ORIGINAL ARTICLE

Importance of dynamics of acquired phototrophy amongst mixoplankton; a unique example of essential nutrient transmission in community ecology

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Abstract

Transfers of energy and nutrients from producers to consumers are fundamental to ecosystem structure and functioning. A common example is the transfer of essential amino acids and fatty acids, produced by phototrophs, up through successive trophic levels. A highly specialised example is the transmission of acquired phototrophy between certain plankton. There are > 250 species of marine plankton that exploit acquired phototrophy; the *Teleaulax-Mesodinium-Dinophysis* (TMD) trinity is the most studied complex. In the TMD-trinity, plastids and nuclear material produced by the cryptophyte *Teleaulax* are transferred during feeding to the ciliate, *Mesodinium* and these acquired plastids are subsequently transferred from *Mesodinium* to its predator, the dinoflagellate *Dinophysis*. These plastidic non-constitutive mixoplankton, *Mesodinium* and *Dinophysis*, are globally ubiquitous and ecologically important organisms. *Mesodinium* can form red-tide blooms, while *Dinophysis* spp. cause diarrhetic shellfish poisoning events and shellfisheries closures. However, very little is known about the impact of different environmental stressors on the transmissions of acquired phototrophy, the subsequent decay of that phototrophic potential over time, and the implications for community trophic dynamics. Here, for the first time, the implications of the transmission dynamics of acquired phototrophy for the success of the TMD-trinity were explored under different nitrogen and phosphorus (N:P) nutrient ratios and loadings (eutrophic, mesotrophic, oligotrophic). Using a multi-nutrient simulator, bloom dynamics were shown to be markedly different under these scenarios, highlighting the importance of variable stoichiometry in community ecology. Importantly, dynamics were sensitive to the longevity (half-life) of the acquired phototrophy (especially for *Dinophysis* at low nutrient high N:P), a feature for which appropriate empirical data are lacking. This work highlights the need to enhance our understanding about how environmental stressors arising from anthropogenic activities (including climate change) will impact transference of acquired phototrophy between trophic levels and thence marine biodiversity and ecosystem services.

Keywords Biodiversity · Harmful algal blooms (HABs) · Marine · Predator–prey · Phytoplankton · Zooplankton

Introduction

The major driver in community ecology is the transfer of biochemicals between different trophic levels (Lindeman, 1942). As a first step, this transfer involves harnessing of energy and utilisation of diverse nutrients to produce different biochemical compounds. The organisms which undertake this crucial activity in the community are termed 'producers'; without their products, in the form of organic compounds, higher trophic levels could not grow. A common example is the dependence of consumers, across different trophic levels (including aquatic invertebrates, fish through to humans), on essential amino and fatty acids (Aristoy & Toldrá, 2009; Glick & Fischer, 2013). These compounds required by all aquatic and terrestrial consumers are produced de novo by phototrophic organisms, such as microalgae (Harwood, 2019), and then transmitted through the food web. An extreme example of transfer of essential biochemicals in the marine ecosystem is the transference of acquired phototrophy (Stoecker et al., 2009). This is seen

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within a group of planktonic organisms, termed mixoplankton (Table 1).

Mixoplankton are protist plankton that engage in osmotrophy (using dissolved organics), phagotrophy (through predation), and also in phototrophy (utilising light and dissolved inorganics) (Flynn et al., 2019; Glibert & Mitra, 2022; Table 1). These protists, which de facto perform activities normally assigned to different trophic levels within the one celled organism (i.e., producers and consumers), have traditionally been side-lined by mainstream ecologists. However, the last decade has witnessed a marked change in the understanding of how the base of marine ecosystem is structured leading to the emergence of the mixoplankton paradigm (Glibert & Mitra, 2022).

Traditional descriptions of how the plankton food webs function are based on the plant-animal dichotomy where plant-like phytoplankton employ photosynthesis (utilising light energy, organic and inorganic nutrients) to fix carbon and produce essential biochemical compounds. The phytoplankton are then consumed by animal-like protist zooplankton which, subsequently, are prey to metazoan zooplankton such as copepods, krill, fish larvae (Mitra & Davis, 2010; Mitra et al., 2014a). Now mixoplankton are recognised as important members of planktonic food webs (Ghyoot et al., 2017; Leles et al., 2021; Le Noac'h et al., 2024; Li et al., 2022; Mitra et al., 2023). Inclusion of mixoplankton in the plankton food webs, resulting in the allied redesignation of various iconic 'phytoplankton' and protist 'zooplankton' as mixoplankton (Mitra et al., 2023), overturns the traditional phytoplankton-zooplankton dichotomy, redefining marine community ecology (Flynn et al., 2019; Mitra et al., 2024) and the dynamics of plankton community ecology (Leles et al., 2018, 2021).

Based on physiological traits, mixoplankton are categorised broadly (Mitra et al., 2023; Table 1) into constitutive mixoplankton (CM) and non-constitutive mixoplankton (NCM). The CM possess a genetically innate capability for photosynthesis while NCM acquire their phototrophic capabilities through transfer of photosynthetic apparatus and nuclear material. This transfer into NCM occurs either from—(i) non-specific prey, these are the generalist-NCM (GNCM); (ii) specific prey, these are the plastidic-specialist-NCM (pSNCM), or, (iii) through harbouring photosynthetic endosymbionts (endosymbiotic-specialist-NCM, eSNCM). This essential acquisition of complete subcellular components into GNCM and pSNCM represents an extreme example of the transfer of essential nutrients between trophic levels. Acquired phototrophy in NCM is not unique to any taxonomic group but is observed across different branches of protists (Mitra et al., 2023; Stoecker et al., 2009). Interrogation of taxonomic and genomic databases have shown NCM to have significant spatial and temporal differences in the biogeographic distributions of the different functional and taxonomic sub-groups (Leles et al., 2017; Mitra et al., 2023). A globally important instance of transmission of acquired phototrophy between NCM, from primary producers to primary and secondary consumers, is the case of the *Teleaulax-Mesodinium-Dinophysis* (TMD)-trinity.

Mesodinium rubrum and *Dinophysis* spp. are plastidic-specialist NCM (pSNCM). The different species within these

Table 1 Definitions and abbreviations of plankton functional groups under the mixoplankton paradigm. List collated from Flynn et al. (2019) and Glibert & Mitra (2022)

Abbreviation	Definition
CM	Constitutive Mixoplankton; protist plankton with an inherent capacity for phototrophy that also engage in phagotrophy and osmotrophy. (cf. NCM)
eSNCM	endosymbiotic Specialist Non-Constitutive Mixoplankton; SNCM that acquire their capacity for phototrophy through harbouring photosynthetic endosymbionts. (cf. pSNCM)
GNCM	Generalist Non-Constitutive Mixoplankton; NCM that acquire their capacity for phototrophy from general (i.e., non-specific) phototrophic prey. (cf. SNCM)
mixoplankton	Plankton protists capable of obtaining nourishment via phototrophy and phagotrophy and osmotrophy. (cf. phytoplankton & protist zooplankton)
NCM	Non-Constitutive Mixoplankton; protist plankton that acquire the capability for phototrophy from consumption (via phagotrophy) of phototrophic prey. (cf. CM)
phytoplankton	Plankton obtaining nourishment via phototrophy and osmotrophy. They are incapable of phagotrophy. These include the eukaryotic diatoms and prokaryotic cyanobacteria. (cf. mixoplankton & protist zooplankton)
protist-zooplankton	Protist plankton obtaining nourishment via phagotrophy and osmotrophy. They cannot engage in phototrophy. (cf. phytoplankton & mixoplankton)
pSNCM	plastidic Specialist Non-Constitutive Mixoplankton; SNCM that acquire their capacity for phototrophy from sequestration of photosynthetic apparatus and nuclear material from specific phototrophic prey. (cf. eSNCM)
SNCM	Specialist Non-Constitutive Mixoplankton; NCM that acquire their capacity for phototrophy from specific phototrophic prey (cf. GNCM). There are two types, pSNCM and eSNCM
zooplankton	Plankton obtaining nourishment via heterotrophy. They cannot engage in phototrophy. (cf. phytoplankton, mixoplankton)

two genera require the photosynthetic apparatus manufactured by the cryptophyte clade *Teleaulax/Plagioselmis/Ge minigera* to provide their acquired phototrophic potential (Wisecaver & Hackett, 2010; Fig. 1). *Teleaulax amphioxeia*, a signature species within the cryptophyte clade, is itself a constitutive mixoplankton (CM) with the innate capability to manufacture chloroplasts to drive phototrophy. After ingestion of *T. amphioxeia*, *M. rubrum* disassembles the *T. amphioxeia* cell, retaining the mitochondria, chloroplast and nuclear material within capture membranes for acquired phototrophy (Fig. 1); the remaining *T. amphioxeia* cell components are processed and assimilated for nutrition, or voided. The pSNCM *Dinophysis* spp., in turn, feeds on *M. rubrum*, from which it obtains the photosynthetic apparatus originating from *T. amphioxeia* to support its own acquired phototrophy. However, unlike *M. rubrum*, *Dinophysis* spp. do not appear to have the ability to retain the mitochondrion and nuclear material of the *T. amphioxeia*; only the chloroplast originating from *T. amphioxeia* is retained in the *Dinophysis* spp. for phototrophy (Fig. 1). These acquired chloroplasts are termed kleptochloroplasts. Thus, *Dinophysis*

spp. require cellular components transferred from the CM *T. amphioxeia* via the pSNCM *M. rubrum* for their own growth and proliferation (Johnson & Stoecker, 2005). The consequence of the differences in material transferences noted above (Fig. 1) is that *Dinophysis* spp. is less able to maintain the acquired phototrophic potential than is *M. rubrum*; neither, however, can reproduce indefinitely without having to 'top-up', with newly acquired subcellular components, to support acquired phototrophy.

The trophic transfer of acquired phototrophy within the TMD-trinity is not only an interesting ecological complex but it is also an important precursor to a trophic transfer pathway which have deleterious impacts on ecosystem services. Under different environmental conditions, *Dinophysis* spp. produce secondary biochemical compounds such as okadaic acid (Reguera et al., 2012). These compounds do not affect the metazoan grazers (e.g., mussels, oysters) of *Dinophysis* spp. but they are toxic to humans; trophic transfer of such toxins to humans via shellfish leads to outbreak of Diarrhetic Shellfish Poisoning (DSP) events (Díaz et al., 2016; Pizarro et al., 2008). Indeed, within the IOC-UNESCO
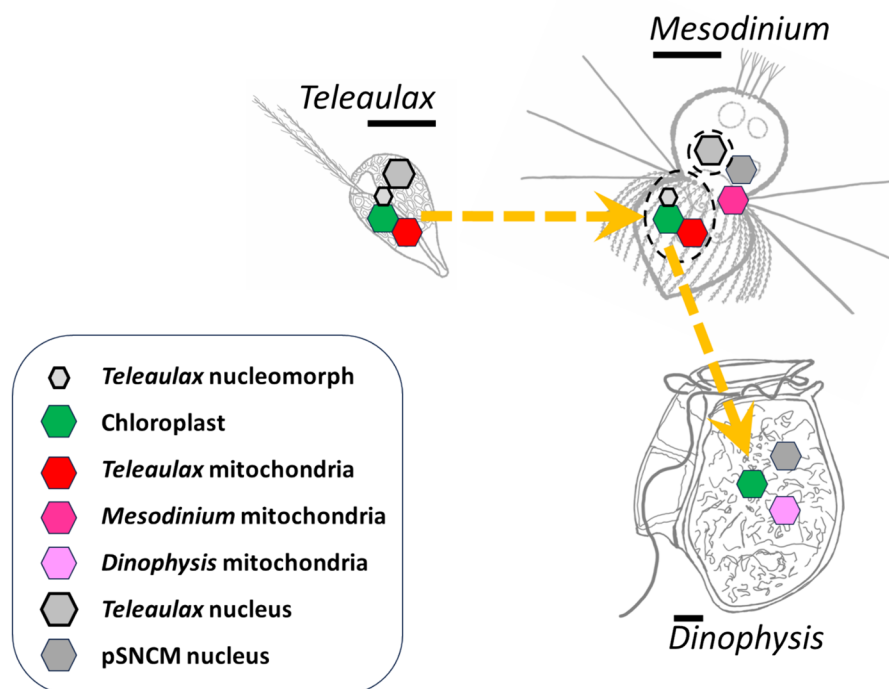

Fig. 1 Schematic showing transmission of acquired phototrophy within the *Teleaulax-Mesodinium-Dinophysis* (TMD)—trinity. The cryptophyte *T. amphioxeia* is a constitutive mixoplankton (CM) with the innate capability to manufacture chloroplasts to drive phototrophy and capable of ingesting prokaryote prey. The pSNCM *Mesodinium rubrum* ingests *T. amphioxeia*, disassembles the cell and retains the *Teleaulax* mitochondria, chloroplast and nuclear material within capture membranes for acquired phototrophy. The remaining *T. amphioxeia* cell components are processed and assimilated for nutrition, or voided. The *Dinophysis* spp., in turn, feeds on *M. rubrum*, from which it obtains the photosynthetic apparatus originating from *T. amphioxeia* to support its own acquired phototrophy. However, unlike the *M. rubrum*, *Dinophysis* spp. do not appear to have the ability to retain the mitochondrion and nuclear material of the *T. amphioxeia*; only the chloroplast originating from *T. amphioxeia* is retained in the *Dinophysis* spp. for phototrophy. Dashed lines are of capture membranes. The dark lines next to each species name is ca. 5 μm, representing the scale bar

database of harmful species (https://marinespecies.org/hab/), several pSNCM species of *Dinophysis* are recognised as Harmful Algal Bloom (HAB) species (Mitra et al., 2023).

Considerable efforts have been expended on research and monitoring of *Dinophysis* spp. blooms. Between 1970 and 2023, 1512 events of DSP producing *Dinophysis* spp. blooms were recorded in the Harmful Algal Event Database (HAEDAT) (Table S1). However, in these studies, *Dinophysis* spp. have traditionally been categorised as 'phytoplankton' (e.g., Carlsson et al., 1995) with research and allied management efforts concentrated on importance of physical oceanography in the proliferation of *Dinophysis* HAB events (e.g., Siemering et al., 2016). In such studies, there has been little, if any, consideration of the physiology of the organisms or biological interactions within the TMD-trinity. Physiological studies typically focus on either the *Teleaulax – Mesodinium* or the *Mesodinium—Dinophysis* couple (e.g., Hernández-Urcera et al., 2018; Johnson et al., 2006; Mafra et al., 2016). Studies focussing on the TMD-trinity as a whole are rare (Anschütz et al., 2022; Fiorendino et al., 2020) with scant information about the implication of transmission of acquired phototrophy on trophic dynamics.

This work presents a first study of how acquired phototrophy within the TMD-trinity under the mixoplankton paradigm could impact plankton ecosystem structure and functioning under different multi-nutrient (N and P) environmental conditions. Using a variable stoichiometric food web simulator, this work investigates the importance of the longevity and functionality of photosynthetic material acquired by the *Mesodinium rubrum* and *Dinophysis* spp. in shaping the community structure.

Methods

Hereafter the members of the TMD-trinity are referred to by their generic names only (i.e., *Teleaulax*, *Mesodinium* and *Dinophysis*) except when reference is made to specific species.

Food web simulator structure

The impact of acquired phototrophy within the TMD-trinity on ecosystem structure and function was explored using a plankton food web simulator (Fig. 2). The ecosystem simulator operated a multi-nutrient (C:N:P:Chl) currency including three inorganic nutrients (carbon, DIC; nitrogen, DIN as ammonium (NH_4^+) and nitrate (NO_3^-); phosphorus, DIP), two pools of dissolved organic matter differentiated by labilities (DOM including labile and semi-labile forms; recalcitrant r-DOM) and one pool of voided organic matter (VOM). The simulator included five plankton functional groups – phytoplankton cyanobacteria, bacteria, CM *Teleaulax*, pSNCM *Mesodinium* and pSNCM *Dinophysis*.

Each of the five functional groups were described using mechanistic acclimative variable stoichiometric biomass-based plankton models. A schematic of the physiological functions incorporated within each plankton functional
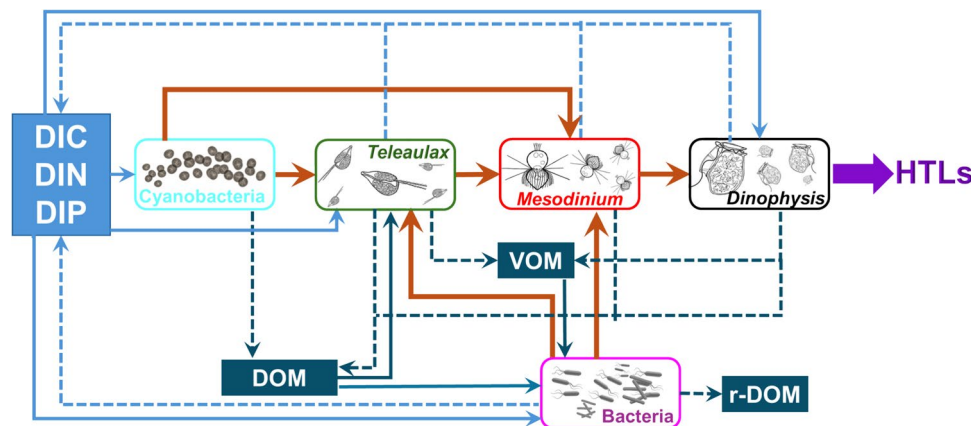

Fig. 2 Schematic of simulated food web used to explore how transmission of acquired phototrophy within the *Teleaulax–Mesodinium–Dinophysis* (TMD) trinity impacts ecosystem structure and functioning under different environmental conditions. The simulator is a multi-nutrient variable stoichiometric model including carbon (C), nitrogen (N) and phosphorus (P) pools as dissolved inorganics and organics. The food web includes five plankton functional types (PFTs)—cyanobacteria (prokaryote phytoplankton), *Teleaulax* (constitutive mixoplankton, CM), *Mesodinium* (plastidic non-constitutive mixoplankton, pSNCM), *Dinophysis* (pSNCM) and heterotrophic bacteria. Blue (light and dark) lines with arrow heads represent linkages between the PFTs and nutrients. Solid lines indicate uptake by the PFTs; dashed lines indicate inputs into the organic and inorganic pools from the PFTs. Solid orange lines represent predation within the plankton community. DIC, dissolved inorganic carbon; DIN, dissolved inorganic nitrogen; DIP, dissolved inorganic phosphorus; DOM, dissolved organic material (labile forms); rDOM, recalcitrant DOM; VOM, voided organic matter; HTLs, higher trophic levels. See also Fig. 3

group sub-module is shown in Fig. 3. Cyanobacteria and bacteria were described according to Flynn (2001) and Flynn (2005), respectively. Cyanobacteria (1.9 μm equivalent spherical diameter, ESD; Mitra & Flynn, 2023) employed phototrophy through utilization of light and dissolved inorganic nutrients and released dissolved organics as waste. Bacteria (1 μm ESD; Mitra & Flynn, 2023), as decomposers, modulated the cycling of voided and dissolved organic matter. The "Perfect Beast" model (Flynn & Mitra, 2009), which can be configured to represent the different protist functional types (Mitra et al., 2023), was used to describe the CM *Teleaulax* (length × width, L × W = 11.5 μm × 5.8 μm ≡ 9.18 μm ESD; Mitra et al., 2023) and the two pSNCM communities – *Mesodinium rubrum* (L × W = 25.5 μm × 21 μm ≡ 26.11 μm ESD; Mitra et al., 2023) and *Dinophysis*

(L × W = 72.2 μm × 41.3 μm ≡ 61.62 μm ESD; average calculated from Mitra et al., 2023). All the communities within the TMD-trinity were phototrophic and able to exploit external ammonium (NH_4^+). *Teleaulax* and *Mesodinium* were also configured to uptake external nitrate (NO_3^-); uptake of nitrate in *Dinophysis* was disabled (García-Portela et al., 2020).

In the community model (Fig. 2), the CM *Teleaulax* grazed on the prokaryote communities (cyanobacteria and bacteria), *Mesodinium* fed on both the prokaryotic communities as well as the CM *Teleaulax* while *Dinophysis* grazed only on *Mesodinium* (Mitra et al., 2023). Predation was described using the Satiation Controlled Encounter Based (SCEB) function of Flynn and Mitra (2016). Losses to higher trophic levels (HTLs) were accounted for via a
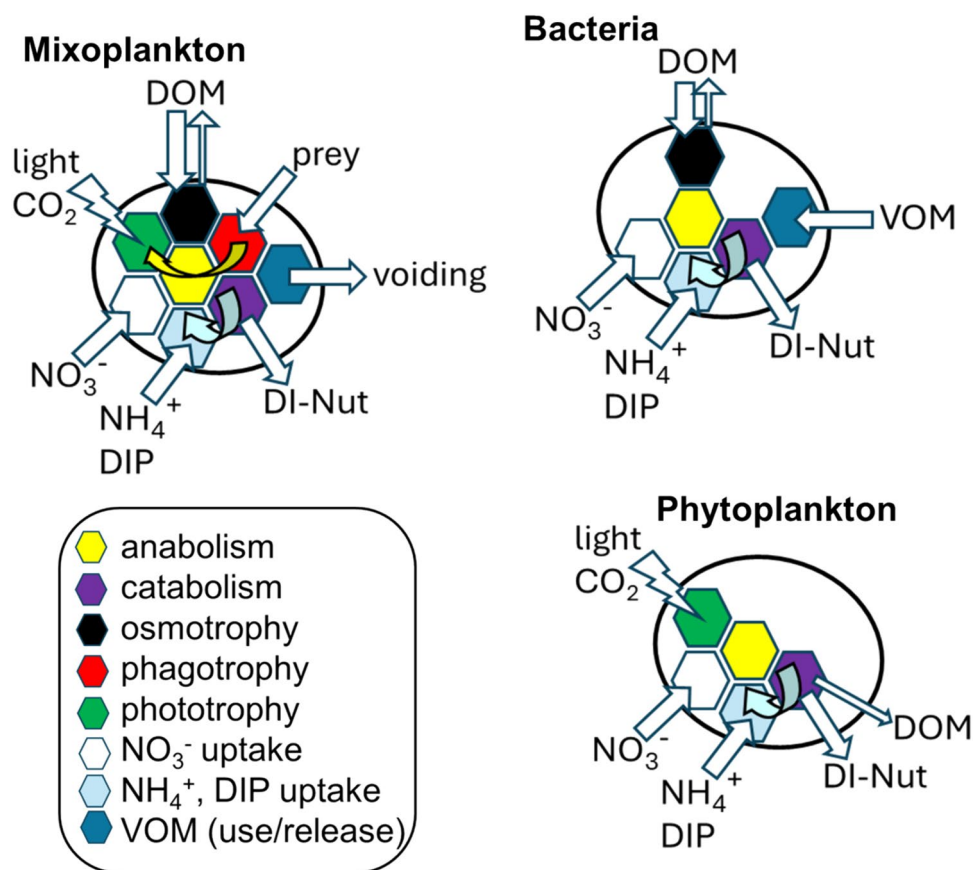

Fig. 3 Schematic showing nutritional strategies employed by the different functional groups in the plankton community framework. Anabolism and catabolism represent core metabolic processes. Mixoplankton (*Teleaulax*, *Mesodinium*, *Dinophysis*) and phytoplankton (Cyanobacteria) are primary producers that use light, carbon dioxide (CO_2) and dissolved inorganic nutrients (NO_3^-, NH_4^+, DIP) for photosynthesis. These groups also leak low molecular weight dissolved organic metabolites (DOM; e.g., sugars, amino acids, purines etc.) due to differences in the cellular versus outside concentrations. In addition to phototrophy, mixoplankton also engage in osmotrophy (uptake of DOM) and phagotrophy (ingestion of prey). During phago-

trophy, a portion of prey biomass is voided due to incomplete digestion (voided organic matter, VOM), and a further portion of digestate is converted into dissolved inorganic nutrients (DIN, associated with specific dynamic action, SDA). SDA liberated dissolved inorganic nutrients (NH_4^+, DIP) from prey biomass, in mixoplankton, are recycled internally (blue and yellow arrows) and exploited by priority, in preference to external inorganic sources, to support phototrophy. Bacteria, as decomposers, utilise DOM and VOM for their nutritional needs releasing DOM of different labilities. Figure modified from Flynn and Mitra (2023) See also Table 1 and Fig. 2

closure function (Mitra, 2009). Consumption and digestion of prey led to voiding of wastes, and regeneration of stoichiometric excesses due to respiration. The latter event, termed specific dynamic action (SDA; McCue, 2006), would, for a non-photosynthesising organism, result in the loss of around 30% of the biomass that is not voided, in the forms of CO_2, ammonium and phosphate. However, for mixoplankton, SDA liberated dissolved inorganic nutrients from prey digestion were recycled internally and exploited by priority, in preference to external inorganic sources, to support phototrophy (Fig. 3, mixoplankton).

Description of acquired phototrophy

A sub-module to describe acquired phototrophy was developed and incorporated within the Perfect Beast model (Flynn & Mitra, 2009) descriptors for pSNCM *Mesodinium* and pSNCM *Dinophysis*. The conceptual basis of this development followed understanding of how organelles and allied material enabling photosynthesis in CM *Teleaulax* is transferred within the TMD-trinity (Fig. 1; Wisecaver & Hackett, 2010). A new state variable (*PLN*, mg N m^{-3}) to describe the acquired phototrophy was introduced (Eq. 1).

$$\frac{d}{dt}\text{PLN} = f(\text{acquisition, maintenance, degradation}) \qquad (1)$$

In Eq. 1, acquisition (*PLN$_{acq}$*, mgN m^{-3} d^{-1}) described the acquisition rate of the material through prey ingestion (*CRC*, d^{-1}) required to ensure functioning of acquired phototrophy related photosynthesis in the pSNCM. Over time, the operational capacity of this acquired material will decline and the pSNCM will need to replace these from fresh prey. Laboratory studies have shown *Mesodinium* and *Dinophysis* to be capable of photosynthetic activity for up to 4 months and 2 months, respectively in the absence of any prey (Johnson & Stoecker, 2005; Johnson et al., 2006; Park et al., 2008). *PLN$_{acq}$* (Eq. 2) is thus described as a function of the number of days the pSNCM can survive in the absence of their special prey (*Enc$_{crit}$*, d) and a maximum value *PLN$_{max}$* (mgN m^{-3}) representing the optimal status of *PLN* for acquired phototrophy. It was assumed that 5% of cell nitrogen was associated with acquired phototrophic potential (i.e., *PLN$_{max}$* = 0.05 • protist N biomass); the exact proportion does not impact the emergent dynamics of the simulation, only the integration time step required to operate the model.

$$\frac{d}{dt}\text{PLN}_{acq} = \left(\text{MIN}\left(1, \text{CRC}/\text{Enc}_{crit}\right)\right)^2 \cdot \frac{\text{PLN}_{max} - \text{PLN}}{\text{TIMESTEP}} \qquad (2)$$

Maintenance of the phototrophic potential (*PLN$_{mgmt}$*, mgN m^{-3} d^{-1}) represents the rate of recycling of material, derived from the special prey from whence the potential is acquired, to enable the continued state of phototrophy in pSNCM (Hansen et al., 2013). Over time there would be a gradual deterioration in the ability of the pSNCM to perform photosynthesis. These errors would be countered by new acquisitions (i.e., *PLN$_{acq}$*) from the appropriate prey providing new copies of the genetic material associated with the maintenance and control of phototrophy. *PLN$_{mgmt}$* (Eq. 3) was thus described as a function of the growth rate of the pSNCM (*Cu*, d^{-1}) and a co-efficient accounting for efficiency of the kleptoplastidic material driving phototrophy (*PLN$_{coeff}$*, dimensionless).

$$\frac{d}{dt}\text{PLN}_{mgmt} = \text{Cu} \cdot \text{PLN}_{coeff} \cdot \text{PLN} \qquad (3)$$

Degradation (*PLN$_{decay}$*, mgN m^{-3} d^{-1}) of the photosynthetic material acquired from the special prey to enable phototrophy in pSNCM was computed (Eq. 4) with reference to a half-life function of the kleptoplastidic material (*halflife$_{PLN}$*, d). The half-life function was computed with reference to the *Enc$_{crit}$* value. Thus, when *Enc$_{crit}$* for *Mesodinium* and *Dinophysis* are 120 days and 60 days, respectively, then the *halflife$_{PLN}$* for *Mesodinium* ≈ 18 and *Dinophysis* ≈ 9 days, assuming basal respiration costs of ca. 10%.

$$\frac{d}{dt}\text{PLN}_{decay} = \frac{\text{Ln}(2)}{\text{halflife}_{PLN}} \qquad (4)$$

Simulation scenarios

Simulations were run in settings akin to eutrophic, mesotrophic and oligotrophic coastal waters with a mixing rate of 0.03 d^{-1} between the photic and subphotic zones and a mixed layer depth of 10 m (de Boyer et al., 2004). Initial concentration of dissolved inorganic nitrogen (DIN as NH_4^+ and NO_3^- at ratio of 0.1:0.9) for the eutrophic, mesotrophic and oligotrophic systems were 50 μM, 20 μM and 5 μM, respectively. In each of the three trophic systems, simulations were run under three different N:P initial mole ratios (DIN:DIP) of 16 (NP16, N-limiting, Redfield ratio), 32 (NP32) or 64 (NP64, P-limiting) (Flynn & Mitra, 2023). To achieve these initial conditions, inorganic phosphate (DIP) was supplied with reference to the initial DIN concentration and the required N:P ratio (Table 2). The surface photon flux density (PFD) was set at 500 μmol m^{-2} d^{-1} (saturating conditions for photosynthesis; Flynn & Mitra, 2023) supplied over 70% of the day. To study the impact of acquired phototrophy on ecosystem structure and functioning, simulations were run with different combinations of the default, 2× and 0.5× of the default values of *Enc$_{crit}$* (thus doubling and halving *halflife$_{PLN}$*) for the functioning of acquired phototrophy in *Mesodinium* and *Dinophysis* within the three nutrient systems. Tables 2 and 3 provide a full list of these

Table 2 Nutrient loads in simulated systems

simulated system	DIN (µM)	DIP (µM) at N:P = 16	DIP (µM) at N:P = 32	DIP (µM) at N:P = 64
eutrophic	50	3.1250	1.56250	0.781250
mesotrophic	20	1.2500	0.62500	0.312500
oligotrophic	05	0.3125	0.15625	0.078125

Table 3 Configuration of parameters describing acquired phototrophy for in silico investigations $halflife_{PLN}$, days; Enc_{crit}, days

acquired phototro-phy parameters	Mesodinium		Dinophysis	
	$halflife_{PLN}$	Enc_{crit}	$halflife_{PLN}$	Enc_{crit}
default	18.062	120	09.031	60
M0.5	09.031	60	09.031	60
M2	36.124	240	09.031	60
D0.5	18.062	120	04.515	30
D2	18.062	120	18.062	120

scenarios and configurations. Simulations were run with an Euler integration routine using Powersim Studio 10.

Results

The community structure and spatial dynamics of all the functional groups appear similar in the eutrophic and mesotrophic systems operating with the default configuration for acquired phototrophy (Table 3). There were, however, differences in the relative peak bloom biomass between the three species depending on the nutrient status of the simulated scenario (Fig. 4). For oligotrophic systems, the community structure differed markedly from the eutrophic and mesotrophic systems with *Mesodinium* dominating the trophic dynamics.

In the eutrophic system, the trophic dynamics of all functional groups followed similar patterns under the three different N:P ratios of 16, 32 and 64 (Fig. 4, top row). In all these simulations, *Dinophysis* bloom occurrence was of the longest duration and produced the highest C-biomass peak; this was followed by *Mesodinium* and then *Teleaulax* (Fig. 5; top row). Termination of blooms was associated primarily with a decline in prey biomass to support acquired phototrophy rather than by nutrient limitation (Fig. S1).

In the mesotrophic system (Fig. 4, middle row), with default configuration for acquired phototrophy (Table 3), under NP16 and NP32 conditions, the community trophic dynamics followed the same pattern as in the eutrophic system with *Dinophysis* dominating. However, under NP64, the C-biomass production for all the members of the TMD-trinity, as well as of cyanobacteria and bacteria, were substantially lower. *Mesodinium* bloom peak was the highest which

was attained with the shortest bloom duration (Fig. 5; middle row). There was a 10 d delay in the temporal dynamics of the recurring bloom in the mesotrophic system compared to eutrophic system (Fig. 4 middle vs. top row). This was associated with nutrient limitation (Fig. S2). In contrast, the eutrophic system had sufficient DIN to support pico-phytoplankton cyanobacteria and CM *Teleaulax* blooms (Fig. S1).

Under default configuration, the trophic dynamics in the oligotrophic system was very different from those seen in the eutrophic and mesotrophic systems (Fig. 4, bottom panel). *Mesodinium* and *Teleaulax* dominated the oligotrophic systems even though, under N:P ratios of 16 and 32, the duration of the *Dinophysis* bloom was greater than that of *Mesodinium* or *Teleaulax* (Fig. 5, bottom panel). Under NP64, *Mesodinium* bloom dominated the system. The system was N and P limited under all the oligotrophic conditions (Fig. S3).

When the parameters describing the longevity of acquired phototrophy in *Mesodinium* ($halflife_{PLN}$) and survival capacity of *Mesodinium* (Enc_{crit}) in the absence of *Teleaulax* were halved or doubled (M0.5 and M2, Table 3), the community dynamics showed similar trends to those from the default configuration under the different N:P conditions within each of the three systems – eutrophic (default versus M0.5 & M2, Fig. S4), mesotrophic (default versus M0.5 & M2, Fig. S5) and oligotrophic (default versus M0.5 & M2, Fig. S6). Likewise, the TMD-trinity bloom duration and bloom peak height outputs matched those from the default configuration (Fig. S7).

When the $halflife_{PLN}$ and Enc_{crit} for *Dinophysis* were halved (D0.5, Table 3), the patterns of temporal dynamics were similar to those from the default configurations in all three systems (default versus D0.5, Figs. S4, S5, S6). The duration of *Dinophysis* blooms were relatively shorter in eutrophic and mesotrophic systems under all three N:P ratios (Fig. S7, top and middle rows). However, all the members of the TMD-trinity achieved similar maximum bloom peak except under NP64 where the maximum peak achieved by the *Dinophysis* population was significantly lower than those achieved under default, M0.5 and M2 configurations.

The *Dinophysis* bloom dynamics persisted for a longer duration compared to the other configurations when Enc_{crit} (and thence $halflife_{PLN}$) for *Dinophysis* was doubled (D2, Table 3) in eutrophic and mesotrophic systems under all three N:P ratios of 16, 32 and 64 (Fig. 6). The duration of the
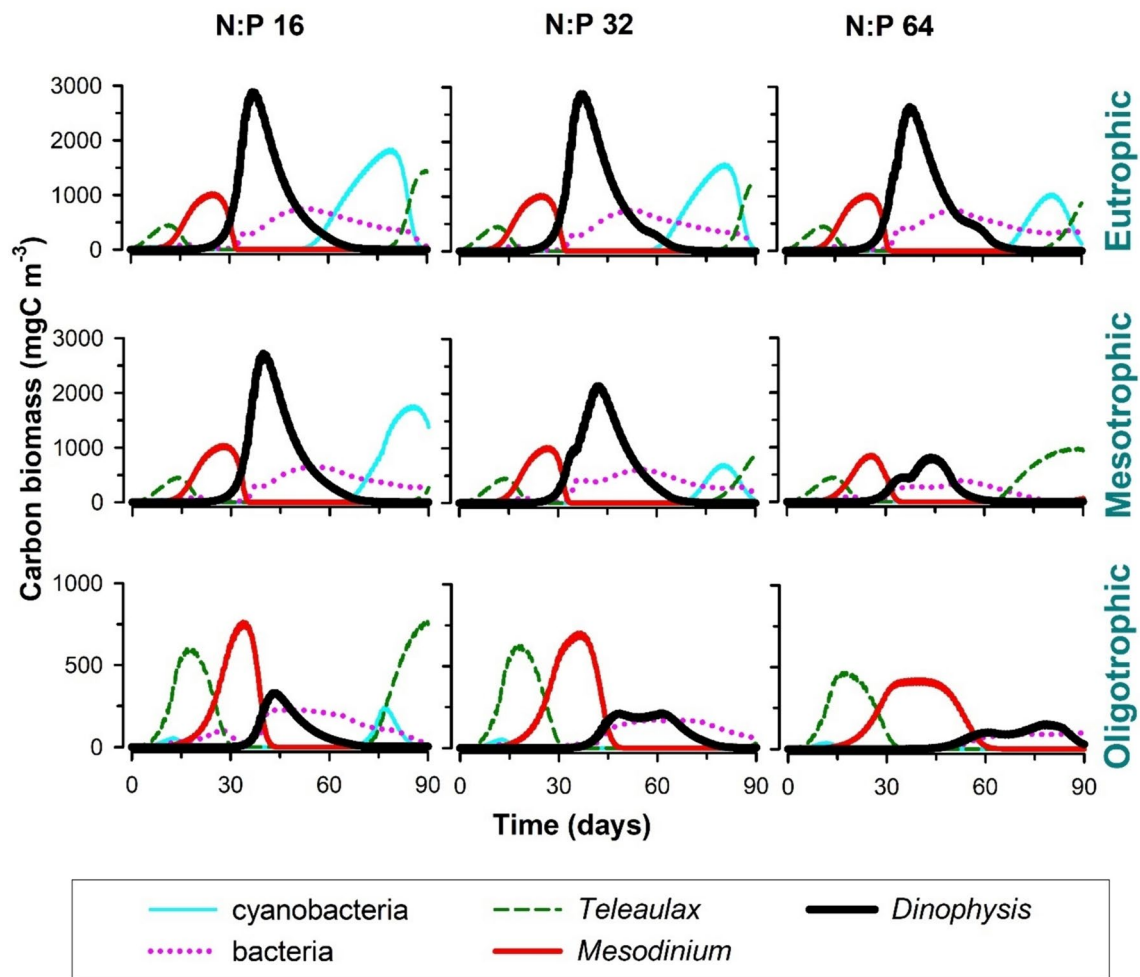
Fig. 4 Temporal patterns of plankton bloom dynamics under different nitrogen and phosphorus (N:P) nutrient ratios and loadings (eutrophic, mesotrophic, oligotrophic) with default configuration for acquired phototrophy. Shown are changes in the carbon biomass for the five plankton functional types (Fig. 3) in the simulated food web (Fig. 2). See also Table 2 for nutrient loads and Table 3 for acquired phototrophy configurations

Dinophysis blooms were extended by 10–20% compared to those under default configurations (Fig. 7 vs. Fig. 5). Different half-life and critical prey availability configurations for acquired phototrophy in *Dinophysis* did not appear to have any obvious impact on the ecosystem structure or functioning in the oligotrophic system except under N- and P- limiting conditions (N:P = 64) where *Teleaulax* blooms attained the maximum C-biomass peak (Fig. S7).

Overall, changes in N:P ratios leading to P-stress (Figs. S1, S2, S3), resulted in a decrease in the maximum bloom density for *Mesodinium* and *Dinophysis* in all conditions (Fig. S7). As noted, in the default scenario, doubling the half-life of kletoplastidic material in *Dinophysis* was advantageous leading to an increase in the *Dinophysis* bloom duration. In contrast, halving the half-life resulted in an early termination of the *Dinophysis* bloom in all trophic scenarios under the different N:P ratios.

Discussions

Transfer of energy and biochemicals from producers to consumers through the trophic levels is the bedrock of community ecology. This study investigated the specialised transfer mechanism of acquired phototrophy from planktonic primary producers to their consumers under different environmental conditions. This transmission pathway provides essential biochemical (actually, subcellular components), while the acquisition then provides additional energy and materials via photosynthesis. The emergent community bloom dynamics is seen to be a function of the trophic interactions within the TMD-trinity, the nutrient status of the system and the stoichiometric ratio of the nutrients within each system (Figs. 4, 6, S4, S5, S6). For the first time, this work shows how changes in different environmental conditions—eutrophic versus mesotrophic versus oligotrophic—can
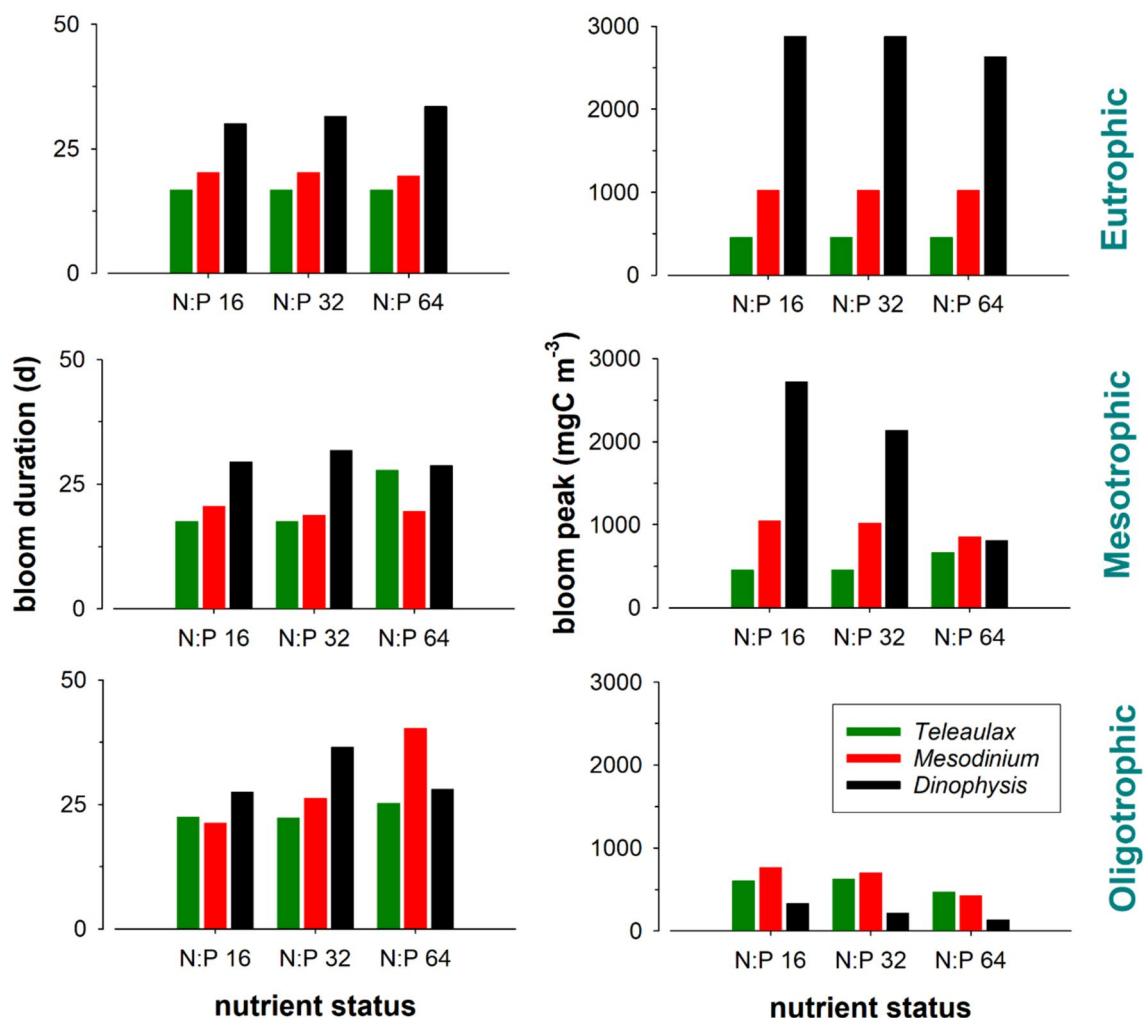
Fig. 5 Bloom duration and bloom peak of the TMD-trinity under different N:P nutrient ratios and loadings (eutrophic, mesotrophic, oligotrophic) with default configuration for acquired phototrophy. See Tables 2 and 3 for nutrient loads and acquired phototrophy configurations, respectively

influence the transference of acquired phototrophy and thus bloom dynamics of the TMD-trinity. While the outputs from the simulations superficially resemble those of the single nutrient N-based fixed stoichiometric TMD-model of Anschütz et al. (2022), here, P was a co-limiting nutrient and hence the impact of variable stoichiometry was included with its attendant stoichiometric ecological implications (Mitra & Flynn, 2005). The findings from this study reveals the additional multi-stressor impact that variable environmental N:P has on the transference of acquired phototropy.

With climate change and anthropogenic activities, the N:P stoichiometric ratios and concentrations of oceanic nutrients are predicted to vary significantly in the future (Sardans et al., 2021). The simulations undertaken in this study demonstrated the importance of considering different N:P stoichiometry to understand implications for community dynamics and production within each of the eutrophic, mesotrophic and oligotrophic systems. In eutrophic system the impact of differing N:P ratios was observed only under more extreme N- and P- limiting conditions (N:P = 64) which yielded a relatively lower biomass (Figs. 4, 5). This is consistent with the work of Mayers et al. (2014), who showed that N:P nutrient ratios of below 32 were insufficient to generate significant P-stress in an individual microalga. However, within each of the mesotrophic and oligotrophic systems, substantial differences were observed in the emergent community dynamics and productivity under the different N:P stoichiometric ratios (Figs. 4, 5, 6, 7, S5, S6, S7). These demonstrate the need for multi-nutrient variable stoichiometric community models to capture the important emergent dynamics of stoichiometric ecology.

Of the three genera within the TMD-trinity, the *Dinophysis* spp. have received most attention within modelling studies due to the socio-economic implications associated
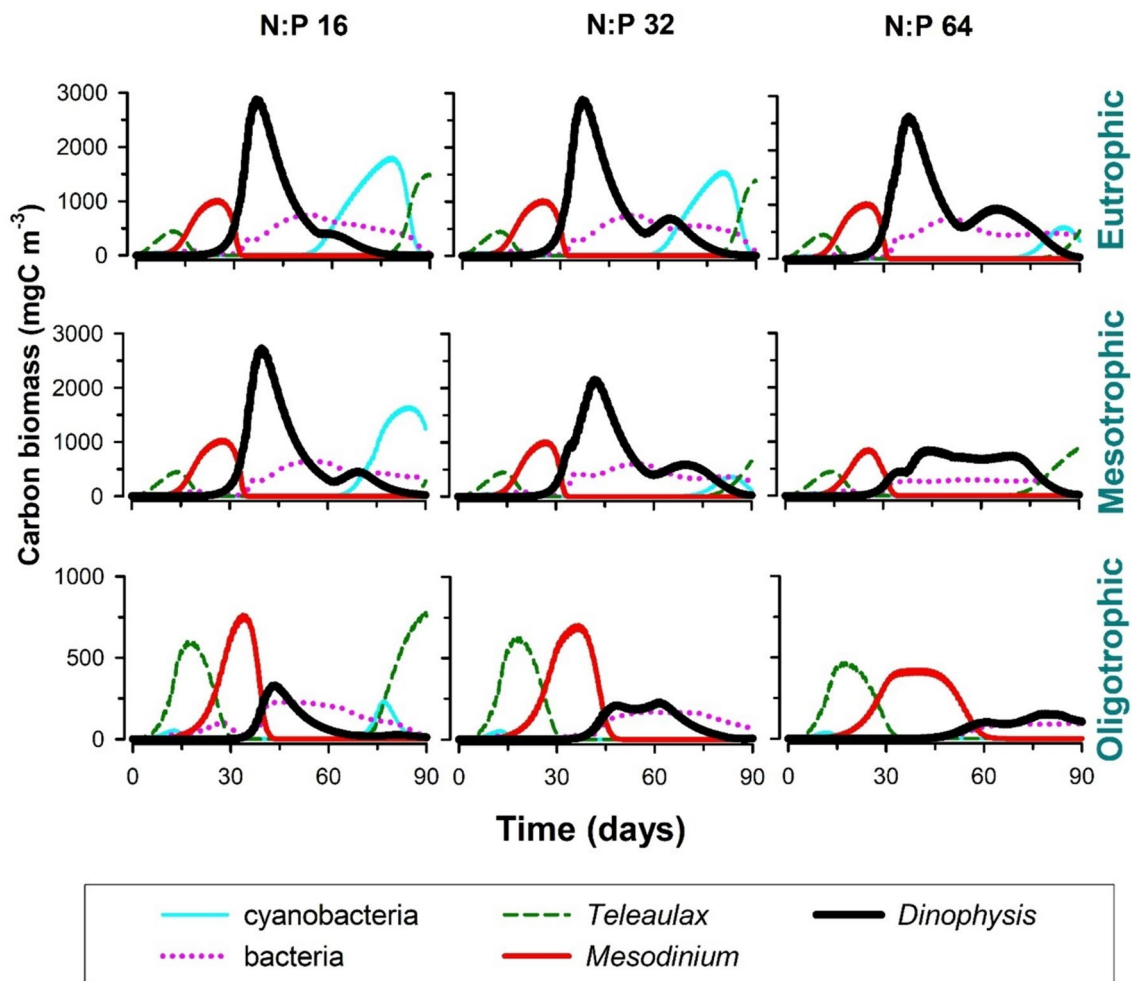
Fig. 6 Temporal patterns of plankton bloom dynamics under different N:P nutrient ratios and loadings (eutrophic, mesotrophic, oligotrophic) with D2 configuration for acquired phototrophy. Shown are changes in the carbon biomass for the five plankton functional types (Fig. 3) in the simulated food web (Fig. 2). See also Table 2 for nutrient loads and Table 3 for acquired phototrophy configurations

with DSP events (Table S1) leading to closures of shellfisheries (Díaz et al., 2016; Fiorendino et al., 2020; Reguera et al., 2012). The importance of acquired phototrophy in *Dinophysis* spp. has been well documented from eco-physiological investigations for over three decades (Fiorendino et al., 2020; Garcia-Portela et al., 2018; Mafra et al., 2016; Jacobsen & Andersen, 1994; Skovgaard, 1998; Reguera et al., 2012). Despite this, information detailing the longevity and functionality of acquired phototrophy in *Dinophysis* spp., and the implications for community ecology thereof, is scant. Under the different conditions, the longevity of acquired phototrophy had a more discernible impact on *Dinophysis* spp. bloom dynamics rather than upon *M. rubrum* (Figs. 4, 6, S4, S5, S6). The halving or doubling of parameters describing acquired phototrophy in *M. rubrum* (Enc_{crit} and $halflife_{PLN}$, Table 3) did not appear to be a strong driver of *M. rubrum* bloom dynamics. Rather, termination of *M. rubrum* blooms appeared to be a function of grazing

pressure from the *Dinophysis*, or of nutrient exhaustion. The pSNCM *M. rubrum* has evolved to acquire not just the plastidic material but also nuclear material from the *Teleaulax* spp. clade. As a result, *M. rubrum* appears to have the unique ability to undergo multiple cell divisions in the absence of *Teleaulax* spp. and survive for up to four months (Johnson & Stoecker, 2005). The bloom dynamics under different N- and P- limiting conditions in the oligotrophic systems showcases the resilience of acquired phototrophy of *M. rubrum*. The different pSNCM *Mesodinium* spp. have evolved to prefer different species of cryptophytes and have different retention rates for acquired phototrophy. For example, acquired phototrophy in benthic *Mesodinium* species, *M. coatsi* and *M. chamaeleon*, has been found to be short-lived; these cannot survive for longer than 2–4 weeks in the absence of their cryptophyte prey (Kim et al., 2019; Moeller & Johnson, 2018). In contrast, the various pSNCM *Dinophysis* spp. appear to have evolved to depend strictly
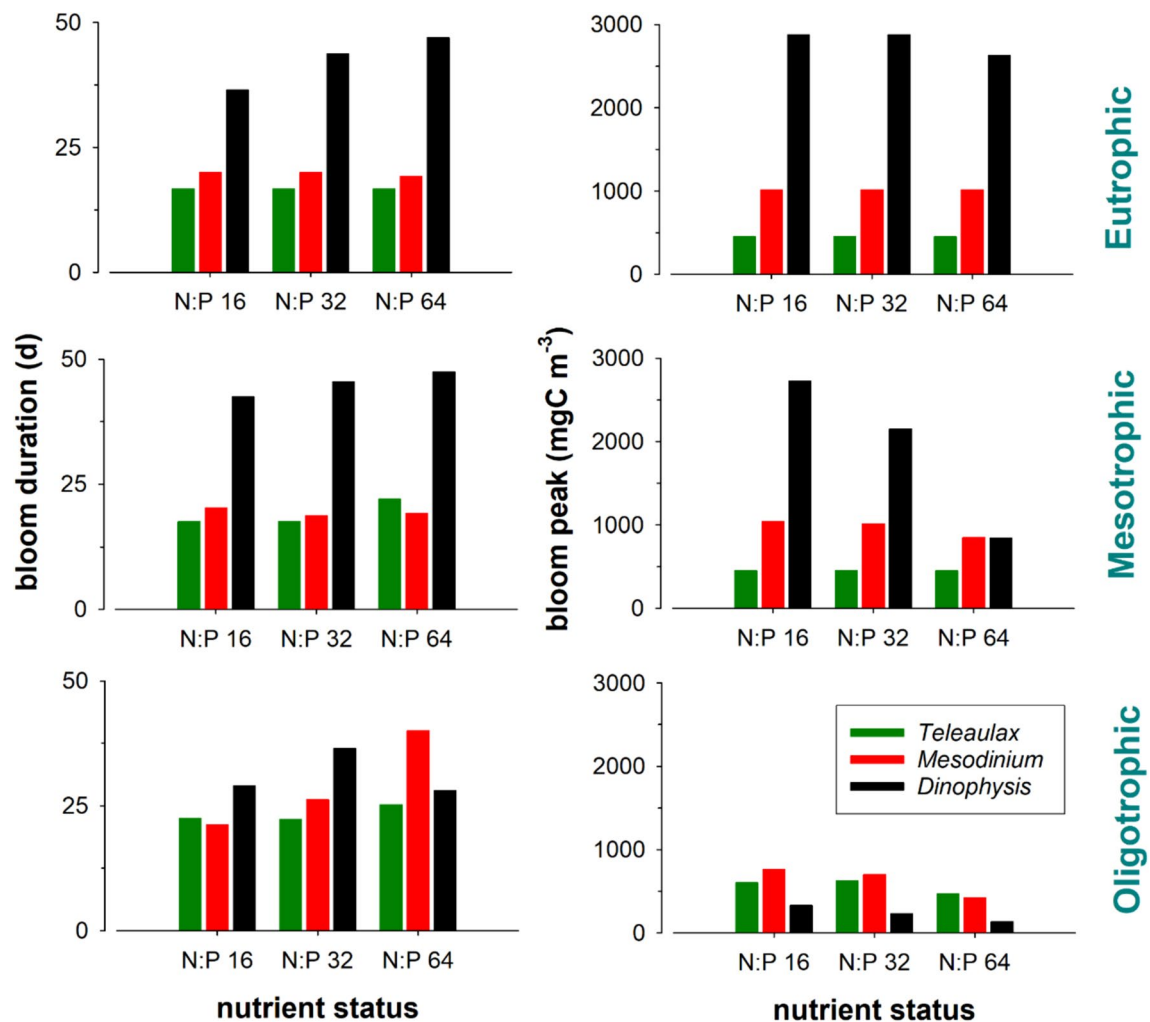
Fig. 7 Bloom duration and bloom peak of the TMD-trinity under different N:P nutrient ratios and loadings (eutrophic, mesotrophic, oligotrophic) with D2 configuration for acquired phototrophy. See Tables 2 and 3 for nutrient loads and acquired phototrophy configurations, respectively

on the planktonic *M. rubrum* for their acquired phototrophy (Hernández-Urcera et al., 2018; Mitra et al., 2023; Velo-Suárez et al., 2014).

Dinophysis spp. have been reported to be capable of maintaining their phototrophic capability for up to 2 months in the absence of *M. rubrum* (Park et al., 2008). However, such studies do not provide sufficient data to constrain a model. The simulation results show that halving or doubling this capability has the potential to terminate or extend the bloom significantly (Figs. 4, 5, 6, 7). The photo-acclimation capacity of *Dinophysis* spp. (Chl:C) was found to differ by up to four-fold over the duration of the bloom; the quality (C:N:P) of *M. rubrum* and *Dinophysis* spp. also declined as the bloom progressed (not shown). Decline in stoichiometric (C:N:P) ratios of organisms leads to mismatch in predator–prey growth dynamics and nutrient regeneration (Flynn et al., 2015; Mitra & Flynn, 2005) impacting

transfer efficiency between trophic levels (Anderson et al., 2013) potentially leading to the formation of harmful algal bloom events (Mitra & Flynn, 2006). The situation here is more complex. All the organisms within the TMD-trinity are mixoplankton. These mixoplankton are not just predators (i.e., consumers); they are also phototrophic producers and can recycle nutrients that would otherwise be regenerated during prey digestion (Fig. 3; Flynn & Mitra, 2023; Mitra & Flynn, 2023).

Most modelling studies of *Dinophysis* spp. bloom prediction fail to take into account the eco-physiological interactions within the TMD-trinity or even recognise that they are mixoplankton (e.g., Pinto et al., 2016; Raine et al., 2010; Silva et al., 2023). In these previous studies, *Dinophysis* spp. have typically been considered to belong to the phytoplankton functional group and modelling efforts have thus focussed mainly on forecasting *Dinophysis* spp.

bloom linked only to physics (cf. Anschütz et al., 2022). In contrast to *Dinophysis* spp., the placement of *Mesodinium* spp. within a plankton functional group has been controversial (Crawford, 1989; Lindholm, 1985) even though the importance of these ciliates in primary production have been documented since the early 1980s (Leppänen & Bruun, 1986; Revelante & Gilmartin, 1983; Stoecker et al., 1989). *Mesodinium* are recognised as ecologically important organisms due to their ability to form high cell density red-tide blooms (Yih et al., 2013). However, as these red-tide blooms are non-toxic, even though in some instances such growths have been reported to lead to localised hypoxia (Hayes et al., 1989), *Mesodinium* spp. bloom dynamics have received no attention in ecosystem modelling studies.

Climate change related environmental stressors are predicted to have diverse implications for marine ecosystem structure and services. For example, changes in levels of precipitation and associated storm water run-offs have been predicted to lead to increased coastal eutrophication (Sinha et al., 2017), favouring and enhancing harmful algal bloom events (Glibert, 2020) such as DSP producing *Dinophysis* blooms (Table S1). In contrast, increasing water temperatures are predicted to result in an increase in oligotrophic zones in the oceans (Irwin & Oliver, 2009). In these systems, picophytoplankton (e.g., cyanobacteria) abundance is predicted to increase (Morán et al., 2015; Zehr et al., 2017) and nano-sized mixoplankton (such as *Teleaulax*) could act as a lynchpin. Thus, in low nutrient systems, the TMD-trinity would have access to nutrients beyond those indicated solely by concentrations of inorganic sources, via *Teleaulax* consuming picoplankton (Yoo et al., 2017) and thence supporting *Mesodinium* (Mitra & Flynn, 2023). The implication of this can be observed in the oligotrophic simulations where *T. amphioxeia* and *M. rubrum* dominate but the low nutrient status of the environment cannot support good quality (optimal C:N:P) *M. rubrum* impacting *Dinophysis* spp. bloom dynamics (Figs. 4, 6, S4, S5, S6). It may be that such nutrient limiting conditions would also impact the quality and longevity of the plastidic material transferred from the *T. amphioxeia* to *M. rubrum* to *Dinophysis* spp. which would then further impact community dynamics. Results shown here indicate the importance of understanding such possibilities.

Irrespective of the environmental conditions, any transfer of kleptoplastidic and nuclear material from the CM *T. amphioxeia* to the pSNCM ciliate *M. rubrum* and then onto the pSNCM *Dinophysis* spp. enables the pSNCM consumers to engage in photosynthesis and contribute towards primary productivity. Carbon fixation by the two pSNCM parties in the TMD-trinity could be a significant contribution to community dynamics (Fig. 8) impacting biogeochemical cycling and trophic dynamics (Leles et al., 2021; Mitra et al., 2014b). Thus, ignoring the TMD-trinity within models
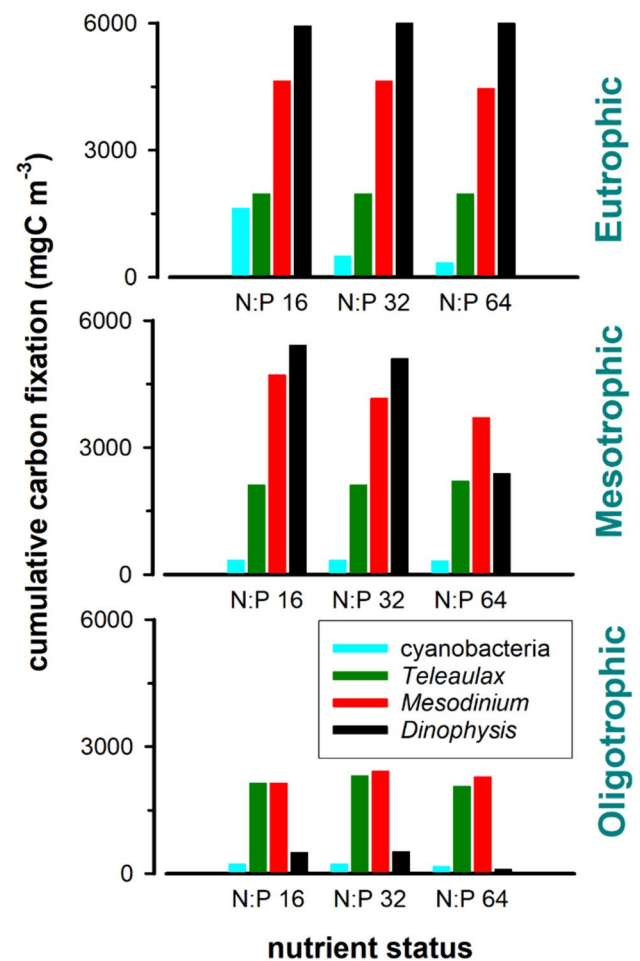

Fig. 8 Cumulative carbon fixation by each of the phototrophic plankton functional groups under different N:P status. Simulations were run with molar N:P of 16, 32, 64 (N:P16, N:P32, N:P64, respectively) in the three systems (eutrophic, mesotrophic, oligotrophic; Table 2) under default configuration for acquired phototrophy (Table 3)

exploring impact of climate change on primary productivity and thence ecosystem services could potentially provide incomplete or, indeed, flawed predictions about future scenarios for these organisms.

There is much uncertainty about how diverse and contrasting environmental stressors arising from anthropogenic activities, including climate change, will impact transference of acquired phototrophy and thence ecosystem structure and function. There are > 250 species of mixoplankton that engage in acquired phototrophy (Mitra et al., 2023); the TMD-trinity is the most studied complex. Research exploring how pSNCM *Mesodinium* spp., especially *M. rubrum* (previously *Myrionecta rubra*), acquire phototrophic capability continues to flow from the first comprehensive studies on this subject (Gustafson et al., 2000; Johnson, 2011; Johnson et al., 2006). However, studies that focus on how different abiotic conditions impact ecophysiology and blooms

dynamics of the TMD-trinity are rare (Anschütz et al., 2022; Fiorendino et al., 2020). As a result, there is very little knowledge that can aid advancement of our understanding about the implications of the transfer of acquired phototrophy and longevity of these acquisitions for community ecology structure and function. This work shows the importance of enhancing our quantitative knowledge of such matters, without which we cannot improve our understanding of this unique and important example of the transfer of essential biochemicals between trophic levels and the subsequent implications for marine biodiversity and ecosystem services.

Declarations

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