The ecological significance of small, eukaryotic parasites in marine ecosystems

LAURE GUILLOU
CATHARINA ALVES-DE-SOUZA
RAFFAELE SIANO
HUMBERTO GONZÁLEZ

As global warming takes hold, research shows that a group of eukaryotic marine parasites could have a far-reaching impact on marine ecology.

Fig. 1. Red tide produced by dinoflagellates in the Bountiful Islands, Gulf of Carpentaria in Queensland, Australia, potentially resulting from the displacement of populations induced by the global warming and the absence of natural pathogens in the area of introduction. *Bill Bachmann / Science Photo Library*

Background. Sun glinting off sea surface. *AbleStock.com / Thinkstock*

PARASITES are typically small organisms that exploit their host both as a food source and as a habitat. Although well-studied as human pathogens and organisms prejudicial to human interests, they have been persistently ignored in microbial aquatic ecology. Increased awareness of the important role of viruses in marine aquatic ecosystems in processes as diverse as species competition, carbon cycling, and gene transfers has recently changed our overall view of aquatic parasites. Recent evidence of the widespread occurrence of small eukaryotic parasites, requiring eukaryotic hosts, has highlighted the existence of another kind of pathogen which potentially has specific ecological roles.

THE (RE-)DISCOVERY OF THE EXISTENCE OF EUKARYOTIC PARASITES AMONG PLANKTON

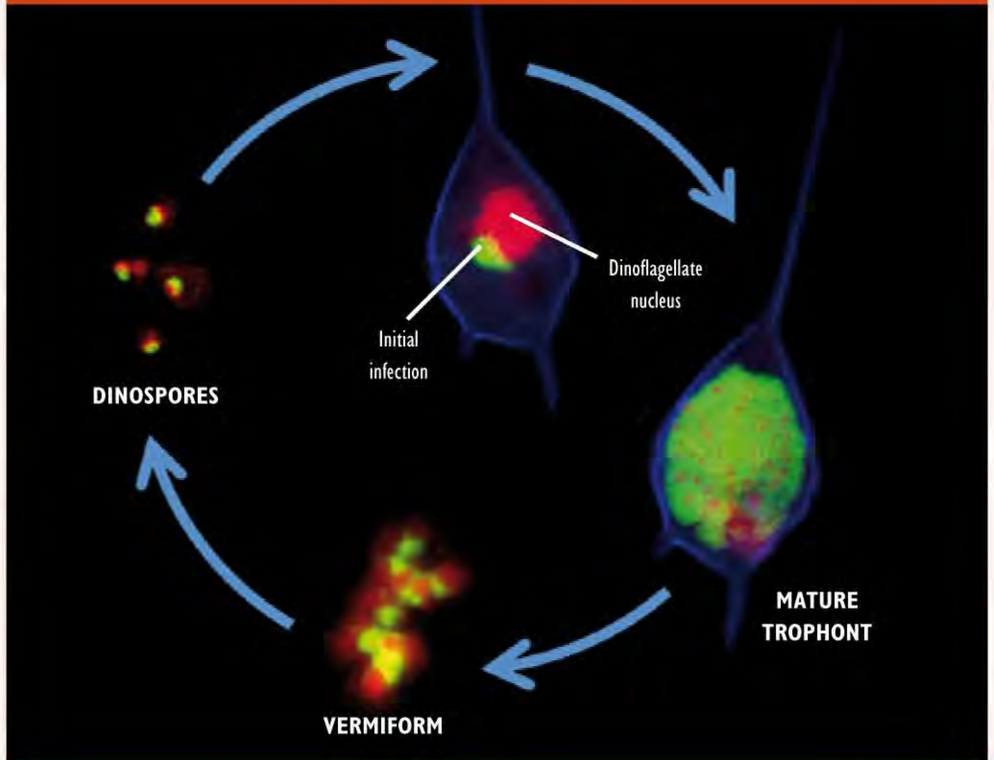
During the last decade, novel eukaryotic lineages have been discovered within the smallest fraction of marine eukaryotic plankton using culture-independent methods (mainly by the analysis of the genetic diversity of the 18S ribosomal RNA gene). All investigations performed so far have shown the overwhelming occurrences of environmental DNA sequences affiliated to novel eukaryotic lineages that have been grouped under the term of MALV (for MArine ALVeolate). These enigmatic new lineages represent up to 50% of sequences retrieved in all marine environments, from coastal waters to deep hydrothermal vents. They are everywhere.

Today, MALV sequences are believed to belong to Syndiniales, a group of species composed to date exclusively of marine parasites, which have been known for more than a century! Indeed, molecular techniques have clearly revealed the widespread occurrence of such parasites in marine waters. Interestingly, recent studies performed with the smallest planktonic fraction taken from lakes also revealed a high proportion of environmental sequences belonging to putative parasites (mainly chytrids, Cercozoa, Perkinsozoa and Colpodellids). Although different lineages have been retrieved from marine and freshwater ecosystems, these converging observations show the ecological significance of small eukaryotic parasites in aquatic environments.

ECOLOGICAL SIGNIFICANCE OF SYNDINIALES

Described Syndiniales species are all obligate parasites, and infect a wide range of hosts such as dinoflagellates, ciliates, cnidarians, crustaceans (like copepods and crabs), chaetognaths, radiolarians and fish eggs. Indeed, these parasites potentially affect most marine planktonic organisms. In particular, Syndiniales includes the widespread genus *Amoebophrya*, known to infect a large number of (if not all) dinoflagellate species, including several responsible for toxic 'red tides' (Fig. 1). The *Amoebophrya* vegetative life-cycle takes about 2–3 days and is characterized by alternation between a small, free-living stage (the dinospore) and an endoparasitic growing stage (the trophont) (Fig. 2). The life-cycle starts when a dinospore, a biflagellate cell 2–10 µm in diameter, invades a host cell. The trophont grows inside the host until it breaks the host cell wall. At this stage, it may produce a synchronous swimming colony (a sort of long filament of cells), called the vermiform stage. To complete the cycle, each cell of the vermiform stage differentiates into many dinospores, which are released rapidly. Considering that one infection eventually produces hundreds of dinospores, each one able to infect a new host, these parasites are likely to have the capacity to control their host population. This hypothesis is in fact supported by numerous field observations reporting episodic outbreaks of hosts infected by Syndiniales, sometimes with significant loss to fisheries (for example *Hematodinium*, a virulent parasite of crustaceans such as crabs and lobsters). However, the ecological role of Syndiniales has been particularly well-studied in the case of *Amoebophrya* species infecting noxious dinoflagellate species able to produce 'red tides'.

Dinoflagellates are important primary producers in coastal areas. Some species may proliferate and change the colour of seawater, forming blooms known as 'red tides'. Dinoflagellates like warm and stratified waters. Thus, global warming favours this group of microalgae. The increasing occurrence and geographical expansion of red tides is consequently a worldwide phenomenon. In addition, such proliferations are often recurrent because many dinoflagellates can produce resistant stages, or cysts, that contaminate sediments for a long time. It has been suggested that these proliferations are favoured by the absence of efficient pathogens in new areas they colonize. Thus, a blooming species is in fact one species escaping its natural enemies for a period of time. This hypothesis, also called the 'Enemy Release Hypothesis', was first introduced in terrestrial ecology, but can be adapted to planktonic organisms. In our case, this is an interesting explanation for the general increase of blooms in the context of global warming and an illustration of the ecological role of eukaryotic parasites.



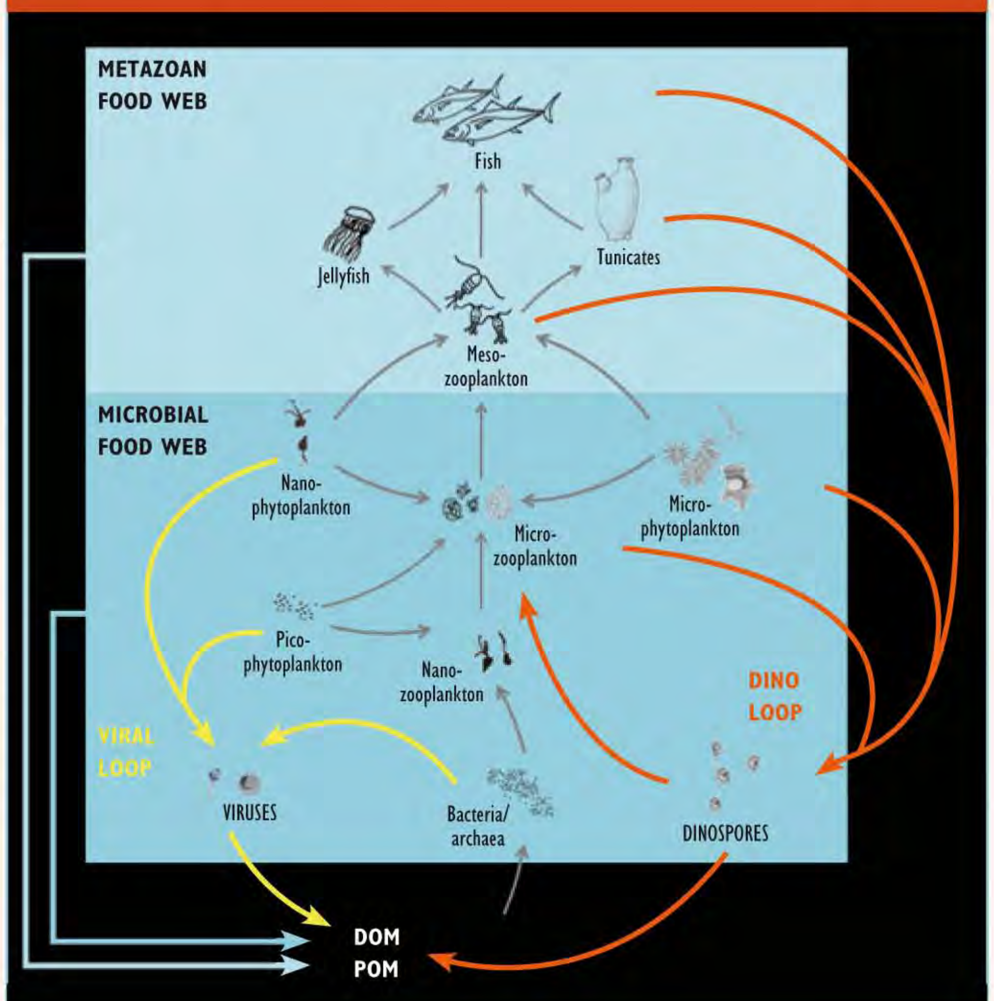


Fig. 2 (*top*). Life cycle of *Amoebophrya* sp. infecting *Neoceratium minutum*. Red, nucleus of the host and the parasite; green, cytoplasm of the parasite detected by fluorescent *in situ* Hybridization. Samples taken from the Mediterranean Sea, collected during the BOUM cruise. *C. Alves-de-Souza*

Fig. 3 (*bottom*). Parasitic loops in marine food webs. A potential role for eukaryotic parasites is highlighted by the dino loop pathway that parallels the viral loop for smaller organisms. DOM, Dissolved organic matter; POM, particulate organic matter. *L. Guillou & C. Alves-de-Souza*

> *"Although different lineages have been retrieved from marine and freshwater ecosystems, these converging observations show the ecological significance of small eukaryotic parasites in aquatic environments."*

IMPLICATIONS OF SYNDINIALES FOR FOOD WEBS AND CARBON FLOW

Considering the wide host range of Syndiniales, these parasites could have a key role in marine planktonic food webs and fisheries. However, the ecological impact of such eukaryotic parasites remains to be conceptualized and considered by biogeochemical models. All species known to date are highly virulent, as infection generally voids host cell replication and results irremediably in death of the host. Estimates based on culture experiments using dinoflagellate hosts suggest that almost half of the host biomass is transformed into dinospores; the rest is rapidly incorporated into the pool of particulate and dissolved organic matter (POM and DOM) and used as substrates by marine bacteria. Syndiniales dinospores can be very abundant within the smallest size fractions of marine eukaryotic plankton. Sometimes they can account for an important proportion (>25%) of nanoplanktonic (2–20 µm) organisms and can constitute a suitable food source for microzooplankton (the heterotrophic protists between 20–200 µm). Like viruses, these parasites reroute a substantial proportion of the carbon invested in the general food webs, and interfere in the competition between species by preferentially infecting the most actively growing species. This process is called the viral loop (or viral shunt) for viruses. The myco loop describes a similar pathway for chytrids infecting freshwater diatoms. Additionally, eukaryotic parasites are particularly efficient infective agents of large, inedible dinoflagellates, releasing carbon biomass potentially refractory to microbial grazing activity. The myco loop describes a similar pathway for chytrids infecting freshwater diatoms.. By homology, Syndiniales produce a 'dino loop' within marine food webs, from microalgae to large metazoans.

CONCLUSION

That fact that Syndiniales parasites constitute a very diverse and widely distributed parasitic group suggests that they could play an important role both in host population regulation and microbial communities. This could be particularly relevant at the surface of all oceans, where microbial food webs usually dominate the transfer of carbon through complex trophic interactions. They may also have a key role in the regulation of invasive species in the context of the recent global warming and host migrations. However, more quantitative studies are required to better evaluate the functional role of these parasites and their contribution to carbon flow in marine food webs.

In comparison, major differences exist between the regulation of viruses and parasitic eukaryotes. Dinospores are known to be actively grazed by microzooplankton, whereas viruses are not consumed. Also, viral infections seem to be particularly relevant for very small organisms, like bacteria and nanoflagellates, while the ecological roles of eukaryotic parasites are directed towards larger hosts. Thus the 'dino loop' could constitute an important trophic pathway in the recycling of carbon through different compartments of marine trophic webs.

DR LAURE GUILLOU works at CNRS (Centre National de Recherche Scientifique), UMR 7144, Station Biologique of Roscoff, Place Georges Teissier, BP 74, 29682 Roscoff Cedex, France (email laure.guillou@sb-roscoff.fr).
CATHARINA ALVES-DE-SOUZA is a PhD student at the University of Paris 6 and University Austral of Chile (email calves@sb-roscoff.fr).
DR RAFFAELE SIANO works at the Taxonomy and Identification of Marine Phytoplankton (TIMP) facility of the Stazione Zoologica A. Dohrn Villa Comunale, 80121 Naples, Italy (email raffaele.siano@szn.it).
DR HUMBERTO GONZÁLEZ is a researcher at the University Austral of Chile, Institute of Marine Biology, Campus Isla Teja, PO Box 567, Valdivia, Chile (email hgonzale@uach.cl)

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