Chapter 5
A Revised Interpretation of Marine Primary Productivity in the Indian Ocean: The Role of Mixoplankton

Aditee Mitra and Suzana Gonçalves Leles

Abstract Traditional interpretations of marine plankton ecology, such as that in the Indian Ocean, mirror the plant-animal dichotomy of terrestrial ecology. Thus, single-celled phytoplankton produce food consumed by single-celled zooplankton, and these are in turn consumed by larger zooplankton through to higher trophic levels. Our routine monitoring surveys, research, models, and water management protocols all reflect this interpretation. The last decade has witnessed the development of an important revision of that traditional vision. We now know that the phytoplankton-zooplankton dichotomy represents, at best, a gross simplification. A significant proportion of the protist plankton at the base of the oceanic food-web can photosynthesise (make food 'like plants') and ingest food (eat 'like animals'), thus contributing to both primary and secondary production simultaneously in the same cell. These protists are termed 'mixoplankton', and include many species traditionally labelled as 'phytoplankton' (a term now reserved for phototrophic microbes that are incapable of phagocytosis) or labelled as 'protist zooplankton' (now reserved for protist plankton incapable of phototrophy). Mixoplankton include various harmful algal species, most likely all the phototrophic dinoflagellates, and even iconic exemplar 'phytoplankton' such as coccolithophorids (which can consume bacteria). Like all significant revisions to ecology, the mixoplankton paradigm will take time to mature but to ignore it means that we fail to properly represent plankton ecology in teaching, science, management, and policy. This chapter introduces the mixoplankton functional groups and provides the first insight into the biogeography of these organisms in the Indian Ocean. A first attempt to consider the implications of the mixoplankton paradigm on marine primary productivity and ecology in the Indian Ocean is also given.

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1 Reassessing Primary Production in the Indian Ocean

The Indian Ocean covers ~30% of the global ocean area (74.92 million km^2, latitude: 25°N–40°S, longitude: 45°E–115°E), has a coastline of ~66,526 km shared by 38 countries and supports, socioeconomically, >30% of the global human population (Wafar et al., 2011). The Indian Ocean (henceforth IO) comprises nine large marine ecosystems and is home to various keystone species; for example, >30% of the global coral population are IO inhabitants (Wafar et al., 2011; Roxy et al., 2016, 2020). The IO also makes a substantial contribution to global fish production through small-scale as well as commercial fisheries; it is one of the top producers of tuna, and ~13% of the global wild-fish catch come from the IO (FAO, 2020; Dalpadado et al., 2021). However, research attention on the IO has been significantly below that applied to the Atlantic and Pacific Oceans. In part, this may be attributed to the complexities and variabilities in the oceanographic and atmospheric conditions (Krey, 1973; Hood et al., 2009), as well as the geopolitics of the area. To advance out knowledge in understanding primary productivity in the IO, it is important to rethink how we perceive the microbial food-web. The subject of this chapter, mixoplankton – protist plankton that photosynthesise and eat, is one that has evaded mainstream oceanography for over a century. As the IO is explored, it is only right for studies of mixoplankton, as contributors to marine primary production, to be embedded in that process with all due haste.

A core component of IO research involves quantification of the primary production, which ultimately supports fisheries as well as biodiversity. Phytoplankton, prokaryotic cyanobacteria and eukaryotic protists, are the primary producers that employ photo-autotrophy to fix carbon. This production is then transferred to fish via their consumers, the zooplankton (Mitra et al., 2014a; Fig. 5.1a). More recently, there has been an increased emphasis on understanding the impact of various climate change stressors on primary productivity. There have been concerns that increasing sea surface temperatures in conjunction with increasing oxygen minimum zones in the IO will lead to a decline in primary productivity and shifts in the dominance of the organisms that drive it. Such a decline will, in turn, impact fish stocks and, thence, regional and global food security (Gomes et al., 2014; Dalpadado et al., 2021).

The study of primary production in any ecosphere needs to take into account the development of paradigms, and this applies equally to the IO. If we do not get the fundamentals underpinning the functioning of an ecosphere correct, then everything else collapses. During various instances, in the past decades, marine science has had cause to reconsider the key foundations of marine ecology (reviewed by Glibert & Mitra, 2022). In the late 1970s, marine ecology saw the advent of the 'microbial loop' introduced by Pomeroy (1974), and more formally described by Azam et al. (1983). This led to the food chain description of microbial components of marine

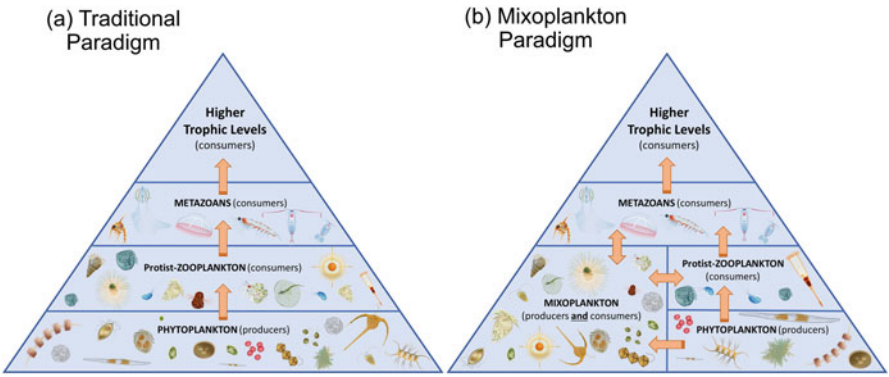

Fig. 5.1 (**a**) Traditional versus (**b**) mixoplankton paradigms for the structure of the Indian Ocean marine food-web. Arrows indicate transfer of energy. Mixoplankton can consume microbial plankton as well as metazoan grazers. Plankton images not to scale. See also Table 5.1 for definitions of the functional groups

ecology to be reimaged as a 'web'. In this web, bacteria play a major role as consumers of dissolved organic matter as well as decomposers of particulate organic matter. The activities of bacteria, and those of their grazers, regenerate nutrients to support primary production, especially in regions where upwellings are of low significance. Nearly two decades after the formalisation of the microbial loop, enhanced understanding of the importance of viruses and processes by which viruses facilitate the movement of nutrients from organisms to pools of dissolved and particulate organic matter led to the concept of the 'viral shunt' (Wilhelm & Suttle, 1999; Jiao et al., 2010). The microbial loop and viral shunt together further enhanced our understanding of how these microbial communities aid the transformation of labile dissolved organic carbon to more recalcitrant forms – important sources of sequestered oceanic carbon – via the 'microbial carbon pump' (Jiao et al., 2010, 2014).

At present, we stand at a point when we need to reconsider something that is arguably more fundamental in marine ecology. It transpires that science did not get the description of the functionalities of the organisms at the base of the plankton food-web correct. Over the last decade, a new paradigm in marine ecology has emerged – a paradigm that reimages the base of all marine food-webs. This is the 'mixoplankton paradigm'.

2 The Mixoplankton Paradigm

Understanding mechanisms that drive life in the single largest ecosystem of our planet, the Ocean, remains a pivotal research theme in natural sciences. About half of Earth's carbon fixation and oxygen production are attributed to the activities of

microscopic marine plankton. Marine systems, and indeed humans, are thus ultimately dependent on the activities of these microscopic plankton. Traditionally the planktonic communities have been considered to occupy clear niches in the ecosystem as phototrophic primary producers (phytoplankton), heterotrophic primary consumers (protist-zooplankton), and remineralisers (bacterioplankton). In this marine food-web structure, the food-producing phytoplankton, comprising prokaryotic cyanobacteria and eukaryotic protist plankton, are consumed by the protist-zooplankton (primary consumers). These zooplankton are then consumed by metazoan plankton (e.g. copepods, krill), which in turn provide food and energy to the higher trophic levels (HTLs; e.g. fish, cetaceans). This traditional view of the marine food-web, following a plant-animal dichotomy, is analogous to the pyramidal structure of the terrestrial food-web (Fig. 5.1a; Mitra et al., 2014a; Glibert & Mitra, 2022).

Over the last decade, there has been an increasing awareness that protist plankton engaging in 'mixotrophy' via photo-autotrophy and phago-heterotrophy are important members of the marine food-web communities (Flynn et al., 2013). Mixotrophy is not new to marine ecology. Indeed, in primary producing phytoplankton, mixotrophy has long been recognised as an important nutritional strategy, especially for harmful algal bloom (HAB) species (Burkholder et al., 2008). Typically, 'mixotrophy' in marine microalgae refers to photo(auto)trophy plus osmo(hetero)-trophy; mixotrophy through phago(hetero)trophy has traditionally been considered to be of relatively minor importance for microalgae (see Table 5.1 for definitions of forms of nourishment). However, various exemplar 'phytoplankton' are now recognised to be capable of consumption of prey; examples include the iconic coccolithophorid *Emiliania huxleyi* (Avrahami & Frada, 2020); the cosmopolitan ecosystem disruptive *Phaeocystis globosa* (Koppelle et al., 2022); the ecologically important *Tripos furca* (Bockstahler & Coats, 1993); the diverse bacterivorous phytoflagellates of the microbial carbon pump (Unrein et al., 2014); toxin-producing HABs *Alexandrium* spp. and *Dinophysis* spp. whose blooms result in shellfish contamination and harvesting closures (Jeong et al., 2005; Reguera et al., 2014). Likewise, over a third of the traditionally labelled 'protist-zooplankton' species, consumers of microalgae, have been found to be capable of engaging in acquired phototrophy through kleptoplastidy (e.g. *Laboea strobila*, Stoecker et al., 2009) or endosymbiosis (e.g. various species of Foraminifera, Bé et al., 1977; Gast & Caron, 1996).

The protist plankton thus includes photosynthetic micro-plankton that also eat, and predatory micro-plankton that also photosynthesise. The base of the oceanic food-web, therefore, does not follow the typical plant-animal dichotomy concept akin to terrestrial systems; textbook and modelling descriptions of marine food-webs are, for the most part, incorrect. This recognition where most oceanic primary producers cannot be analogised as 'miniature plants' and their primary consumers as 'miniature animals' has led to a paradigm shift in the understanding of marine ecology (Mitra et al., 2016; Flynn et al., 2019; Glibert & Mitra, 2022; Fig. 5.1b). To help emphasise the shift in categorisation of plankton functional type and in the usage of the term 'mixotroph' (noting that mixotrophy does not have to involve

Table 5.1 Glossary to terms describing forms of nourishment and functional groups (types) of microbial plankton; terminologies and definitions collated from Flynn et al. (2019), Glibert & Mitra (2022) and Mitra et al. (2023b).

Forms of nourishment	**Definitions**	
Autotrophy	Nutrition involving the synthesis of complex organic substances using photosynthesis (phototrophy) or chemosynthesis. Typically associated with the use of inorganic nutrients.	
Heterotrophy	Nutrition involving the consumption and interconversions of sources of organic carbon; this includes osmotrophy and phagotrophy.	
Mixotrophy	Nutrition involving both autotrophy and heterotrophy. Autotrophy may be via photosynthesis or chemosynthesis. Heterotrophy may be via osmotrophy and/or phagotrophy.	
Osmotrophy	A mode of heterotrophy involving the uptake and consumption of dissolved organic compounds; includes auxotrophy (uptake of vitamins). Also referred to as osmo(hetero)trophy.	
Phagotrophy	A mode of heterotrophy involving the engulfment of particles (often whole organisms) into a phagocytic vacuole in which digestion occurs. Also referred to as phago(hetero)trophy.	
Phototrophy	A mode of autotrophy involving the fixation of CO_2 using energy derived from light. Also referred to as photo(auto)trophy.	
Plankton functional groups (types)	**Abbreviations**	**Definitions**
Bacteria	–	Prokaryote plankton acquiring nourishment via osmo(hetero)trophy, and some also via chemo (auto)trophy (rendering them mixotrophic).
Constitutive Mixoplankton	CM	Mixoplankton with an inherent capacity for photo(auto)trophy (cf. NCM) in addition to osmo(hetero)trophy.
Cyanobacteria	–	Prokaryote members of the phytoplankton acquiring nourishment via photo(auto)trophy and osmo(hetero)trophy rendering them mixotrophic.
endosymbiotic Specialist Non-Constitutive Mixoplankton	eSNCM	SNCM that acquire their capacity for photo (auto)trophy through harbouring photosynthetic endosymbionts (cf. pSNCM).
Generalist Non-Constitutive Mixoplankton	GNCM	NCM that acquire their capacity for photo (auto)trophy from general (i.e. from a range of potential non-specific) phototrophic prey (cf. SNCM).
Mixoplankton	M	Plankton protists capable of obtaining nourishment via photo(auto)trophy *and* osmo(hetero)-trophy *and* phago(hetero)trophy; that is, they are photo-osmo-phago-mixotrophic (cf. phytoplankton and protist-zooplankton).
Non-Constitutive Mixoplankton	NCM	Mixoplankton that acquire the capability for photo(auto)trophy from consumption (via phago(hetero)trophy) of phototrophic prey. There are three functional forms of NCM: GNCM, pSNCM, and eSNCM (cf. CM).

(continued)

Table 5.1 (continued)

Phytoplankton	P	Plankton obtaining nourishment via photo (auto)trophy and osmo(hetero)trophy rendering them mixotrophic. They are incapable of phago (hetero)trophy. Exemplars include the eukaryotic diatoms and prokaryotic cyanobacteria (cf. mixoplankton and protist-zooplankton).
Protist	–	Single-celled eukaryotic organism. These include 6 functional types of plankton: pZ, GNCM, pSNCM, eSNCM, CM, and P.
Protist-Zooplankton	pZ	Protist zooplankton obtaining nourishment via heterotrophy (phagotrophy and osmotrophy). They cannot engage in autotrophy. (cf. phytoplankton and mixoplankton).
plastidic Specialist Non-Constitutive Mixoplankton	pSNCM	SNCM that acquire their capacity for photo (auto)trophy from sequestration of photosynthetic apparatus and nuclear material from specific phototrophic prey (cf. eSNCM).
Specialist Non-Constitutive Mixoplankton	SNCM	NCM that acquire their capacity for photo (auto)trophy from specific phototrophic prey. There are two functional types of SNCM: pSNCM and eSNCM (cf. GNCM).

predation, Table 5.1), Flynn et al. (2019) coined the term 'mixoplankton' to describe planktonic protists that engage in photo(auto)trophy *plus* osmo(hetero)trophy *plus* phago(hetero)trophy. This distinguishes them from the non-phagotrophic phytoplankton (e.g. diatoms) and the non-phototrophic protist-zooplankton (e.g. tintinnids). The descriptor 'phytoplankton' is thus now reserved for phototrophs (both protists and cyanobacteria) that are incapable of phagotrophy though capable of mixotrophy through osmotrophy (Flynn et al., 2019; Glibert & Mitra, 2022, Table 5.1).

A widespread role for mixotrophy through osmotrophy is demonstrated by many decades of research illustrating the use of sugars, amino acids, and other dissolved organics (Antia et al., 1981; Flynn & Butler, 1986; Meyer et al., 2022). The term 'mixotroph' and 'mixotrophy' are often used indiscriminately to refer to traits and ecological implications of the mixotrophic phytoplankton as well as of the mixoplankton. While all mixoplankton are mixotrophs by virtue of their ability to engage in photo-osmo-phago-trophy, all mixotrophs are not mixoplankton (see Table 5.1 for definitions of microbial plankton functional types). Photo-osmo-mixotrophy (of phytoplankton) versus photo-osmo-phago-mixotrophy (of mixoplankton) has very different implications for ecology and biogeochemical cycling. A mixoplankter actively removes a wide range of competitors (bacteria to metazoans) from the ecosystem through hunting, killing, and eating (Fig. 5.1b). For example, the HAB-forming mixoplankton *Karlodinium armiger* have been observed to predate on metazoans (e.g. copepods; Berge et al., 2012); within the traditional marine food-web, metazoan grazers are categorised as predators of the microalgae

K. armiger. We thus see a reversal of the traditional trophic 'role' with mixoplanktonic activity directly impacting the food-web dynamics. Further, the processes of prey digestion and assimilation by mixoplankton results in the release of a range of different end products – dissolved and particulate organics – through excretion and defecation (voiding), potentially contributing towards the biological and/or microbial carbon pumps (Mitra et al., 2014b; Glibert & Mitra, 2022). In contrast, the photo-osmo-mixotrophy employed by phytoplankton neither removes any prey, competitors, or grazers from the food-web nor does this type of mixotrophy lead to the production of any defecated particulate matter that further structures the plankton food-web.

Another aspect of mixoplankton that is often confused in discussions on the topic is the evolutionary lineage of protist evolution. The ancestral protist was phagotrophic (Raven et al., 2009) and would have retained at least a level of the osmotrophic capabilities present in the earliest microbes, if only to recover leaked metabolites (Flynn & Berry, 1999). From these, ancestral mixoplankton evolved by the integration of photosystems from their prey (originally cyanobacteria-like species; Ponce-Toledo et al., 2017; Sánchez-Baracaldo et al., 2017). What are now (sensu Flynn et al., 2019) termed 'phytoplankton protists' then evolved from the loss of phagotrophy. Mixoplankton did not, therefore, evolve through combining traits from protist zooplankton and protist phytoplankton; the latter evolved by loss of an important trait for protist evolution, namely, phagotrophy (Mitra et al., 2023a).

3 Mixoplankton in the Indian Ocean

Mixoplankton comprise a diverse group of protist plankton which can be functionally divided between those with a constitutive ability to photosynthesise (constitutive mixoplankton; CM), and those which need to acquire phototrophic capabilities (non-constitutive mixoplankton; NCM) (Flynn et al., 2019; Mitra et al., 2023b). NCM acquire their phototrophic potential by stealing photosynthetic machinery from (i) many prey types (generalists: GNCM; e.g. *Laboea strobila*, McManus & Fuhrman, 1986; Stoecker et al., 1987; *Strombidinium conicum*, Stoecker et al., 1988/89), (ii) from only specific prey (plastidic specialists: pSNCM; e.g. *Mesodinium rubrum*, Gustafson et al., 2000; Johnson et al., 2016; *Dinophysis acuminata*, Jacobson & Andersen, 1994; Park et al., 2006), or, (iii) by harbouring endosymbionts (endosymbiotic specialists: eSNCM; e.g. green *Noctiluca scintillans*, Subrahmanyan, 1954; Wang et al., 2016; foraminiferans such as *Globigeria bulloides*, *Orbulina universa*, Spindler & Hemleben, 1980; Gastrich, 1987). Accordingly, marine protist plankton can be broadly divided into six functional groups (types), with the phago-heterotrophic protist-zooplankton and the photo-osmo-mixotrophic phytoplankton occupying the two ends of the trophic spectrum (Mitra et al., 2016; Flynn et al., 2019; Mitra et al., 2023b). Figure 5.2 provides a key to this plankton functional group (type) classification specifically providing examples from the IO plankton communities; this has been modified from Mitra et al. (2016), Mitra

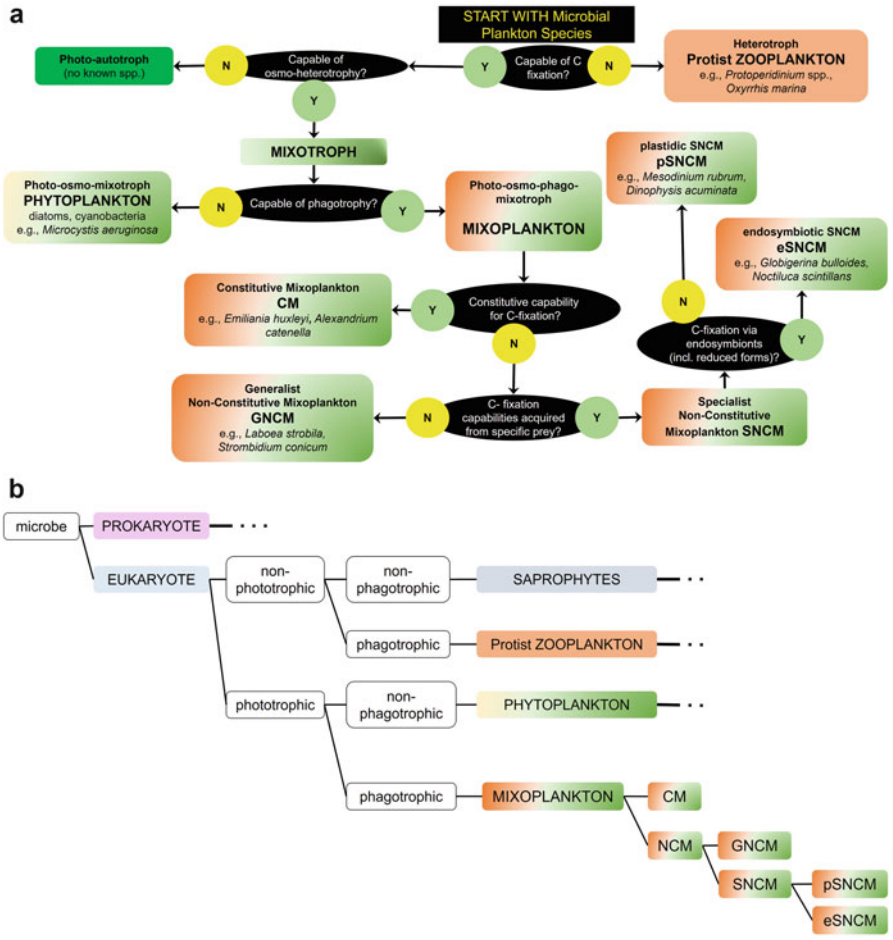

Fig. 5.2 Classification of the Indian Ocean marine microbial plankton under the mixoplankton paradigm. (**a**) Functional group classification key for marine microbial plankton. N no, Y yes. (Modified from Mitra and Flynn et al. (2021) and Mitra et al. (2023b)). (**b**) Marine microbial plankton traits tree leading to mixoplankton. Dash-dotted lines indicate additional tree branches. (Modified from Mitra et al. (2023b)).

and Flynn (2021) and Mitra et al. (2023b), to take into account the coining of the term 'mixoplankton'. Figure 5.3 provides a schematic of the physiological processes associated with the different forms of nourishment employed by the different protist plankton functional groups; this has been modified from Mitra et al. (2023a). Functional group descriptions are commonly used by scientists to partition the numerous taxonomic classes into categories more relevant to ecology; it is also referred to as 'functional type' especially in modelling studies (Mitra et al., 2016). Accordingly, in this chapter, we will use the terminologies 'functional group' and 'functional type' synonymously.

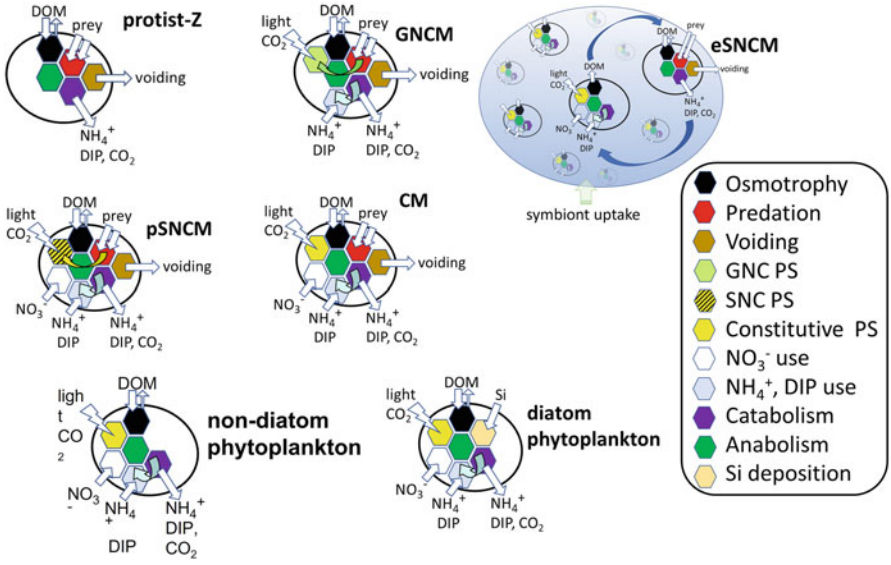

Fig. 5.3 Schematic representations of the six protist functional type configurations under the mixoplankton paradigm. Physiological functions of each functional group are indicated by the hexagons. The six protist functional groups are: zooplankton (with no phototrophy; pZ), generalist non-constitutive mixoplankton (with acquired phototrophy; GNCM), plastidic specialist non-constitutive mixoplankton (with acquired phototrophy from specialist prey; pSNCM), endosymbiotic specialist non-constitutive mixoplankton (with symbionts for acquired phototrophy; eSNCM), constitutive mixoplankton (inherent phototrophic capability; CM) and phytoplankton (with no phagotrophy). All protist types can use dissolved organic matter (DOM); phytoplankton are thus mixotrophs by combining photo(auto)trophy with osmo(hetero)trophy. See also Table 5.1 for definitions of the functional groups and nutritional strategies. Schematics are not to scale; see Table 5.2 for size ranges of IO mixoplankton. (Figure modified from Mitra et al. (2023a)

3.1 Mixoplankton Biogeography in the Indian Ocean

Different mixoplankton functional groups have diverse spatial and temporal distributions (Leles et al., 2017, 2019; Faure et al., 2019), but collectively include representatives with global significance throughout the wide size range of protist plankton (Flynn et al., 2019; Mitra et al., 2023b). The size range is extensive, ranging from some of the smallest CM of a few micrometre diameter (e.g. *Florenciella* sp., Li et al., 2020) to single-celled Rhizaria exceeding 1 cm (e.g. *Orbulina universa*, Spindler & Hemleben, 1980; Gastrich, 1987). Here we present, a biogeographic study of the different mixoplankton functional groups that occur in the IO.

In order to undertake this study, we aligned the mixoplankton species listed in 'The Mixoplankton Database' (Mitra et al., 2023b) to those reported in the Ocean Biogeographic Information System database (OBIS; http://www.iobis.org/) for the IO. For this purpose, data from OBIS were oriented by the division of the global

ocean into subsets defined by 54 biogeographic provinces according to Longhurst (2007). We considered the following Longhurst biogeographic provinces (LP) to encompass the IO: North-western Arabian Coastal Upwelling (ARAB), Archipelago Deep Basins Oligotrophic Gyres (ARCH), Australia-Indonesia Coastal Seas (AUSW), Eastern Africa Coastal Seas (EAFR), Eastern India Coastal Seas (INDE), Western India Coastal Seas (INDW), Red Sea and Persian Gulf Coastal Seas (REDS), Indian South Subtropical Gyres (ISSG), Indian Monsoon Gyres (MONS), Sunda-Arafura Shelves (SUND), parts of Subantarctic Water Ring (SANT), and parts of South Subtropical Convergence province (SSTC). This division of the IO was similar to that employed by Dalpadado et al. (2021). At least one record was necessary to assume the occurrence of mixoplankton in any province. Grids corresponding to Longhurst's provinces used in the maps were obtained from http://www.marineregions.org/.

Figure 5.4 shows the biogeographic distribution of the different mixoplankton functional types in the IO. The constitutive mixoplankton species (CM) would all have been traditionally labelled as 'phytoplankton' and, therefore, identified only as primary producers with no role in predation. The species within the three non-constitutive mixoplankton groups (GNCM, pSNCM, eSNCM) would have been traditionally considered to be 'protist-zooplankton'. Their food-web activity would have been labelled as 'consumers' of primary producers and prey for metazoan grazers (secondary consumers), with no consideration of their contribution towards primary production.

3.2 Mixoplankton Traits

The biogeography data revealed that 150 mixoplankton species have been recorded within the OBIS database for the IO. Of these, 58 species are constitutive mixoplankton (CM), and 92 species are non-constitutive mixoplankton (NCM) (Fig. 5.5a; see also Table 5.2 and Mitra et al. (2023b)). Of those 150 species, 33 species are recorded as HABs in the IOC-UNESCO harmful algal bloom database (https://marinespecies.org/hab/). Ten of the HAB species belong to the plastidic specialist NCM (pSNCM) functional group, while the remaining species belong to the CM functional group.

The size range of the observed mixoplankton species in the IO is highly diverse between and within each functional type (Fig. 5.5b). The CM species encompass pico to micro size ranges (e.g. *Florenciella* sp.: ESD 0.6 µm, Li et al., 2020; *Tripos furca*: 150 µm × 50 µm, Mitra et al., 2023b), while the sizes of pSNCM and eSNCM species range from nano to meso (e.g. pSNCM *Pfiesteria piscicida* ESD: 10–20 µm, Parrow & Burkholder, 2004; eSNCM *Dinothrix paradoxa* ESD: 12–20 µm, Pascher, 1914; eSNCM *Globigerina bulloides*: ~200 µm, Bé et al., 1977). Only two GNCM plastidic ciliates (*Laboea strobila*, *Strombidium conicum*) are reported as present in the OBIS database for the IO, and the sizes of these range between 40 and 150 µm (Stoecker et al., 1988/89; McManus & Fuhrman, 1986). An analysis of the size

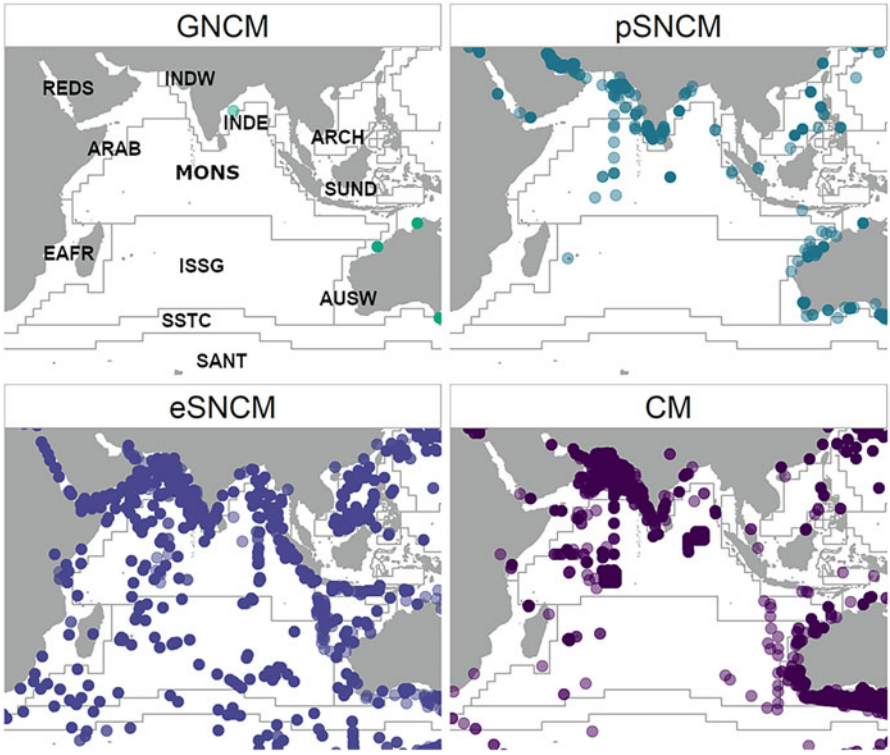

Fig. 5.4 Occurrence of mixoplankton across the Indian Ocean. The number of records are derived from the OBIS database and plotted according to Longhurst's biogeographic provinces of the IO (Longhurst, 2007). Outputs are provided for each of the four mixoplankton functional groups: generalist non-constitutive mixoplankton (GNCM), plastidic specialist non-constitutive mixoplankton (pSNCM), endosymbiotic specialist non-constitutive mixoplankton (eSNCM), and constitutive mixoplankton (CM). See also Fig. 5.2 and Tables 5.1 and 5.2. The IO and neighbouring IO provinces are indicated in the panel showing GNCM distribution

relationship between the mixoplankton predator and their prey also shows the diverse size range of prey ingested by these different mixoplankton functional groups (Fig. 5.5c). This is indicative of the role that mixoplankton must play in the plankton dynamics of the IO.

Analysis of the mixoplankton taxonomic groups revealed Dinoflagellata to be the most observed taxonomic group in the IO (Fig. 5.6a), while the most frequently and highest recorded species belong to the Foraminifera taxonomic group (Table 5.2). Indeed, the top 10 species recorded from the IO all belong to the Formanifera, and 60% of these species were observed in all of the IO Longhurst provinces. Within the specialist non-constitutive mixoplankton types, eSNCM showed greater diversity in their ability to acquire phototrophy compared to pSNCM (Fig. 5.6b vs. Fig. 5.6c).

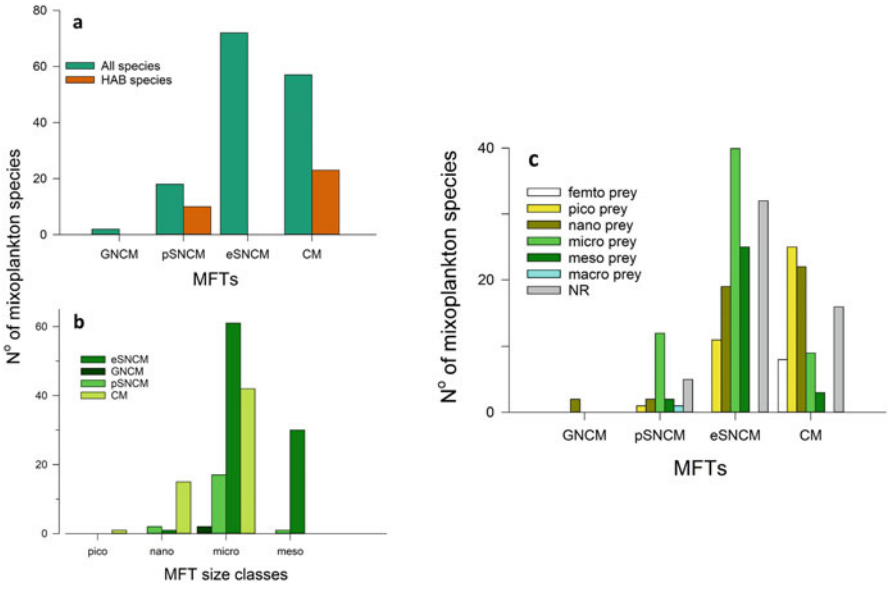

Fig. 5.5 Diversity of the IO mixoplankton species and their prey. (**a**) Species categorised according to mixoplankton functional types (MFT). (**b**) Size class distribution of the species within each MFT. (**c**) Relationship between prey size class and mixoplankton size class for each of the MFTs: generalist non-constitutive mixoplankton (GNCM), plastidic specialist non-constitutive mixoplankton (pSNCM), endosymbiotic specialist non-constitutive mixoplankton (eSNCM), and constitutive mixoplankton (CM). NR indicates not recorded. See also Table 5.1 and Fig. 5.3

3.3 Primary Production and Bacterial Farming by Mixoplankton

An obvious question that arises is as follows: what are the implications of the mixoplankton paradigm for primary production? One of the 'common' taxonomic prey groups associated with the top 30 IO species in the OBIS database (Table 5.2) are the prokaryotic Bacteria and Cyanobacteria. These prokaryotes have been shown to be resilient to multi-stressors (Oliver et al., 2014), with evidence that climate change is seeing an up-shift in the abundance of these picoplankton at the expense of the larger, protist, primary producers across the global Ocean (Morán et al., 2010, 2015).

Mitra et al. (2014b) explored the importance of accounting for the mixoplankton-prokaryote predator-prey interactions in marine systems. In that study, the 'traditional paradigm' configuration considered the simple plant-animal dichotomy where primary production was a function of phytoplankton (diatoms and cyanobacteria) activity (phototrophy + osmotrophy), and remineralisation was due to bacteria. The phytoplankton and bacteria were consumed by protist-zooplankton (phagotrophy), which in turn were consumed by metazoan grazers. In this system, the

Table 5.2 Top 30 frequently recorded species from the Indian Ocean in the OBIS database

#	MFT	Species	Taxonomy	HABs	OBIS	#LP	% LP	Size	Example prey taxonomy
1	eSNCM	*Globigerina bulloides*	Foraminifera	No	9953	11	100	Micro-meso	Bacteria, Copepoda, Sarsostraca
2	eSNCM	*Globigerinoides ruber*	Foraminifera	No	8581	11	100	Micro-meso	Ciliophora, Copepoda
3	eSNCM	*Globigerinita glutinata*	Foraminifera	No	8336	10	91	Micro-meso	Bacteria, Ciliophora, Copepoda
4	eSNCM	*Orbulina universa*	Foraminifera	No	6916	11	100	Micro-meso	Ciliophora, Copepoda
5	eSNCM	*Trilobatus sacculifer*	Foraminifera	No	6756	9	82	Micro-meso	Bacteria, Copepoda, Sarsostraca
6	eSNCM	*Globigerinella siphonifera*	Foraminifera	No	6364	11	100	Micro-meso	Bacteria, Copepoda, Sarsostraca
7	eSNCM	*Globorotalia menardii*	Foraminifera	No	5665	10	91	Micro-meso	Diatomeae, Ochrophyta
8	eSNCM	*Neogloboquadrina dutertrei*	Foraminifera	No	5514	11	100	Micro-meso	Diatomeae
9	eSNCM	*Globigerina falconensis*	Foraminifera	No	4751	10	91	Micro-meso	Bacteria, Copepoda, Sarsostraca
10	eSNCM	*Pulleniatina obliquiloculata*	Foraminifera	No	4265	11	100	Micro-meso	Ochrophyta
11	eSNCM	*Globigerinoides conglobatus*	Foraminifera	No	3490	9	82	Micro-meso	Bacteria, Copepoda, Sarsostraca
12	eSNCM	*Globorotalia tumida*	Foraminifera	No	1833	10	91	Micro-meso	Ciliophora, Copepoda
13	CM	*Emiliania huxleyi*	Haptophyta	No	1668	8	73	Nano	Bacteria
14	eSNCM	*Globoquadrina conglomerata*	Foraminifera	No	1289	7	64	Micro-meso	Bacteria, Copepoda, Sarsostraca
15	CM	*Phaeocystis globosa*	Haptophyta	Yes	1278	3	27	Nano	Bacteria
16	CM	*Tripos furca*	Dinoflagellata	No	1175	9	82	Micro	NR◆
17	eSNCM	*Globorotalia hirsuta*	Foraminifera	No	1137	8	73	Micro-meso	Bacteria, Copepoda, Sarsostraca
18	eSNCM	*Noctiluca scintillans*	Dinoflagellata	No	971	8	73	Meso	Diatomeae, Dinoflagellata
19	CM	*Tripos fusus*	Dinoflagellata	No	905	7	64	Micro	NR◆
20	CM	*Tripos muelleri*	Dinoflagellata	No	901	7	64	Micro	NR◆
21	CM	*Gonyaulax spinifera*	Dinoflagellata	Yes	820	7	64	Micro	Cyanobacteria
22	eSNCM	*Candeina nitida*	Foraminifera	No	807	7	64	Meso	Bacteria, Copepoda, Sarsostraca
23	CM	*Heterocapsa rotundata*	Dinoflagellata	No	647	1	9	Nano	Bacteria, Diatomeae

(continued)

Table 5.2 (continued)

#	MFT	Species	Taxonomy	HABs	OBIS	#LP	% LP	Size	Example prey taxonomy
24	CM	*Protoceratium reticulatum*	Dinoflagellata	Yes	594	7	64	Micro	NR◆
25	eSNCM	*Turborotalita humilis*	Foraminifera	No	589	9	82	Micro-meso	Bacteria, Copepoda, Sarsostraca
26	pSNCM	*Mesodinium rubrum*	Ciliophora	No	492	3	27	Nano-micro	Cryptophyceae
27	CM	*Gymnodinium catenatum*	Dinoflagellata	Yes	474	3	27	Micro	Cyanobacteria, Cryptophyceae, Dinoflagellata
28	CM	*Calcidiscus leptoporus*	Haptophyta	No	336	5	45	Nano	Bacteria
29	pSNCM	*Dinophysis acuminata*	Dinoflagellata	Yes	288	3	27	Micro	Ciliophora
30	CM	*Prorocentrum micans*	Dinoflagellata	No	222	7	64	Micro	Cyanobacteria,Diatomeae, Cryptophyceae, Dinoflagellata, Haptophyta, Ochrophyta

Data obtained from Mitra et al. (2023b)

Species classified according to mixoplankton functional groups/types (MFT): constitutive mixoplankton (CM), and non-constitutive mixoplankton (NCM); NCM species classified according to source of acquired phototrophy (generalists: GNCM; plastidic specialists: pSNCM; endosymbiotic specialists: eSNCM). 'HABs' indicates whether the mixoplankton is recorded as a harmful algal bloom species in the IOC-UNESCO HABs list. 'OBIS' indicates total number of observations per species recorded in the OBIS database. #LP indicate number of Longhurst provinces where ≥5 observations have been reported for the species while %LP indicates % occurrence of the mixoplankton species in the 11 Longhurst provinces in the Indian Ocean. femto, <0.2 μm; pico, 0.2–2 μm; nano, 2–20 μm; micro, 20–200 μm; meso, 200 μm–20 mm. *NR*◆ prey not recorded; mixoplankton activity evidenced through presence of food vacuoles

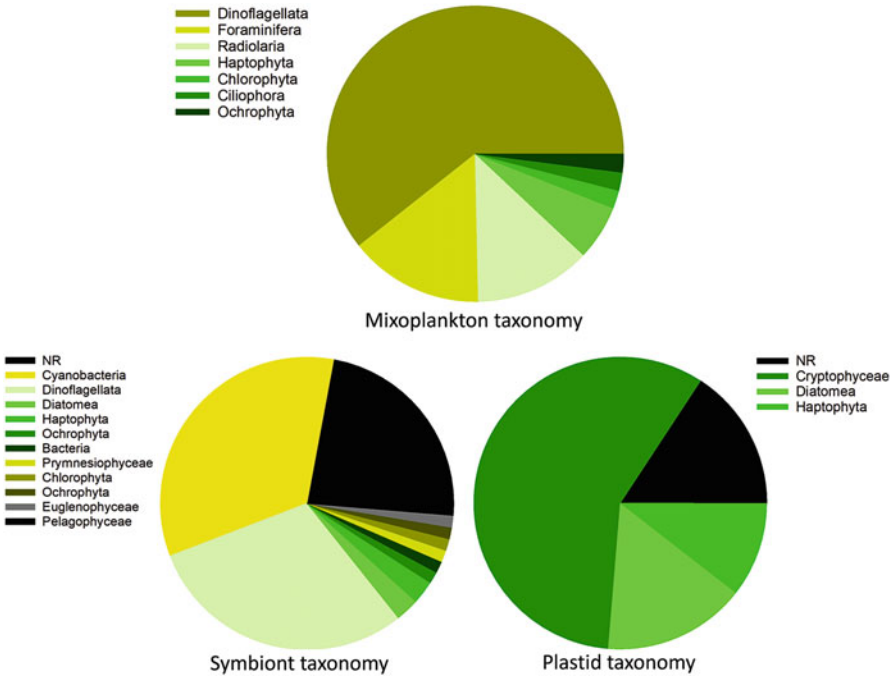

Fig. 5.6 Diversity of IO mixoplankton species and the sources of acquired phototrophy for the IO specialist non-constitutive mixoplankton (SNCM). Symbiont taxonomy, sources of endosymbionts for acquired phototrophy in endosymbiotic specialist non-constitutive mixoplankton (eSNCM). Plastid taxonomy, taxonomic groups contributing photosynthetic material to plastidic specialist non-constitutive mixoplankton (pSNCM). NR indicates not recorded. See also Fig. 5.3 and Table 5.1

phytoplankton and bacteria thus competed for dissolved inorganic nutrients (Fig. 5.7a). Within the 'mixoplankton paradigm', the protist 'phytoplankton' functional group was replaced with a 'constitutive mixoplankton' (CM) group. CM preyed upon cyanobacteria and bacteria (via phagotrophy) as well as engaged in C-fixation (via phototrophy). Thus, in this configuration, the CM are not competing with the prokaryote community for nutrients, rather the CM-bacterial activities were argued to be akin to 'farming' of the bacterial prey supported by the release of dissolved organics by the mixoplankton (Fig. 5.7b). Mixoplanktonic activity resulted in higher C-fixation due to enhanced nutrient feedbacks (Fig. 5.7c). This study thus showed that consideration of mixoplankton in food-web studies could have profound impacts on the ecosystem dynamics.

Ecosystem functioning has been shown to depend crucially on the description of the plankton functional types (phytoplankton vs. CM vs. NCM) with open ocean plankton dynamics. Description of the food-web organisms under the mixoplankton paradigm could potentially have a more stable equilibrium resulting in higher production rates due to variable (enhanced) nutrient feedbacks (e.g. Mitra et al., 2016; Leles et al., 2018). Leles et al. (2021) further demonstrated the importance of

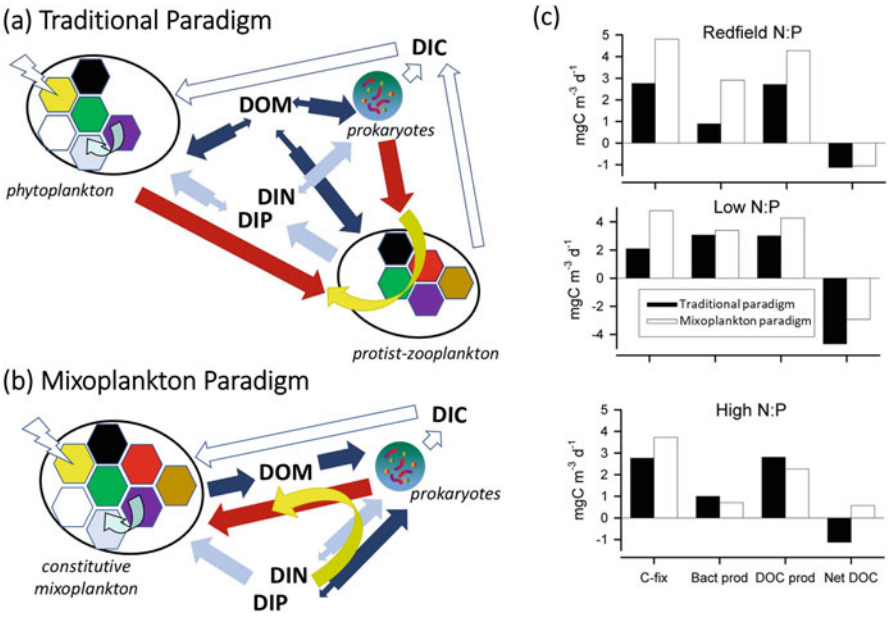

Fig. 5.7 Impact of 'Bacterial farming' on primary production under the mixoplankton paradigm. Schematic showing the detailed involvement of bacteria and DOM for the supply of nutrients to support primary production (yellow arrows) in (**a**) the traditional paradigm versus (**b**) the mixoplankton paradigm. Red arrows indicate predatory links. (**c**) Results from in silico experiments conducted under the traditional versus mixoplankton paradigms. Cfix, rates of primary production; Bact prod, bacterial production; DOC prod, production of dissolved organic carbon (from all sources, including voiding of material by grazers and primary production leakage), and Net DOC = biological production of DOC – bacterial uptake of DOC (negative value indicates reliance of bacteria on DOC in part from outside of the mixed layer). The inorganic nutrient regimes (all with an inorganic N input of 1 μM) are in Redfield N: P (molar ratio 16), low N: P (molar ratio 4), or high N: P (molar ratio 64). (Figures and results modified from Mitra et al. (2014b)). See also Fig. 5.3 and Table 5.1 for plankton functional group physiology and definitions

different mixoplankton functional types coupled with different sizes to plankton bloom dynamics and, thence primary production. For example, within the European regional seas' ecosystem model, the magnitude of the spring bloom differed when micro-phytoplankton were replaced by micro-mixoplankton; further, the timing of nano-plankton bloom altered when considered under the mixoplankton paradigm.

4 Discussion

The term 'mixoplankton' is relatively new, but the activities of these organisms are not new. Yet even after decades of marine research, species of the mixoplankton communities still remain enigmatic. Studies of the base of the oceanic food-web still follow the false plant-animal dichotomy (Fig. 5.1a) with primary production

focussing solely on phytoplankton (diatoms and cyanobacteria) activity. The mixoplankton paradigm sees a major shift in our understanding of the ecosystem functioning of various protist plankton (Fig. 5.1b); consumers of primary producers are now also contributing to carbon fixation (Glibert & Mitra, 2022). It is important to reflect on why and how science managed to miss this important community of marine ecology for so long; there are a few key reasons that warrant reflection.

4.1 Sampling Bias in Monitoring

From microscopic analyses to molecular data, ocean colour, and ecosystem models, all share one common aspect – these approaches are traditionally rooted in the phytoplankton-zooplankton paradigm, and thus neglect the mixoplankton communities. Current field monitoring methods do not reflect the complexity of the marine food-web under the mixoplankton paradigm, where different mixoplankton functional groups play a diverse and important role (Fig. 5.1b; Mitra et al., 2014b; Leles et al., 2021; Glibert & Mitra, 2022). Routine field sampling techniques are also based on the plant-animal phytoplankton-zooplankton dichotomy. Critically, such techniques are not well adapted to provide quantitative data for mixoplankton where phototrophy and phagotrophy are concurrent and synergistic processes (Mitra & Flynn, 2010). Research is too often conducted by experts in phytoplankton or zooplankton, with separate sampling and measurement approaches. For example, the presence of chlorophyll is typically used as an indicator of phytoplankton biomass and, thence, carbon fixation in surveys and ecosystem monitoring. However, chlorophyll is actually not just an indicator of the presence of phytoplankton; it may also indicate the presence of mixoplankton, which are not just primary producers, but also consumers, and include harmful species (Fig. 5.1b, Mitra & Flynn, 2021). It is thus important that plankton monitoring programmes take into account the mixoplankton communities. Their proliferation is not driven solely by light and inorganic nutrients as that of phytoplankton communities; therefore, they have a much wider and diverse impact on marine trophic dynamics (Anschütz et al., 2022; Larsson et al., 2022).

Traditional sampling protocols, based on microscopic identification and quantification, are commonly biased towards certain taxonomic groups or size classes of protists. In our interrogation of the OBIS database for the IO, we found ca. 70% of the species to belong to the Dinoflagellata group (Fig. 5.6); previous studies on mixoplankton biogeography in global oceans (Faure et al., 2019; Leles et al., 2019) have observed a similar bias towards this group. Such a bias towards dinoflagellates can be attributed to a focus on global HAB events due to their deleterious impact on aquaculture and fisheries (Al Shehhi et al., 2014; Reguera et al., 2014; Kudela et al., 2015; Harrison et al., 2017); we found records of dinoflagellates in 27–64% of the Longhurst provinces within the IO (Table 5.2).

The IO biogeography data show a wide range of functional diversity within the mixoplankton community (Fig. 5.5). While species of sizes ranging from pico-meso (1–800 μm) have been recorded across the different mixoplankton functional groups (Table 5.2), the majority of the recorded species fall within the micro (20–200 μm) size range (Fig. 5.5b). Previous studies have suggested that sampling bias adversely affects investigations of small mixoplankton, occurring within the pico- and nano-plankton size spectrum (Leles et al., 2019), as well as the larger (>600 μm) mixoplankton (Leles et al., 2017). Microscopy still remains the primary and best methodology for identification of organisms to species level. However, that approach is problematic for smaller (pico- and nano-) mixoplankton.

Protist species have been traditionally defined based on morphological differences, but this is compounded by the presence of cryptic species with very similar body forms but different physiologies, particularly among nanoplankton (Lie et al., 2018). While DNA sequence information has been proposed as a potential tool to address such shortcomings in the detection of protistan diversity (De Vargas et al., 2015), it should be noted that estimates from DNA sequences are strongly dependent on primer choice, amplification protocols, and sequencing and can also be biased towards certain groups (Caron & Hu, 2019; Strzepek et al., 2022). The study by Faure et al. (2019), for instance, identified a gap in sequence data in the GNCM and pSNCM groups compared to the CM and eSNCM groups. At best, sequences provide semi-quantitative data only. We need quantitative data for presence and for vital rates of not just mixoplankton but also their prey and predators to understand ecosystem functioning – 'omics cannot provide such data (Strzepek et al., 2022).

Various rhizarian taxa, including eSNCM Foraminifera and Radiolaria, occur within the 'larger' meso-plankton (>500 μm) size category. However, when considering plankton within the meso size range, sampling and monitoring studies typically focus on the metazoan planktonic grazers (e.g. copepods) (Leles et al., 2017). Yet, imaging surveys have revealed that nearly 30% of total zooplankton biomass across the oceans are rhizarians, most of which are eSNCM (Biard et al., 2016). Within routine monitoring surveys, these meso- mixoplankton are typically under-represented because their cells are severely damaged by plankton nets and also because they slowly dissolve during attempts to preserve samples (Biard et al., 2016). We found the most frequently recorded mixoplankton species in the IO to be the eSNCM rhizarian Formanifera occurring in all the Longhurst biogeographic provinces (Table 5.2; Fig. 5.4). A recent study reports that mixoplanktonic rhizarians dominate the oligotrophic waters of the IO (110°E, Davies et al., 2022; i.e. comprising parts of the AUSW, MONS, ISSG Longhurst provinces, Longhurst, 2007). This important group would traditionally be labelled as predatory protist-zooplankton, and therefore, their potentially significant contributions towards primary production in the IO through carbon fixation would be ignored.

4.2 Challenges for Aquaculture and Fisheries

Over 80% of the world's human population lives within 100 km of the coast, and the IO coastline is ~66,526 Km, shared by 38 countries (Wafar et al., 2011). The majority of the coastal zone belts of the IO are densely populated, with the Ocean playing a substantial socioeconomic role in the provision of ecosystem services to these communities (De Young, 2006). The Sustainable Development Goals of the United Nations highlight the importance of ocean health and sustainability, especially under climate change (Arora & Mishra, 2019). This, in turn, highlights the need for revision of the ocean health indicators in line with the mixoplankton paradigm. In marine systems, chlorophyll is typically used as a proxy for measuring phytoplankton productivity, including for fisheries and aquaculture management. This is because chlorophyll and its analogues in remote sensing or ocean colour provide a ready and sensitive monitor of 'phytoplankton' (see Sect. 3.3 above). The concept that, on occasions, this signature is due to organisms other than strict phototrophs creates a challenge. This is especially important for predictions of algal blooms and their impacts on aquaculture and fisheries (Jeong et al., 2005; Reguera et al., 2014). Various HAB species are mixoplanktonic (Mitra & Flynn, 2021), and the growth of these HABs is not controlled simply by light and dissolved organics and inorganics (i.e. nutrients that support phototrophy and osmotrophy). Competitors and even grazers could provide food for the proliferation of HABs (Berge et al., 2012).

New types of ecosystem disruptive mixoplankton blooms are also appearing in the IO – such as the eSNCM dinoflagellate green *Noctiluca scintillans* (Gomes et al., 2014) and the mucosphere-producing CM dinoflagellate *Prorocentrum* cf. *balticum* and *P. cordatum* (Larsson et al., 2022; Tillmann et al., 2023) – and are expanding across coastal oceans with climate change. In the Arabian Sea sector of the IO, green *N. scintillans* blooms are leading to the collapse of the traditional phytoplankton-zooplankton-fisheries link in the food-web with severe food security and socioeconomic hardships to a population of over 140 million people (Goes et al., 2018). Other mixoplankton blooms affect recreational activities, and the property market – discolouration of water caused by *Karlodinium veneficum* blooms have been known to result in a decrease in prices of highly sought-after waterside properties; this species has been recorded (in OBIS) as occurring in the INDE and INDW Longhurst provinces of the IO.

There is also a potential interaction with aquaculture, as fish farms release both the nutrients needed for photosynthesis, but also the organic matter used directly or indirectly (via support of prey species) by mixoplankton. Algal blooms are a major issue for aquaculture all around the globe, and the IO supports a range of different aquacultures such as sea cucumbers, seaweeds, and shell- and fin-fisheries (De Young, 2006; FAO, 2020). Studies on fisheries and aquaculture without considering mixoplanktonic activity leave gaps in our understanding of what controls the many algal blooms that impact these ecosystem services.

4.3 Primary Production in Ecosystem and Climate Change Models

Carbon fixation through primary production is one of the cornerstone processes in marine ecology and oceanography; in the IO, primary production studies have been focussed mainly in the Arabian Sea and the 110°E sections (Krey, 1973; Hood et al., 2009). Modelling is a widely used tool to study the impact of climate change on primary productivity. However, the traditional split between 'phytoplankton' and 'zooplankton' still defines the means by which plankton are structured within climate change models, with a few exceptions (Ghyoot et al., 2017; Leles et al., 2018, 2021; Li et al., 2022). The majority of global models of primary productivity thus ignore the diverse strategies adopted by protist plankton, leaving us largely ignorant of how photo-osmo-phago-trophy of mixoplankton affect the competitive outcomes within protist communities. Modellers generally avoid complexity, and mixoplankton are complex; they are more than merged 'phytoplankton' and 'zooplankton' (Flynn & Mitra, 2009; Mitra & Flynn, 2010; Mitra et al., 2023a). Introducing mixoplankton to models is thus an uphill battle. The challenge in embedding the well-established microbial loop and virus shunt descriptions in models (both are typically absent from models) perhaps warns us of the challenge ahead. However, the absence of mixoplankton in models is more than just another simplification, for it also reflects a flawed description of the organisms that are currently included in the models and labelled as 'phytoplankton' and 'zooplankton'.

Biogeochemical models, particularly 3D models, tend to compare simulations against ocean colour data due to the availability of continuous global estimates of surface Chl-a concentrations (Bracher et al., 2017; Dalpadado et al., 2021). However, such data do not capture the diversity of forms and functions among phototrophic taxa, including phytoplankton and mixoplankton. From the 1990s, increasing efforts have been applied to developing algorithms that can retrieve information on the composition and size structure of phototrophic communities from ocean colour (Sathyendranath, 2014). These methods utilise information from (presumed) phytoplankton abundance, cell size, and bio-optical properties such as pigment composition, absorption, and backscattering (reviewed in Bracher et al., 2017). Most algorithms provide information about the dominance or the presence/absence of a particular group, or the fraction of Chl-a associated with three different size classes (pico-, nano-, and micro-plankton). Such information is not, however, easily transferable to the plankton functional types within biogeochemical models, and the situation will be more complex when considering mixoplankton as the 'colour' in those organisms could be due to acquired phototrophy or ingested prey.

There are various other challenges with acquiring and using remote sensing data. For example, biogeochemical models are typically biomass-based (e.g. carbon, nitrogen); currently, there is no reliable algorithm to convert chlorophyll data to carbon biomass as the Chl:C ratio varies significantly under different environmental conditions (as does the C:N ratio) and with different species. There are limitations

with acquiring data using remote sensing as the methodology can be applied to the ocean surface only, while plankton are distributed throughout the vertical water column. This limitation is further compounded in coastal areas – the most important areas for ecosystem services and thus primary productivity, and the habitat for many mixoplankton – due to the presence of c-DOM and particulate matter (Flynn & McGillicuddy Jr, 2018; Flynn et al., 2021).

An argument voiced for ignoring mixoplankton in the ecosystem and climate change models is a paucity of data. However, given the new lines of evidence for the global ubiquity of the different mixoplankton functional types (Leles et al., 2017, 2019) and their not in-substantial impact on primary production (Fig. 5.7; Ghyoot et al., 2017; Leles et al., 2021), this argument can no longer be considered to be justifiable. The data labelled as 'phytoplankton' or 'zooplankton', are not just representative data for those functional groups, but they are confused by the presence of data for mixoplankton.

5 Conclusions and Future Directions

There is as yet no definitive answer to the most profound question, '*what is the significance of mixoplanktonic activities?*'. This applies equally to the IO as to any other oceanic area. The available data and metrics are insufficient to determine the actual contribution of mixoplanktonic species. Indeed, there is very little quantitative knowledge that is holistic on these ubiquitous but often cryptic species. Thus, no synthesis or consensus exists for how to best estimate the contribution of mixoplankton to primary and secondary productivities, to biogeochemical cycling, to the microbial carbon pump, or how these important plankton may react to climate change events such as ocean acidification (Flynn & Mitra, 2023). A major problem in attaining holistic quantitative data is attributed to the methodologies used in routine oceanographic science; field and laboratory methodologies for protist physiology are designed for phototrophy or phagotrophy – for mixoplankton both are required simultaneously.

One important challenge is that neither traditional sampling protocols nor high-throughput sequencing captures the presence of mixoplankton and/or indicate their potential activity, while analyses of metabarcoding data must rely on previous experimental evidence to classify the operational taxonomic units as mixoplankton (Faure et al., 2019; Leles et al., 2019). Even though not a common practice, it is relatively simple to quantify the biomass of non-constitutive mixoplankton versus that of their heterotrophic counterparts. Mixoplanktonic ciliates (e.g. GNCM *Laboea strobila*, *Strombidium conicum* in IO), for example, are easily identifiable from the heterotrophic ones through the examination of samples under epifluorescence microscopy or with a FlowCAM (e.g. Stoecker et al., 2014; Haraguchi et al., 2018). The same does not apply to CM because these are not necessarily actively feeding at all times. Constitutive mixoplankton smaller than 20 μm are usually distinguished from their phytoplanktonic counterparts by experiments on measuring

rates of bacterivory. Such experiments are limited by a series of assumptions, including that community ingestion rates can be approximated from ingestion rates measured in a few individuals (Safi & Hall, 1999; Anderson et al., 2017). In reality, feeding varies over the diel cycle, and only a proportion of the total mixoplankton assemblage will be actively feeding at any time during an experiment (e.g. Avrahami & Frada, 2020; Koppelle et al., 2022; Mitra & Flynn, 2023). Paradoxically, most bacterivory studies do not provide information on protistan diversity (Unrein et al., 2014; Beisner et al., 2019). Without quantifying mixoplankton activity, we cannot have a clear understanding of the impact of mixoplankton on primary production, plankton trophodynamics, and global biogeochemical cycles.

Climate change is impacting the biodiversity and the food-web structure of the IO (Gomes et al., 2014). Given the socioeconomic importance of the IO, it is important that the mixoplankton paradigm is integrated into studies of ocean productivity from research through to monitoring and management (e.g., of aquaculture and fisheries). Various methods have been developed or repurposed to isolate and culture mixoplankton for laboratory and fieldwork to gain a quantitative understanding of their functionality (Hansen et al., 2021; Flynn et al., 2021; Mitra et al. 2021a, b, c). While suggestions have been made for the need to develop high-end research methodologies (e.g. single-cell transcriptomics, 'nanoSIMS') for in situ mixoplankton identification (Beisner et al., 2019 but cf. Strzepek et al., 2022), such methods are too expensive for regular monitoring of food-web dynamics not only in the IO but in coastal seas and oceans globally. There is thus a need to repurpose or develop more cost-effective in situ methods. For example, a recent study has demonstrated how the 'dilution technique', traditionally used to study zooplankton predator-prey dynamics, can be repurposed for quantification of mixoplankton predator-prey interactions (Duarte Ferreira et al., 2021).

Now science (belatedly) recognises the presence and importance of different mixoplankton. At the very least, all future plankton research and monitoring programmes need to caveat their work as being incomplete unless mixoplankton are explicitly studied. What is really needed, however, is to make mixoplankton studies as routine as studies of phytoplankton. To do otherwise not only ignores mixoplankton but it damages the value of 'phytoplankton' science by contaminating it with information on non-phytoplankton species.

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