benthos are not independent of each other and cannot be studied as discrete units. Supply-side ecology warned against ignoring the supply of propagules when interpreting benthic communities, and the same warning is appropriate for planktonic communities, supplied continuously or periodically with propagules from the benthos. The study of harmful dinoflagellate blooms encompasses the study of what Dale called 'benthic plankton'<sup>20</sup>, a concept that applies to other phytoplankters, such as diatoms<sup>21</sup>, and to, at least, part of the zooplankton, from copepods to jellyfish<sup>23</sup>. Recent findings show that copepod eggs can remain in lake sediments for 300 years before hatching<sup>22,23</sup> and such a 'strategy' is turning out to be widespread also in the seas. This idea was expressed long ago by Hensen<sup>24</sup>, who proposed the alternation of planktonic and benthic stages as a way of phytoplankton function. The discovery of the 'holoplanktonic' nature of some phytoplankters distracted attention from this model, but the time is ripe to revive it<sup>25</sup>, and to change fundamentally our approach to the study of marine systems (Box 1).

We need concurrently to widen and narrow our focus, taking account of both single organisms (or even molecules) and whole communities, without forgetting that organisms make no sense when isolated from their communities, and that communities are made by organisms. Organisms, furthermore, are not simple energy containers. Even though behaviour cannot be measured with precision, it is through their behaviour that organisms play their parts in the communities.

If there is to be further progress in the study of ecology and evolution, there needs to be a thorough re-appraisal of the elements of these disciplines. It is time to rest in our search for data and models and to focus on more theoretical-philosophical issues. Our envy of the certainties of physics attaches great importance to the patterns or laws that physicists discover, but neglects the epistemological processes that led to the discovery of such patterns. Theoretical physics is a strong discipline, and the backbone of physics: theorization and experimentation are two stages of the same research process. Theoretical biology (with some outstanding exceptions) is rather weak, and often tries to mimic theoretical classical physics, tending to forget history and multiple causality. Pianka<sup>26</sup> rightly warned against giving too much weight to the first 'cause' identified for a given pattern (for instance, nutrient availability to explain plankton dynamics). This could distract our attention, in terms of research performed, from other causes

that may be as important as the first one (for instance, propagule availability or behavioural patterns). Many experimental biologists and ecologists (fortunately not all; see Refs 27,28) regard theory as a bad word, showing some cultural sterility. Do we explore these issues enough, or do we take them for granted? If we do take them for granted can we afford to continue to ignore or, at least, underevaluate them?

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## Genetic and evolutionary consequences of metapopulation structure

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**Extinction and recolonization of populations may have various effects on the degree and distribution of genetic variation, but turnover is generally associated with low levels of among-population variation, in both 'classical' and other types of metapopulation. Therefore, adaptive evolution is unlikely to be promoted by selection among populations. Whether adaptation is promoted or slowed by population subdivision, with or without turnover, remains a subject of theoretical debate.**

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Spatial subdivision, local extinction and recolonization are ubiquitous phenomena in natural populations, and their effects on genetic variation and adaptive evolution have interested evolutionists since Wright discussed these issues in 1931<sup>1–3</sup>. Exploration of these issues using metapopulation models began with Richard Levins' studies on interdemec selection<sup>4</sup>, and continues with great vigor today<sup>5</sup>. Despite the profusion of theory and interest, however, it remains unclear what patterns in genetic variation are associated with metapopulation structures in nature. In this article we attempt to clarify seemingly conflicting ideas on how metapopulation processes affect, or are related to, the partitioning of neutral

genetic variation within and among populations. We then review recent work on the still unresolved question of whether and how metapopulation structure can promote adaptive evolution.

### Is turnover associated with high or low variation among populations?

Theoretical work reviewed by McCauley<sup>6</sup> has explored the effects of local extinction and recolonization on the distribution of genetic variation within and among populations. Interest in this question stemmed from Wright's proposition that differential rates of extinction could drive natural selection at the among-population level. Slatkin<sup>7</sup> argued that such interdemec selection is inherently unlikely, because ongoing local extinction implies ongoing recolonization, recolonization constitutes gene flow, and gene flow will prevent local populations from becoming differentiated. However, Wade and McCauley<sup>8</sup> showed that the outcome depends on the mode of founding of new populations. If colonizing propagules tend to be large and contain individuals from many populations, turnover will have the homogenizing effect described by Slatkin. But if propagules tend to be small and homogeneous, coming from only one or a few source populations, then the turnover of local populations can actually enhance their differentiation. It is important to note that the latter effect does not increase total variation in the metapopulation, but only redistributes it from within to among populations.

These theoretical results leave unclear where, in nature, we may expect to find the combination of moderate to high population differentiation and appreciable rates

of turnover. (Differentiation among populations is usually measured as Wright's  $F_{st}$ , that is, the proportion of total heterozygosity in the metapopulation that is found at the among-population level.) Milkweed beetles on patches of their host plants<sup>9</sup> and fungus beetles on rotting logs<sup>10</sup> exhibited high rates of local extinction ( $2\text{--}10\% \text{y}^{-1}$ ) combined with relatively modest gene flow – conditions that, theoretically, could permit the maintenance of differentiation and the potential for interdemec selection. But in general, 'weedy' species with naturally high rates of local extinction tend to show low values of differentiation among populations, presumably because such species tend to be excellent dispersers (Refs 11–13). Hence, on ecological grounds, the combination of high rates of local extinction with low rates of gene flow among populations seems an improbable one.

Local extinction and recolonization have also been studied by workers in conservation genetics, where most emphasis has been placed on the negative consequences of these phenomena (Refs 14,15). Population turnover accelerates genetic drift, because alleles are lost when populations disappear, so that the genetically effective size of a metapopulation with turnover may be only a tiny fraction of its census size<sup>15</sup>. Examples of low heterozygosity in certain species are therefore sometimes ascribed to a history of population turnover. Because the total genetic variation of the metapopulation is depleted in such cases, there will also be low variation among local populations, in absolute terms (that is, the average number of alleles added per population sampled, and not the proportional among-population variation that is measured by  $F_{st}$ ).

These apparently contradictory effects are reconciled in a path diagram (Fig. 1). The 'direct' path from population turnover to differentiation among populations can be either positive or negative, depending on the mode of recolonization<sup>8</sup>. The indirect and longer-term effect is negative,