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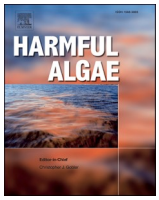

# Why do some dinoflagellates produce toxins, whereas ciliates rarely do?

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ABSTRACT

Dinoflagellates and ciliates dominate marine microzooplankton, yet widespread toxin production is largely restricted to dinoflagellates. This perspective synthesizes evolutionary, genomic, and ecological drivers of that asymmetry with direct relevance to harmful algal events. From a molecular and biochemical point of view, dinoflagellates possess vast, repeat-rich genomes that support modular PKS/NRPS pathways yielding chemically diverse metabolites, whereas ciliates generally lack complete PKS/NRPS clusters (apart from a few predatory lineages) and instead emphasize behavioral defenses and rapid reproduction. Most confirmed toxic dinoflagellates are photosynthetic or mixotrophic; robust cases in purely heterotrophic taxa are lacking. Despite environment-dependent costs, dinoflagellate metabolites confer grazer deterrence, allelopathy, prey lysis, and potential nutrient acquisition. Socio-economically, paralytic shellfish toxins (saxitoxins) produced by *Alexandrium* spp., *Gymnodinium catenatum*, and *Pyrodinium bahamense*—non-PKS alkaloids associated with sxt genes—are among the most consequential. An integrated approach coupling genomics, metabolomics, targeted bioassays, and in situ observations will clarify when chemical versus behavioral strategies prevail across ocean regimes, thereby improving HAB risk assessment, monitoring, and mitigation.

## Introduction

Ciliates (7500 species estimated; Lynn and Small, 1991) and dinoflagellates (2956 described species; Guiry, 2024) account for a large fraction of daily primary production turnover in the sea, typically grazing 30–70 % of phytoplankton standing stock each day (Calbet and Landry, 2004; Sherr and Sherr, 2007; Schmoker et al., 2013). Both groups are unicellular eukaryotes of comparable size and display striking trophic plasticity (Calbet, 2025), spanning strict heterotrophy to obligate phototrophy (primarily among dinoflagellates) with diverse forms of mixotrophy (Jeong et al., 2010; Stoecker et al., 2017). The recently curated Mixoplankton DataBase (MDB) quantifies this breadth across photosynthetic–phagotrophic plankton, including dinoflagellates and ciliates, and provides a robust foundation for comparative analyses of trophic modes (Mitra et al., 2023). Early ultrastructural syntheses also emphasized shared alveolate features—such as cortical alveoli—framing long-standing discussions of evolutionary proximity between ciliates and dinoflagellates (Corliss, 1975; Taylor, 1978, 1988). Yet the two lineages diverge along multiple axes (Table 1): dinoflagellates glide or spin using two flagella, whereas ciliates coordinate thousands of cilia; dinoflagellates often harbor permanent or kleptoplastic plastids of diverse origin, while most ciliates rely on transient chloroplast retention; dinoflagellates include bioluminescent taxa, whereas ciliates excel in millisecond mechanochemical escape bursts; and their genomes follow different blueprints—gigantic, permanently condensed chromosomes in dinoflagellates versus dual nuclei with programmed rearrangement in ciliates (Lin, 2011; Nowacki and Landweber, 2009). For completeness, the third alveolate branch—the Apicomplexa—comprises obligate endoparasites; unlike dinoflagellates they do not typically deploy diffusible phycotoxins, although malaria parasites (*Plasmodium*) shed glycosylphosphatidylinositols that act as inflammatory agonists in vertebrate hosts, engaging TLR2/TLR4 and provoking cytokine release (e.g., TNF-α). (Debierre-Grockiego and Schwarz, 2010; Gubbels and Duraisingh, 2012).

Genetic surveys highlight an additional, consequential divergence in secondary metabolism. A targeted PCR screen detected type I polyketide synthase (PKS) genes—the biosynthetic machinery underlying many complex metabolites—in seven of nine strains spanning seven dinoflagellate species (Snyder et al., 2003). Broader transcriptomic analyses subsequently demonstrated extensive PKS/fatty-acid–synthase domain expansions across dozens of dinoflagellate strains relative to other protists (Kohli et al., 2016). Physiological and toxicological studies identify multiple toxin-producing clades, including *Alexandrium–Pyrodinium, Karenia, Karlodinium, Dinophysis, Gambierdiscus, Ostreopsis, and Azadinium/Amphidoma* (Landsberg, 2002), and contemporary compilations (IOC-UNESCO HAB database, 2025) now enumerate well over a

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**Table 1**
Comparative summary of dinoflagellates and ciliates.

| TRAIT/FEATURE | DINOFLAGELLATES | CILIATES |
|---|---|---|
| PHYLOGENETIC LINEAGE | Alveolata (divergent from ciliates) | Alveolata |
| GENOME COMPLEXITY | Extremely large, with PKS genes | Nuclear dualism; mostly lack PKS machinery |
| TOXIN PRODUCTION | Yes – endogenous, diverse, potent | None (with rare exceptions) |
| PREDOMINANTLY DEFENSE STRATEGY | Chemical (toxins) | Behavioral (escape, reproduction) |
| TROPHIC STRATEGY | Mixotrophy common | Mostly heterotrophy, some kleptoplasty |
| ECOLOGICAL ROLE OF TOXINS | Predator deterrence, allelopathy, prey capture | Marginal in some groups |
| ENERGY INVESTMENT | From low to high (depending on nutrients availability) | Low; focused on rapid division |
| BLOOM DYNAMICS | Often toxic, persistent | Rapid bloom–crash cycles |
| CLIMATE CHANGE PROJECTION | Likely favored (stable, warm, low-nutrient) | Vulnerable to reduced nutrient flux |

hundred toxigenic dinoflagellate species worldwide. In contrast, planktonic ciliates—apart from a few haptorian predators with toxicysts (*Didinium, Dileptus, Spathidium*, etc.),—show no evidence for widespread, complete PKS/NRPS clusters or for broad toxin production (Li et al., 2024) Moreover, most claims of endogenous toxicity in strictly heterotrophic dinoflagellates have not survived genomic, toxicological, or trophic-transfer scrutiny. The *Pfiesteria* case is emblematic: *P. shumwayae* killed fish in some assays, but released no dissolved ichthyotoxin and showed no amplifiable PKS/NRPS genes consistent with polyketide/NRPS toxin biosynthesis, pointing instead to non-toxin mechanisms and experimental confounds (e.g., stressed fish, bacteria, ammonia) (Berry et al., 2002). *Phalacroma rotundatum*—once listed among DSP producers—now appears to act as a vector, retaining okadaate congeners acquired via prey (tintinnids that had in turn fed on toxic *Dinophysis*), rather than synthesizing them de novo (González-Gil et al., 2011). Likewise, *Protoperidinium crassipes* was initially implicated in azaspiracid events; subsequent work isolated *Azadinium spinosum* and demonstrated it as the primary producer of AZAs, reassigning *Protoperidinium* to a trophic-transfer role (Tillmann et al., 2009).

Seasonal dynamics further reinforce functional separation by trophic mode. Mixotrophic or phototrophic dinoflagellates and ciliates exhibit patterns distinct from obligate heterotrophs across environments, with well-documented cases from Arctic and temperate systems to tropical waters and fjords (Nielsen and Kiørboe, 1994; Levinsen and Nielsen, 2002; Hansen et al., 2025). Together, these lines of evidence motivate the central question addressed here: why has widespread toxin production evolved in dinoflagellates but remains rare in ciliates, and under what environmental filters do chemical versus behavioral strategies prevail?

## Evolutionary and genomic foundations

Dinoflagellate genomes range from 3 Gb to 245 Gb, overshadowing those of most eukaryotes. They are packaged into permanently condensed chromosomes rich in tandem repeats and trans-spliced transcripts (Lin, 2011). Long-read genome studies show that dinoflagellate PKS and NRPS (non-ribosomal peptide synthetase) genes are often organized into large clusters of repeated segments. These clusters probably evolved through gene duplication and mixing of functional domains, creating a modular 'toolkit' for synthesizing diverse secondary metabolites without demanding complex new regulatory pathways (Beedessee et al., 2019). Supporting this, experiments using full-length cDNA and protein localization techniques in *Karenia brevis* revealed that PKS genes are expressed as separate single-domain transcripts. Notably, toxin levels correlate better with the abundance of the resulting proteins (many chloroplast-targeted) than with the amount of mRNA, suggesting that toxin production is mainly regulated after transcription has occurred (Monroe et al., 2010). At the scale of the marine microbial eukaryote tree, systematic surveys document a pronounced expansion and diversification of PKS domains in dinoflagellates relative to many other groups, strengthening the argument that genome architecture enabled chemical diversification (Kohli et al., 2016).

Ciliates, though also genome-rich, adopt a dual strategy: a polyploid macronucleus executes somatic transcription, while a diploid micronucleus stores a silent germline (Nowacki and Landweber, 2009). During sexual cycles, the macronuclear genome is shredded and reassembled, generating extraordinary genic plasticity. Yet chromosome-scale assemblies for representative oligotrichs, choreotrichs, and strombidiids reveal few, if any, complete PKS modules (Li et al., 2024). The main exception is the predatory order Haptoria (*Didinium, Monodinium*), where duplicated PKS and l-amino-acid-oxidase genes appear linked to toxicyst biogenesis (Li et al., 2024). These data imply at least two independent origins of toxin pathways within the Alveolata, but only one lineage has radiated through major planktonic clades.

Evolutionary contingency, therefore, set the stage: dinoflagellates retained and elaborated a modular chemical toolkit, whereas ciliates channeled their genomic plasticity into motility, prey capture, and rapid life-cycles (Rzeszutek et al., 2020; Li et al., 2024).

## Trait trade-offs: chemistry versus behavior

Toxin production in dinoflagellates carries environment-dependent costs—often negligible under nutrient-replete conditions but exceeding 20 % of growth under nitrogen limitation with intense grazing—yet remains advantageous because chemically defended cells achieve higher net fitness than undefended ones (Chakraborty et al., 2019). Ciliates pursue a different path. Growth rates of common oligotrichs exceed one doubling per day at 20 °C (Strom and Morello, 1998) and can triple under brief warming pulses (Ferreira et al., 2022). Escape bursts in some species exceed 20 body-lengths $s^{-1}$, triggered by mechanosensory cilia (Jakobsen, 2001). Such speed sidesteps predation without chemical expenditure. Because many ciliates forage in ephemeral, centimeter-scale patches, selection favors rapid numerical responses over slow-yield chemical defenses. In turbulent surface layers, hydrodynamic noise dissolves deterrents, whereas behavioral agility remains effective.

Both strategies have limits. Dinoflagellates often divide more slowly than equally sized ciliates and, therefore, they prosper where nutrient pulses are rare (Sailley and Buitenhuis, 2014). Consistent with long-term observations, heterotrophic dinoflagellates and ciliates show distinct seasonal signatures across regions—post-bloom peaks in temperate seas, cold-season troughs at high latitudes, and strong coupling to prey fields and mixing in fjords—arguing for context-dependent advantages of "chemical" vs "behavioral" strategies (Levinsen and Nielsen, 2002; Nielsen and Kiørboe, 1994; Hansen et al., 2025).

## Ecological roles of dinoflagellate secondary metabolites

Dinoflagellate secondary metabolites play diverse ecological roles (Fig. 1). High-speed video experiments revealed that the copepod Temora longicornis routinely "tastes" toxic dinoflagellate cells and then spits them out: in 10 of the 12 species/strains tested (*Alexandrium tamarense, A. pseudogonyaulax, Karlodinium armiger, Karenia selliformis, K. brevis, K. mikimotoi, Dinophysis acuminata, Protoceratium reticulatum*), the copepods rejected, in some cases, more than 80 % of captured cells—clearly evidencing that these toxins work as a pre-ingestive grazing deterrent rather than a poison that acts after ingestion (Xu and Kiørboe, 2018). Similar capture-and-spit or outright avoidance reactions have been documented in other copepods that encounter *Alexandrium* spp. (Teegarden and Cembella, 1996; Teegarden, 1999), and even dinoflagellate predators are paralyzed by karlotoxins released from

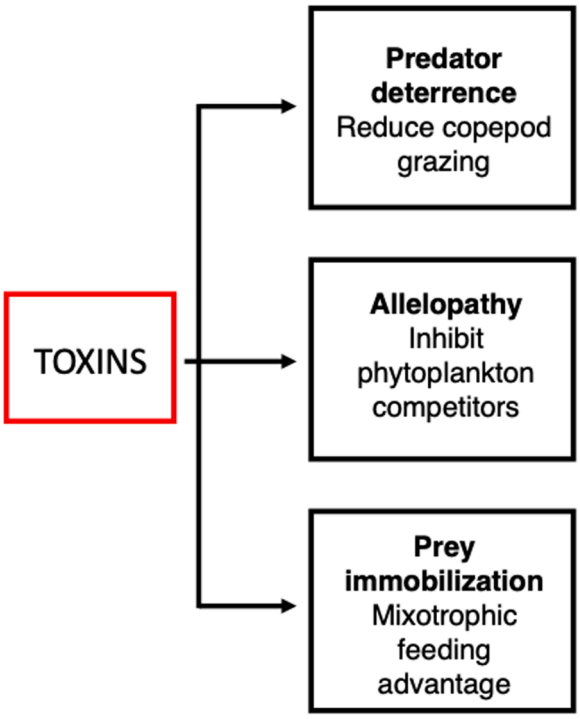


**Fig. 1.** Different effects of dinoflagellate toxins.

*Karlodinium veneficum* (=*K. micrum*) (Adolf et al., 2006), underscoring the broad effectiveness of dinoflagellate chemical defenses across multiple grazer groups. *Karlodinium* spp. secrete karlotoxins that perforate prey membranes, allowing ingestion of slow-moving cells (Adolf et al., 2006; Sheng et al., 2010). Allelopathy extends the reach: filtrates from *Alexandrium ostenfeldii* suppress diatom growth at sub-micromolar concentrations (Hakanen et al. 2014), and the mere presence of *Gymnodinium catenatum* at very low concentrations was enough to decrease overall copepod grazing on phytoplankton in open ocean waters of the Mediterranean (Calbet et al., 2002). Finally, toxins may mediate consortia: toxin-producing strains harbor distinct bacterial partners enriched in xenobiotic-degrading taxa (Deng et al., 2023), suggesting mutualistic detoxification loops.

Beyond PKS/NRPS products, PSTs (saxitoxin family) exemplify *non-PKS* alkaloids with major public-health impact. Genomic and transcriptomic work in *Alexandrium* and related genera identifie core sxt genes (notably *sxtA4*) associated with PST production, although the full dinoflagellate pathway and its regulation remain under study (Akbar et al., 2020). Recognizing this biochemical diversity is essential when comparing dinoflagellate "toxins" to the largely fatty-acid-derived cytotoxins of ciliate toxicysts.

In ciliates, toxicyst discharges (e.g., *Coleps hirtus*) are enriched in free fatty acids, a profile consistent with fatty-acid–rich cytotoxic mixtures implicated in ichthyotoxic events by some bloom-forming protists, underscoring convergent defensive chemistries despite distinct biosynthetic routes (Buonanno et al., 2014).

Not all secondary metabolites are strictly "toxins". Some may function primarily as signaling molecules, attracting prey or inhibiting competitors at sub-lethal concentrations (Larsson et al., 2022; Güell-Bujons et al., 2024). Disentangling these roles will require experiments that couple metabolomics, isotope tracers, and single-cell transcriptomics—approaches still in their infancy. The multifunctionality of dinoflagellate metabolites nevertheless explains why they persist despite metabolic cost: they act as ecological currency redeemable in multiple contexts.

## Outlook

Together, the evidence indicates that chemically defended, often photo-/mixotrophic dinoflagellates prevail under stable, stratified, nutrient-poor and low-turbulence conditions with high grazer pressure, whereas behaviorally agile, fast-growing ciliates dominate during and after mixing events, in nutrient-replete regimes, turbulent surface layers, and ephemeral prey patches.

The contrasting prevalence of toxin production between dinoflagellates and ciliates encapsulates alternative solutions—chemical versus behavioral—to shared ecological pressures. Progress now hinges on trait-explicit measurements that link toxin quotas, PKS/sxt expression, allelopathic/lytic activities, and behavioral escape metrics to realized grazing outcomes across hydrographic regimes relevant to HAB monitoring (fronts, stratified layers, and post-mixing periods). Coordinated multi-omics time series, standardized grazer-deterrence bioassays, isotopic allocation to secondary metabolism, and high-speed videography of capture–rejection will enable quantitative cross-taxon comparisons and distinguish chemical effects from covarying environmental and community factors. These contrasting filters lead to concrete, testable predictions: (i) toxin quotas and PKS/sxt expression will covary positively with hydrographic stability indices; (ii) low-turbulence nocturnal periods should coincide with elevated expression of defense/attack metabolites; and (iii) mesocosms with intermittent mixing should show transient ciliate surges followed by chemically mediated dinoflagellate dominance as stability returns.

Outstanding gaps remain. Field estimates of the true metabolic cost of toxin production under nutrient limitation are scarce; isotope flux approaches could quantify carbon and nitrogen allocation in situ. Moreover, extended, full-season time-series across contrasting regimes (upwelling margins, subtropical gyres, polar fronts, fjords) are essential to separate trait filtering from taxonomic turnover and to ground these trait-based inferences in observation.

In conclusion, dinoflagellates and ciliates exemplify chemical versus behavioral solutions to the same pressures; resolving when each dominates now requires standardized trait-explicit assays and seasonally resolved, multi-omics field programs tightly coupled to HAB monitoring.

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## CRediT authorship contribution statement

**Albert Calbet:** Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

## Declaration of competing interest

The author declare that he has no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Data availability

No data were used for the research described in the article.

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