

POTENTIAL AND REALIZED DIVERSITY OF COASTAL PLANKTON: THE ROLE OF RESTING STAGES IN ECOSYSTEM FUNCTIONING

Diversidade potencial e realizada do plâncton costeiro:
o papel dos estágios de repouso no funcionamento do ecossistema

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ABSTRACT

Resting stages are the strategy for species to avoid the variability of environmental conditions. In coastal confined marine habitats, variability of conditions is higher than in the open sea, and bottoms accumulate plankton resting stages in the so-called "marine cyst banks". The benthic-pelagic coupling generated by this bi-location of plankton, however, is not clearly evident for all the involved species. This result is due to the still scant knowledge of the life cycles and life histories of single species. The study of plankton dynamics from the benthos point of view is useful and informative and it increases the potential complexity of a planktonic community in a confined area.

Keywords: plankton, life cycles, resting stages, cysts, benthic-pelagic coupling, resurrection ecology.

RESUMO

Estágios de repouso são a estratégia das espécies para evitar a variabilidade das condições ambientais. Em habitats marinhos costeiros confinados, a variabilidade das condições é maior do que em mar aberto, e os fundos acumulam estágios de repouso de plâncton nos chamados "bancos de cistos marinhos". O acoplamento bentônico-pelágico gerado por essa bilocalização do plâncton, entretanto, não é claramente evidente para todas as espécies envolvidas. Esse resultado é devido ao

conhecimento ainda escasso dos ciclos de vida e das histórias de vida de uma única espécie. O estudo da dinâmica do plâncton do ponto de vista dos bentos é útil e informativo e aumenta a complexidade potencial de uma comunidade planctônica em uma área confinada.

Palavras-chave: *plâncton, ciclos de vida, estágios de repouso, cistos, acoplamento bentônico-pelágico, ecologia da ressurreição.*

FRAMEWORK

In a well-known paper on the plankton, Hutchinson (1961) asked biologists to think about the reasons for the seemingly illogical coexistence of so many species in the apparently isotropic water habitat.

Certain species are perennial and are always present in the plankton albeit with variable abundance tuned with seasons. Other species, the so-called “seasonal”, show a period of intermittent presence in the plankton, and absences that are sometimes very long.

The existence of such a strategy for many plankters is well known in freshwater organisms but has been little studied in marine ones. In detail, if the disappearance of freshwater organisms could be linked to excessively adverse conditions (seasonal) including the complete drying up of the water habitat itself, this has never been considered as a possibility for the sea. Notwithstanding this, also marine plankton is composed by species with alternate presences.

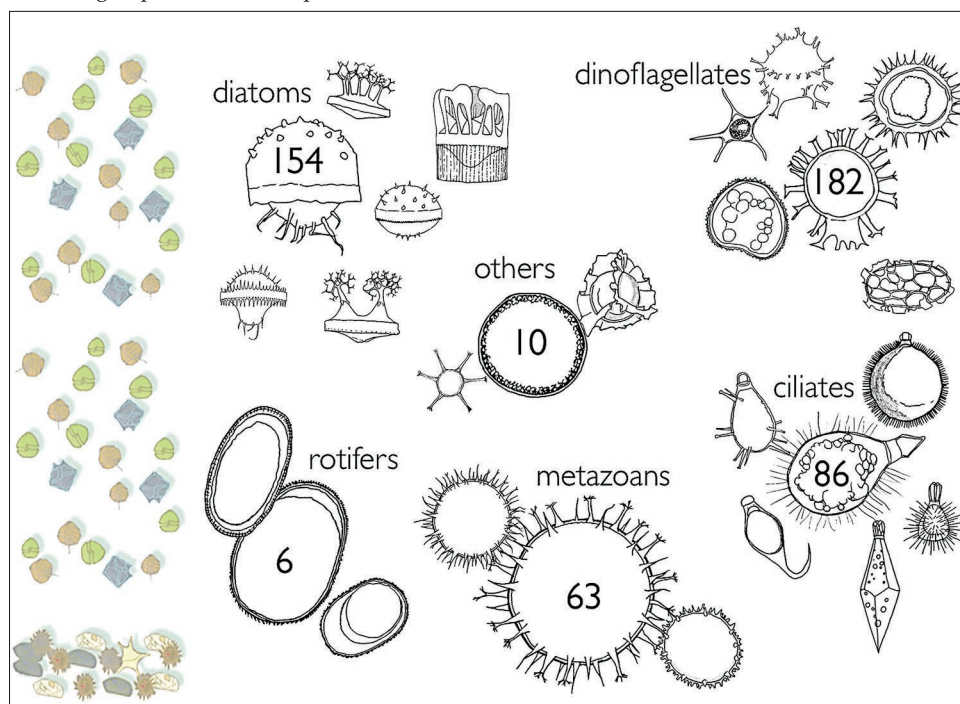
The recognition that species could perform such an alternate presence thank to cycles of encystment-germination to/from resting stages is an important contributor to the understanding of their presence/disappearance from the water column.

The production of encysted resting stages is typical of unicellular organisms, while it is not the only way to rest for planktonic Metazoa which, apart from resting eggs, can enter a lethargic phase also as larvae, juveniles, or adults (see Williams-Howze, 1997; Baumgartner & Tarrant, 2017, for marine copepods).

Marine resting stages of hundreds of species of Protista and Metazoa (501 are listed in Rubino and Belmonte, 2019, Figure 1) share a spherical shape and a spiny surface (Belmonte *et al.*, 1997). The main morphological difference between marine and freshwater Metazoa is the surface (smooth in freshwater resting eggs) and the brooding behaviour (Belmonte, 2021) by the producer organism, i.e., the mother, in the case of freshwater Metazoa. Being laid free in the water column, marine resting stages are equally affected by the dynamic processes which involve the sediment particles, making it possible to share methodologies of investigations with the study of sedimentology and meiobenthos.

The ecological role of resting stages is still underestimated in marine biology textbooks, up to the point that terms like “cyst,” “resting,” or “diapause” are absent from the list of arguments at the end of each volume (see, e.g., Valiela, 1995; Barnes & Hughes, 1999; Levington, 2001; Kaiser *et al.*, 2005). Nevertheless, resting stages are considered responsible for many of the intermittent occurrences of species and for their abundance/rarity cycles in the marine coastal environment (Giangrande; Geraci & Belmonte, 1994; Boero *et al.*, 1996; Belmonte *et al.*, 2013; Rubino & Belmonte, 2019a, 2019b).

Figure 1 - Graphical representation of the number of *taxa* known as resting stage producers in the different groups of the marine plankton



The injection of active stages from bottom sediments was put at centre of the “resurrection ecology” (Kerfoot & Weider, 2004) and, in contrast to supply side ecology (Gaines & Roughgarden, 1985; Lewin, 1986) where recruits arrive from adjacent areas, it pivots on species which subtract themselves from a planktonic role, resting as cysts in the same area of the active forms.

Besides this, resting stages give to the species a high potential of dispersion. Their walls confer mechanical and chemical protection, they can be passively transported in the gut of fishes swallowed by migrating birds (Reznick, 2011) or in the ballast tanks cargo ships, able to survive to the harsh conditions in those environments (Carlton, 1985) and can maintain their vitality also for centuries (Ribeiro *et al.*, 2011).

Many potentially toxic or harmful phytoplankton species produce cysts and this opens another scenario concerning safeguard of human health or the management of economic activities such as aquaculture. But also the contrary is true; the presence of a well structured cyst bank is an insurance for the functioning of the planktonic compartment. Some studies demonstrated as aquaculture farms may negatively affect the survival of the encysted community in the sediments below (Wang *et al.*, 2016) or as fish and shellfish farms may cause a reduction of the hatching success in zooplankton resting eggs.

During recent years, another element was added to the plankton ecology framework, i.e., the finding of resting stages within ice formed in periodically frozen seas (Horner *et al.*, 1992; Brierley & Thomas, 2002). When the ice melts, the resting stages are re-inoculated in the water and germinate to seed new planktonic populations (Garrison, 1991; Horner *et al.*, 1992; Riaux-Gobin *et al.*, 2003; Rozanska; Poulin & Gosselin, 2008). The rest condition, contrarily to the ecological origin of resting stages, is the common feature that probably allows us considering together phytoplankton and zooplankton in a shared study approach.

The state of the art of knowledge about resting stages is mature enough to suggest some future directions of the research.

RESEARCH PERSPECTIVES

Not all plankton groups, even in highly variable environments as confined marine waters are, produce encysted and/or recognizable resting stages. Consequently, a cyst-based strategy to survive unfavourable periods is part (although predominant) of a general framework of species strategies and community dynamics, for each site.

The still not known strategies used by many seasonal species or groups may simply mean that resting stages have yet to be discovered, as suggested by the recent impressive increase of knowledge registered for dinoflagellate life cycles. On the other hand, some species can escape studies on resting stages (cysts or eggs) simply because they undergo a period of rest as larvae or juveniles. Thus, the resting strategy remains the pivotal argument of the dynamics of planktonic communities in variable environments, suggesting that we need to add to the resurrection ecology models, also the species able to rest in the water column.

On the other side, concerning the low knowledge of actors playing the resurrection ecology, we must not forget that not all the resting stages at a particular site are easily assignable to a *taxon* (Rubino *et al.*, 2013; Rubino & Belmonte, 2019), and much effort is still required to resolve this 'simple' descriptive question of "who is who". In such a field probably a solution could derive from e-metabarcoding techniques, which could accelerate the recognition of planktonic species in the form of cryptic stages inside the sediments, thus contributing to depict the complex dynamics of this aspect, i.e., the living link of the benthic-pelagic coupling (Boero *et al.*, 1996).

Another dark side of this framework is the existence of benthic species able to profit of such a rain of encysted biomass sinking from the above water column. Cysts have been somehow recognized as protected from bacterial degradation (Stabili; Miglietta & Belmonte, 1999), chemical aggression (Pati & Belmonte, 2003, 2007), and even immune to intestine juices after ingestion (Marcus, 1984; Redden & Daborn, 1991; Montresor; Nuzzo & Mazzocchi, 2003). Nevertheless, Viitasalo and Viitasalo (2004) and Viitasalo (2007) demonstrated that *Mysida* selectively feed on certain cyst types, thus possibly affecting the plankton composition by differentiated subtraction of propagules.

If any existing organism is specialized in feeding on cysts as an energy source for its own metabolism, is still a matter of debate. The recognition of such an organism is of paramount importance for the ecology of coastal environments because the population dynamics of plankton may depend partially or totally on this benthic predation.

A suggestion is that the abundance of cyst bank assemblages is directly correlated with the instability of the environment. Cyst abundance, from this point of view, may be used as an indicator of environmental instability. Indeed, in unstable environments, the investment of species in the future may be higher. In stressed situations, species could be adapted to invest more in the long-term future by means of diapause and a bet-hedging strategy (as in forest seed banks) (Philippi & Seger, 1989; Gremer & Venable, 2014) than in creating an immediately subsequent generation.

In temporary freshwaters, species that produce long-resting cysts are more common (Moscatello & Belmonte, 2004; Alfonso *et al.*, 2016). Such species (including Anostraca;

Cladocera & Calanoida) produce just one generation per year. The difficulty of obtaining hatchlings of the previous generation is responsible in part (if at all) for the composition of the year by year populations.

In such a frame, most cysts are designed to ‘travel in time’ (Belmonte & Rossi, 1998), each clutch hatching in small percentages every year for many years. This is consistent with the general impression of the numerical predominance of cysts over active stages in the species of very temporary environments, but studies explicitly concerned with this topic are still rare.

Stress situations, e.g., in variable environments, can be differently intense or they are differently perceived by species. This does not allow the species to stay all together at each time, and the diversity, in terms of species richness, which has a large unexpressed portion, gives the system a powerful resilience. This process is not perceivable with simple or short time investigations (Belmonte *et al.*, 2013).

One of the most interesting issues that deserves research efforts is sediment dating. Although some work already indicated the direction (Hairston Jr. *et al.*, 1995; Rubino *et al.*, 2013), it is evident that the dating of layered sediments, coupled with a knowledge of species that produce cysts and their biology, is a powerful tool in the reconstruction of the history of planktonic communities. In the present period of global climate change, it is important to distinguish what is a ‘new arrival’, and what is the effect of long-term resilience.

Finally, there is a pressing need for a unification of the terminology used to describe and measure various cysts and eggs. Methods need to be shared, and an integrated approach adopted for the study of dormant resting cysts and eggs is relevant to studies of the plankton and benthos, but also to sedimentology, palaeontology, microbiology, environmental chemistry, and marine coastal management.

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