Review

Towards a resolution of 'the paradox of the plankton': A brief overview of the proposed mechanisms

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ABSTRACT

In plankton ecology, it is a fundamental question as to how a large number of competing phytoplankton species coexist in marine ecosystems under a seemingly-limited variety of resources. This ever-green question was first proposed by Hutchinson [Hutchinson, G.E., 1961. The paradox of the plankton. Am. Nat. 95, 137–145] as 'the paradox of the plankton'. Starting from Hutchinson [Hutchinson, G.E., 1961. The paradox of the plankton. Am. Nat. 95, 137–145], over more than four decades several investigators have put forward varieties of mechanisms for the extreme diversity of phytoplankton species. In this article, within the boundary of our knowledge, we review the literature of the proposed solutions and give a brief overview of the mechanisms proposed so far. The proposed mechanisms that we discuss mainly include spatial and temporal heterogeneity in physical and biological environment, externally imposed or self-generated spatial segregation, horizontal mesos-cale turbulence of ocean characterized by coherent vortices, oscillation and chaos generated by several internal and external causes, stable coexistence and compensatory dynamics under fluctuating temperature in resource competition, and finally the role of toxin-produc-ing phytoplankton in maintaining the coexistence and biodiversity of the overall plankton population that we have proposed recently. We find that, although the different mechan-isms proposed so far is potentially applicable to specific ecosystems, a universally accepted theory for explaining plankton diversity in natural waters is still an unachieved goal.

Contents

1. Introduction

Phytoplankton are the basis of most aquatic food chains. Most of the species of phytoplankton are phototrophs. These phototrophic phytoplankton species "… reproduce and build up populations in inorganic media containing a source of CO_2, inorganic nitrogen, sulphur and phosphorous compounds and a considerable number of other elements (Na, K, Mg, Ca, Si, Fe, Mn, B, Cl, Cu, Zn, Mo, Co and V) most of which are required in small concentrations and not all of which are known to be required by all groups" (Hutchinson, 1961). However, in many natural waters, only nitrate, phosphate, light and carbon are limiting resources regulating phytoplankton growth. The principle of *competitive exclusion* (Hardin, 1960; Armstrong and McGehee, 1980) suggests that in homogeneous, well-mixed environments, species that compete for the same resource cannot coexist, and that in such competitions one species should win over the others so that in a final equilibrium, the cluster of the competing species should turn into a population consisting of a single species. Indeed, simple competition models and laboratory competition experiments also suggest that the number of species that can coexist in equilibrium cannot be greater than the number of limiting factors, unless additional mechanisms are involved (Tilman, 1977, 1981; Sommer, 1985, 1986; Rothhaupt, 1988, 1996).

However, in most aquatic ecosystems, hundreds of species of phytoplankton are found to coexist throughout the year. Even in summer, when the natural waters suffer from a striking nutrient deficiency and the resource competition becomes extremely severe, *in situ* measurements show prolonged coexistence of a large number of phytoplankton species (Hutchinson, 1961). In the famous paper '*The paradox of the plankton*', Hutchinson (1961) addressed the key question as to "… how it is possible for a number of species to coexist in a relatively isotropic or unstructured environment all competing for the same sorts of materials". Antithetical to the *competitive exclusion* principle, the coexistence of a large number of phytoplankton species on a seemingly limited variety of resources in aquatic ecosystems, that Hutchinson first pointed out 45 years ago, is one of the most famous classical problems in plankton ecology.

To explain the plankton paradox, several possible solutions have been proposed by numerous investigators over the last four decades. The aim of this article is to review briefly the extensive literature related to the paradox, and present an overview of the mechanisms that have been proposed. We restrict ourselves to the literature related to plankton ecology only, and do not cover the generalization of Hutchinson's paradox that applies to terrestrial ecosystems (see Wilson, 1990, for a review). We classify the existing mechanisms into different categories, and place in an appropriate category our

recent approach on this topic. Instead of emphasizing any particle class of mechanisms in detail, we try to present in brief the importance of all the mechanisms regulating the plankton dynamics and diversity in real world.

2. Classification of the proposed mechanisms

Because the principle of competitive exclusion says that the number of coexisting species in equilibrium cannot exceed the number of limiting factors, there may be, in principle, two possible solutions of the plankton paradox:

(i) due to some reasons, the dynamics of real-world plankton never approach to the equilibrium;

(ii) there exist some additional limiting factors that regulate the overall dynamics.

The mechanisms proposed so far for the coexistence of many phytoplankton species, either in non-equilibrium or in equilibrium conditions, are driven by the following two factors:

a. external factors;

b. self-organizing mechanisms.

In general, the proposition of non-equilibrium dynamics as the cause of coexistence is based on several external factors such as fluctuation in the environment, periodic forcing and spatial heterogeneity. Further, self-organized cycles, self-organized complex dynamics, spatio-temporal chaos have also been cited as the cause for non-equilibrium dynamics. On the other hand, other than the limiting resources in aquatic ecosystems, several behavioural effects such as life cycles, predator–prey interactions and chemical signaling processes have been reported as potential limiting factors. Various explanations based on above classification is represented in a chart (Fig. 1). In the following two sections, we discuss these mechanisms, their plausibility and applicability to various aquatic environments.

3. Out-of-equilibrium system (no eqilibrium)

3.1. *External forcing dynamics*

3.1.1. *Purely temporal effects*

Hutchinson (1961) emphasized that a probable reason for the paradoxical coexistence and high diversity of the phytoplankton species "… was explicable primarily by a permanent failure to achieve equilibrium as the relevant external factors

MECHANISMS OF PLANKTON PARADOX

A. Out-of-equilibrium system
B. Additional limiting factors

A1. External Forcing Dynamics
A2. Self Organized Dynamics

A1.1 Purely temporal effects
(i)Environmental fluctuations
(ii)Periodic/quasi-periodic forcing

A1.2 Spatiotemporal effects
(i) Spatial heterogeneity

A2.1 Purely temporal effects
(i)Self organized cycles
(ii) Self organized complex dynamics

A2.2 Spatiotemporal effects
(i)Spatio-temporal chaos
(ii)Self organized segregation

B.1 Behavioral effects
Life cycles

B.2 Interactions with others
Switching predators
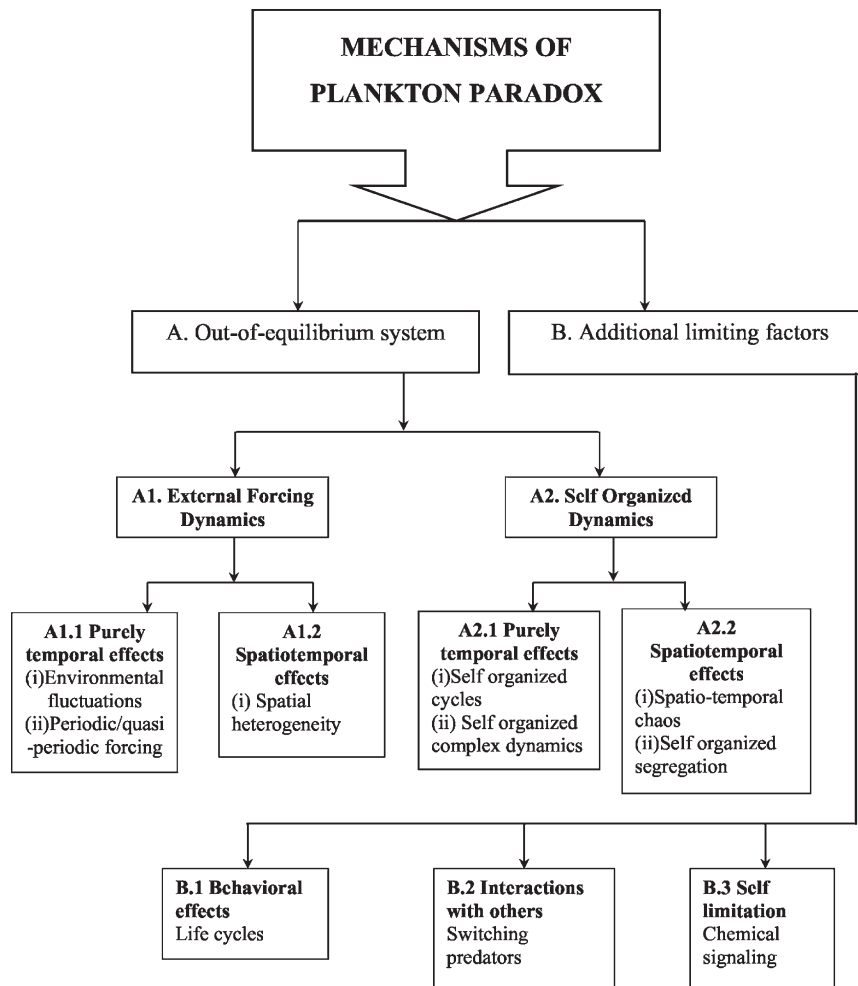
B.3 Self limitation
Chemical signaling

Fig. 1 – Various mechanisms for explaining the plankton paradox.

changed''. He proposed that for a class of organisms, whose reproduction rates are such that the time required (say, t_c) for a complete competitive exclusion under constant physical conditions is of the same order as the time taken (say, t_e) for a significant seasonal change in that environment, a permanent equilibrium is never possible. Because the two times t_c and t_e are of the same order to most organisms whose generation times are measured approximately in days or weeks, the proposition of non-equilibrium is potentially applicable to phytoplankton communities (Hutchinson, 1961). Based on these arguments, he suggested that the cause for the paradoxical coexistence of phytoplankton lies in the fact that the physical environment of natural waters, especially in marine waters, changes continuously due to factors such as weather. Authors such as Richerson et al. (1970), Levins (1979) and Powell and Richerson (1985) argued in a fashion similar to Hutchinson (1961) that continuous variation in environmental conditions, due to the seasonal cycle and factors such as weather, offer the most likely explanation.

Ebenhöh (1988) proposed a simple mathematical model for many competing phytoplankton with input of a single nutrient in pulses. This model showed that a variation of nutrient pulses that modulates the biological parameters such as growth and mortality, results in transitions of species dynamics from simple periodic to complex periodic and finally to chaotic behaviour. In this process, an unlimited number of competing phytoplankton can coexist on a single nutrient (Ebenhöh, 1988).

Moreover, some models taking into account the effects of seasonal forcing on plankton dynamics suggested that chaos can be expected for some parameter values that are sufficiently close to natural situations (Doveri et al., 1993; Scheffer et al., 1997; Heerkloss and Klinkenberg, 1998).

Temperature has a significant effect on the maximum growth rate of phytoplankton (Richardson et al., 2000), and is considered as a primary factor determining phytoplankton succession. Temperature influences the physiology of resource utilization (Rhee and Gotham, 1981; Tilman, 1982). Conducting a long-term laboratory experiment combined with simulation of a mathematical model of resource competition, Descamps-Julien and Gonzalez (2005) demonstrated that an addition of temperature fluctuations leads to the persistence of two phytoplankton species on one limiting resource. This study suggested that fluctuations in the temperature of an aquatic environment might ensure a stable coexistence of

species of phytoplankton (Descamps-Julien and Gonzalez, 2005). However, in open oceans, water temperatures generally do not fluctuate to a high extent, and consequently its influence on phytoplankton physiology might be rather restricted. Thus, stable coexistence through temperature fluctuations, although valid for laboratory set up, needs further investigations.

3.1.2. Spatio-temporal effects

Similar to the marine ecosystem, the diversity of lake phytoplankton is also very high. Sampling in Castle Lake, California (Richerson et al., 1970) showed a high degree of patchiness for many phytoplankton species, "... indicating that the rate of mixing is slow enough relative to the reproductive rate of the algae for many different niches to exist simultaneously". The observations from the real-life data suggested a 'contemporaneous disequilibrium model' to explain the diversity of the lake phytoplankton. This hypothesis stated that at any time, many patches of water might exist in which one species is at a competitive advantage relative to the others (Richerson et al., 1970). In general, the water masses in lakes are stable enough to permit a considerable degree of patchiness to occur in phytoplankton, "... but are obliterated frequently enough to prevent the exclusive occupation of each niche by a single species". The hypothesis of Richerson differs from that of Hutchinson by the fact that the former stressed the contemporaneous, rather than temporal, heterogeneity of the plankton habitat.

Bracco et al. (2000) proposed that coherent vortices in a turbulent environment might lead to strongly non-uniform spatial planktonic patterns that might in turn lead to prolonged survival of competing phytoplankton species by preventing the less-fit species from being driven out completely from the water during the nutrient-deficient months. This explanation captured the previous concern of Hutchinson (1961), that the plankton diversity remains unaffected even in summer, a period when the natural waters suffer from a severe nutrient deficiency. Because environmental conditions in real-world waters are highly fluctuating, resulting to continuous generation mesoscale turbulence, the species that is a stronger competitor than the others at any space and time, may not be the same one that occupies the same space at some other times as a strong competitor. In this way, due to the influence of mesoscale vortices, competing phytoplankton species may persist on a large time scale in non-equilibrium biomass (Bracco et al., 2000). However, the influences of vortices in marine environment differ significantly from that in small lakes and fresh water ponds, whereas the dazzling diversity of phytoplankton is observed in almost all aquatic ecosystems. Thus, the extensive role of the mesoscale vortices in various aquatic ecosystems such as lakes, ponds and coastal regions are still to be explored.

Authors such as Levin (1974), Atkinson and Shorrocks (1981) and Tilman (1994) proposed that incomplete mixing should promote coexistence of species. In aquatic environments, mixing processes largely determine the absorption of light by phytoplankton species, and thus incomplete vertical mixing through a light gradient affects the growth of the phytoplankton species (Huisman et al., 1999). In this process, vertical heterogeneity is generated by incomplete vertical mixing, which might in some cases promote the coexistence and diversity of phytoplankton species (Weissing and Huisman, 1994). However, the magnitude of this diversity is low compared with that of the real-world aquatic environments. In light-controlled environments, incomplete mixing cannot promote coexistence of hundreds of species. Consequently, phytoplankton blooms of eutrophic waters exhibit low species diversity, and different phytoplankton species dominate under different mixing regimes (Huisman et al., 1999). Reduced mixing process in marine environments can also have destabilizing effect in the oceanic deep-chlorophyll maxima, which in turn influences the diversity of phytoplankton species in a vertically-structured water column (Huisman et al., 2006).

3.2. Self-organized dynamics

3.2.1. Purely temporal effects

Analyses of competition models (Armstrong and McGehee, 1976, 1980) have shown that the presence of limit cycles allows the coexistence of two or more consumer species in systems with a single resource. More recently, simulating a resource competition model, Huisman and Weissing (1999) showed that competition for limiting resources leads to oscillations and chaotic dynamics if multiple species compete for at least three resources. The chaotic behaviour thus found was reported to be quite robust, because it was found over a relatively wide range of the model parameters and for different mathematical formulations of resource competition (Huisman et al., 2001; Huisman and Weissing, 2002; review by Scheffer et al., 2003). These theoretical studies showed that, in chaotic situation generated by resource competition itself many species might persist with fluctuating biomass. However, the theories that proposed species coexistence through chaos, showed sudden crashes in species biomass (Huisman and Weissing, 1999) and suggested a fundamental unpredictability of ranking the phytoplankton species according to their competitive ability.

3.2.2. Spatio-temporal effects

Some trophic interaction models of *Daphnia* grazing on competing cyanobacteria and green algae suggested that the chaotic nature of plankton dynamics might be expected under realistic conditions (Gragnani et al., 1999). Trophic interactions between phytoplankton–zooplankton systems, when nutrients and planktivorous fishes are treated as environmental control variables, generate spatial, temporal and spatio-temporal patterns (Malchow, 1993). Nutrient–phytoplankton–zooplankton systems also show a fascinating variety of spatio-temporal patterns such as rotating spiral pattern (Malchow, 2000). These studies suggested that competing species might coexist through trophic interactions under suitable conditions of pattern formation.

In an homogenous environment, incomplete mixing combined with differences in interspecific growth and dispersal rates may lead to spatial segregation of the competitive species. Spatial segregation of competing species reduces interspecies competition, which in turn favours the coexistence of the species (Ives and May, 1985; Britton, 1989; Hassel et al., 1994).

Petrovskii et al. (2003) have shown that persistence of a community of three competing species may occur as a result of self-organized spatial inhomogeneity, while the corresponding spatially homogeneous system goes extinct. This result suggests that self-generated inhomogeneity may also promote coexistence of real-world phytoplankton.

4. Additional limiting factors (density dependent effects)

4.1. Behavioural effects

Different physiological and life-cycle patterns are important factors determining the coexistence and biodiversity of plankton populations. Huisman et al. (2001) have shown that, when biological parameters are considered as a reflection of physiological and life-history traits, different dynamics of coexistence are obtainable. For random biological parameters, biodiversity obtained by simulations is generally low. However, simulations assuming plausible physiological trade-offs have revealed switches of dynamics between equilibrium and non-equilibrium, which lead to a high biodiversity (Huisman et al., 2001). Thus, the physiological and life-history patterns have significant influence on the likelihood of non-equilibrium dynamics and on the biodiversity of plankton communities. Further, adaptive changes in the physiological behaviour of prey due to the presence of a predator also promote coexistence in many cases (e.g., Bolker et al., 2003; Krivan and Schmitz, 2004).

4.2. Interactions with others

In predator–prey interactions, predation often promotes the coexistence and biodiversity of the species (Darwin, 1859; Paine, 1966, 1980; Lubchenco, 1978). Mainly two mechanisms have been proposed whereby predation promotes coexistence: (i) a predator switches to prefer the most common prey (Murdoch and Oaten, 1975; Roughgarden and Feldman, 1975) and (ii) a predator prefers the dominant competitor (Armstrong, 1979; Holt et al., 1994; Leibold, 1996). Generally, the coexistence of competitors for a common resource becomes feasible when a predator imposes a higher predation rate on the dominant competitor (Armstrong, 1979; Leibold, 1996). However, a number of studies have shown that predator switching due to several reasons promotes coexistence of prey species (e.g., Gleeson and Wilson, 1986; Fryxell and Lundberg, 1993, 1994; Krivan, 1996, 1997). More recently, Krivan (2003) has shown that adaptive switching of a shared predator increases the probability of species coexistence. There is another (i.e., a third) potential mechanism: predation can cause changes in the resource used by prey, which reduces the amount of competition between them (Pianka, 1972). But this mechanism does not always work (Abrams, 1977). Analysis of two non-competitive prey-species and a shared predator also showed that, when there are sustained cycles, the prey species exhibit apparent mutualism rather than competition (Abrams et al., 1998). However, further studies have showed that sometimes cycles make predator-mediated coexistence less likely (Abrams, 1999).

4.3. Self limitation by toxin-producing phytoplankton

Recently, using the marine plankton data collected from the north-west coast of the Bay of Bengal, we have proposed a new internal mechanism for the regulation of plankton dynamics in marine environments. In our study area, a significant number of species of phytoplankton have been found that have the ability to produce some toxic or inhibitory compounds (Hallegraeff, 1993; Steidinger et al., 1996; Chattopadhyay et al., 2002a,b; Sarkar and Chattopadhyay, 2003), which are well known to reduce the grazing pressure of zooplankton thereby influencing its the predatory activity (e.g., Kirk and Gilbert, 1992; Buskley and Stockwell, 1997; Nielsen et al., 1990; Ives, 1961; Kozlowsky-Suzuki et al., 2003).

The release of toxic chemicals by TPP plays two significant roles: the inhibition on consumption of toxic substances reduces the abundance of zooplankton, and the toxic materials released by TPP significantly compensate for the competitive disadvantages among phytoplankton species (Fig., also Roy et al., submitted for publication). The toxic chemicals released act as a potential allelopathic agent thereby affecting the growth and competitive ability of other non-toxic phytoplankton species. At species level interaction, the presence of toxic species significantly reduces the competition among other non-toxic species (Hulot and Huisman, 2004; Solé et al., 2005); primary empirical data of our study supports this claim (Roy and Chattopadhyay, 2007; Roy et al., 2006, submitted for publication). This 'additional' effect due to toxic phytoplankton, when put into a simple mathematical model, potentially overturns the possibility of competitive exclusion of those species that would otherwise not coexist (Roy and Chattopadhyay, 2007). The allelopathic effect of toxic chemicals here acts as a potential candidate for stabilizing the dynamics of phytoplankton species both in a deterministic and a stochastic environment (Roy and Chattopadhyay, 2007). In other words, in the absence of the predator zooplankton, toxin-allelopathy favours the weak competitors to survive. The effect of allelopathic interaction at species level thus influences positively the interaction at groups level thereby depicting an apparent passive mutualism between the TPP and NTP groups (Fig. 2, also Roy et al., submitted for publication).

When then effect of grazer zooplankton on the dynamics of phytoplankton is taken into account, toxic phytoplankton species plays another important role. Grazing on toxic species leads to a negative effect on zooplankton growth (e.g, Kozlowsky-Suzuki et al., 2003; Roy et al., 2006). When we consider the entire plankton species as a combination of three functional groups, namely, NTP, TPP and zooplankton, the effect of toxin inhibition on the grazer zooplankton gives a significant feedback to overall plankton dynamics, and its intensity regulates the dynamic stability. Our study (Roy et al., 2006) has suggested that the so-called 'planktonic non-equilibria' can be viewed as a consequence of the switching of dynamics through self-sustained oscillations of different amplitudes and fragile–stable state. The variation in the intensity of toxin inhibition acts as a driving force for switching of plankton dynamics through oscillation and stability, which might be a possible cause for the prolonged coexistence of the plankton species in fluctuating biomass. In
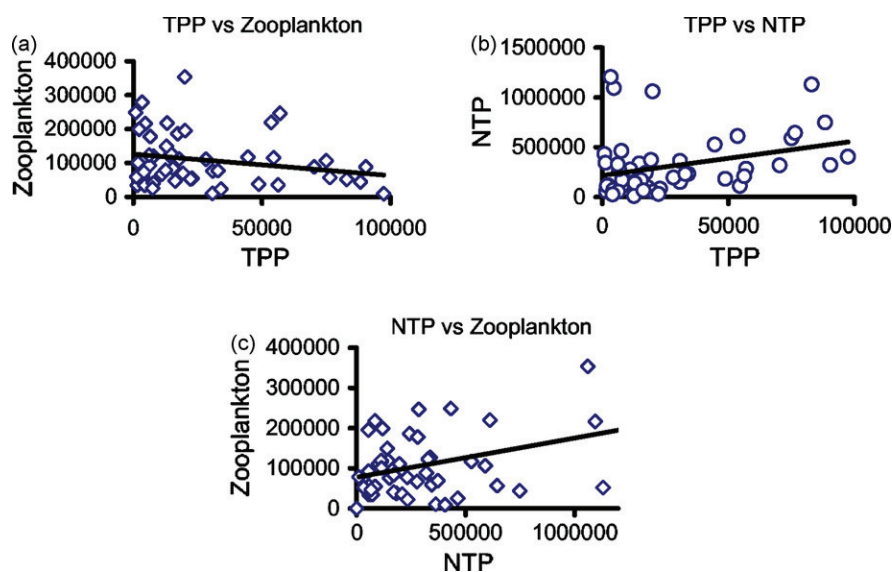
Fig. 2 – Scatter plot between (a) TPP-zooplankton-negative correlation between the abundances, representing an antagonistic relationship, (b) TPP-NTP-positive correlation, representing passive mutualism and (c) NTP-zooplankton-positive correlation, this represents that NTP is favourable for the growth of zooplankton.

sum, the toxic species present in aquatic environments by regulating the dynamics of other phytoplankton and grazer zooplankton species, helps in maintaining the diversity of many plankton species.

5. Discussions

The question as to how a large number of competing phytoplankton species coexist in marine ecosystem under a seemingly limited variety of resources (Hutchinson, 1961), is a fundamental and ever-green question in plankton ecology. A vast literature has followed over more than four decades after this paradox was first pointed out. These literatures propose varieties of mechanisms, out of which we have discussed the spatial and temporal heterogeneity in physical and biological environment (Levins, 1979; Powell and Richerson, 1985), externally imposed or self-generated spatial segregation (Ives and May, 1985; Britton, 1989; Hassel et al., 1994), incomplete vertical mixing (Huisman et al., 1999), horizontal mesoscale turbulence of ocean characterized by coherent vortices (Bracco et al., 2000), oscillation and chaos generated by resource competition among the phytoplankton species (Huisman and Weissing, 1999; review by Scheffer et al., 2003), stable coexistence and compensatory dynamics under fluctuating temperature in resource competition (Descamps-Julien and Gonzalez, 2005), and finally the role of toxin-producing phytoplankton in maintaining the coexistence and biodiversity of the overall plankton population. These theories propose different processes due to which a non-equilibrium condition is generated among many phytoplankton species, which allow them to coexist in fluctuating biomass. Non-equilibrium again may be due to external factors or internal organizations. Generation of spatial patchiness due to external forces, cycles due to variations in physical and biological parameters including temperature fluctuations,

externally driven chaotic dynamics, impulsive physical forcing are the potential external factors that lead to planktonic non-equilibrium (see Fig. 1). On the other hand, chaotic dynamics generated by resource competitions, switching of dynamics between stability and oscillations due to the presence of toxin-producing phytoplankton are the potential internal causes leading to planktonic non-equilibrium (see Fig. 1). Although the coexistence of species through non-equilibrium dynamics does not violate competitive exclusion principle, in natural waters there are some additional limiting factors that may potentially be supportive for equilibrium coexistence of many species. The presence of predators and toxin-producing phytoplankton may be included in this category. However, we would like to mention that, for going beyond the specificity of sampling region and investigating the generality the toxin hypothesis for various natural waters, further efforts are needed.

One might wonder that the diversity of the different mechanisms that have been proposed so far is, nevertheless, not less fascinating than the dazzling diversity of the phytoplankton species in real-world. However, nature is much more complex than models and laboratory environments. Although most mechanisms discussed in the literature allow the coexistence of a few extra competitors, unlike the real-world, very few theories would allow the coexistence of hundreds of species on a small number of resources (an exception is the model of Ebenhöh, 1988, discussed). Present-day theories could not overcome this serious limitation. Even if each of the proposed mechanisms potentially explain the paradox in a fairly convincing way, the question that still remains open is to ask, which one or which combination of the mechanisms hold in real-world plankton communities. Although the proposed mechanisms seems to offer an explanation of the diversity of certain systems, an investigation of a universally accepted theory, that alone could explain the species diversity of phyto-

plankton in laboratory waters, fresh waters and marine environments, is still an unachieved goal. In view of the ever-persisting unpredictability of plankton dynamics, there is still wide scope for extensive investigations of the diverse mechanisms for the real-world plankton, even 45 years after Hutchinson (1961).

Acknowledgements

REFERENCES

Abrams, P.A., 1977. Density independent mortality and interspecific competition: a test of Pianka's niche overlap hypothesis. Am. Nat. 111, 539–552.

Abrams, P.A., Holt, R.D., Roth, J.D., 1998. Apparent competition or apparent mutualism?: shared predation when populations cycle. Ecology 79, 201–211.

Abrams, P.A., 1999. Is predator mediated coexistence possible in unstable systems? Ecology 80, 608–621.

Armstrong, R.A., 1979. Prey species replacement along a gradient of nutrition enrichment: a graphical approach. Ecology 60, 76–84.

Armstrong, R.A., McGehee, R., 1980. Competitive exclusion. Am. Nat. 115, 151–170.

Atkinson, W.D., Shorrocks, B., 1981. Competition on a divided and ephemeral resource: a simulation model. J. Anim. Ecol. 50, 461–471.

Bolker, B., Holyoak, M., Krivan, V., Rowe, L., Schmitz, O., 2003. Connecting theoretical and empirical studies of trait-mediated interactions. Ecology 84, 1101–1114.

Bracco, A., Provenzale, A., Scheuring, I., 2000. Mesoscale vortices and the paradox of the plankton. Proc. R. Soc. Lond. B 267, 1795–1800.

Britton, N.F., 1989. Aggregation and the competitive exclusion principle. J. Theor. Biol. 136, 57–66.

Buskley, E.J., Stockwell, A.J., 1997. Effect of persistent ''brown tide'' on zooplankton population in the Laguna Madre of southern Texas. In: Smayda, T.J., Shimuzu, Y. (Eds.), Toxic Phytoplankton Bloom in the Sea. Elsevier, Amsterdam, Netherlands, pp. 659–666.

Chattopadhyay, J., Sarkar, R.R., Mandal, S., 2002a. Toxin-producing plankton may act as a biological control for planktonic blooms-field study and mathematical modelling. J. Theor. Biol. 215, 333–344.

Chattopadhyay, J., Sarkar, R.R., Elabdllaoui, A., 2002b. A delay differential equation model on harmful algal blooms in the presence of toxic substances. IMA J. Math. Appl. Med. Biol. 19, 137–161.

Darwin, C.R., 1859. On the Origin of Species by Natural Selection. John Murray, London, UK.

Descamps-Julien, B., Gonzalez, A., 2005. Stable coexistence in a fluctuating environment: an experimental demonstration. Ecology 86 (1), 2815–2824.

Doveri, F.M., Scheffer, S., Rinaldi, S., Muratori, S., Kuznetsov, Y.A., 1993. Seasonality and chaos in a plankton–fish model. Theor. Popul. Biol. 43, 159–183.

Ebenhöh, W., 1988. Coexistence of an unlimited number of algal species in a model system. Theor. Popul. Biol. 34, 130–144.

Fryxell, J.M., Lundberg, P., 1993. Optimal patch use and metapopulation dynamics. Evol. Ecol. 7, 379–393.

Fryxell, J.M., Lundberg, P., 1994. Diet choice and predator–prey dynamics. Evol. Ecol. 8, 407–421.

Gragnani, A., Scheffer, M., Rinaldi, S., 1999. Top–down control of cynobacteria: a theoretical analysis. Am. Nat. 153, 59–72.

Gleeson, S.R., Wilson, D.S., 1986. Equilibrium diet: optimal foraging and prey coexistence. Oikos 46, 139–144.

Hallegraeff, G.M., 1993. A review of harmful algae blooms and the apparent global increase. Phycologia 32, 79–99.

Hassel, M.P., Comins, H.N., May, R.M., 1994. Species coexistence and self-organizing spatial dynamics. Hydrobiologia 344, 87–102.

Hardin, G., 1960. The competitive exclusion principle. Science 131, 1292–1298.

Heerkloss, R., Klinkenberg, G., 1998. A long-term series of a planktonic foodweb: a case of chaotic dynamics. Verh. Int. Ver. Limnol. 26, 1952–1956.

Holt, R.D., Grover, J.P., Tilman, D., 1994. Simple rules for interspecific dominance in systems with exploitative and apparent competition. Am. Nat. 144, 741–771.

Huisman, J., Weissing, F.J., 1999. Biodiversity of plankton by species oscillation and chaos. Nature 402, 407–410.

Huisman, J., Van Oostveen, P., Weissing, F.J., 1999. Species dynamics in phytoplankton blooms: incomplete mixing and competition for light. Am. Nat. 154, 46–68.

Huisman, J., Johansson, A.M., Folmer, E.O., Weissing, F.J., 2001. Towards a solution of the plankton paradox: the importance of physiology and life history. Ecol. Lett. 4, 408–411.

Huisman, J., Weissing, F.J., 2002. Oscillation and chaos generated by competition for interactively essential resources. Ecol. Res. 17, 175–181.

Huisman, J., Pham Thi, N.N., Karl, D.M., Sommeijer, B., 2006. Reduced mixing generates oscillations and chaos in the oceanic deep chlorophyll maximum. Nature 439, 322–325.

Hulot, F.D., Huisman, J., 2004. Allelopathic interactions between phytoplankton species: the role of heterotrophic bacteria and mixing intensity. Limnol. Oceanogr. 49, 1424–1434.

Hutchinson, G.E., 1961. The paradox of the plankton. Am. Nat. 95, 137–145.

Ives, J.D., 1961. Possible mechanism underlying copepod grazing responses to levels of toxicity in red tide dinoflagellates. J. Exp. Mar. Biol. Ecol. 112, 131–145.

Ives, A.R., May, R.M., 1985. Competition within and between species in a patchy environment: relations between microscopic and macroscopic model. J. Theor. Biol. 115, 65–92.

Kirk, K., Gilbert, J., 1992. Variation in herbivore response to chemical defence: zooplankton foraging on toxic cynobacteria. Ecology 73, 2208.

Kozlowsky-Suzuki, B., et al., 2003. Feeding, reproduction and toxin accumulation by the copepods Acartia bifilosa and Eurytenora affinis in the presence of the toxic cynobacterium Nodularia Spumigena. Mar. Ecol. Prog. 249, 237–249.

Krivan, V., 1996. Optimal foraging and predator–prey dynamics. Theor. Popul. Biol. 49, 265–290.

Krivan, V., 1997. Dynamic ideal free distribution: effects of optimal patch choice on predator–prey dynamics. Am. Nat. 149, 164–178.

Krivan, V., 2003. Competitive coexistence caused by adaptive predators. Evol. Ecol. Res. 5, 1163–1182.

Krivan, V., Schmitz, O.J., 2004. Trait and density mediated indirect interactions in simple food webs. Oikos 107, 239–250.

Leibold, M.A., 1996. A graphical model of keystone predators in food webs: trophic regulation of abundance, incidence, and diversity patterns in communities. Am. Nat. 147, 784–812.

Levin, S.A., 1974. Dispersion and population interactions. Am. Nat. 108, 207–228.

Levins, R., 1979. Coexistence in a variable environment. Am. Nat. 114, 765–783.

Lubchenco, J., 1978. Plant species diversity in a marine intertidal community: importance of herbivore food preference and algal competitive abilities. Am. Nat. 114, 765–783.

Malchow, H., 1993. Spatio-temporal pattern formation in nonlinear non-equilibrium plankton dynamics. Proc. R. Soc. B 251 (1331), 103–109.

Malchow, H., 2000. Non-equilibrium spatio-temporal patterns in models of non-linear plankton Dynamics. Fresh. Biol. 45 (2), 239–251.

Murdoch, W.W., Oaten, A., 1975. Predation and population stability. Adv. Ecol. Res. 9, 1–131.

Roughgarden, J., Feldman, M., 1975. Species packing and predation pressure. Ecology 56, 489–492.

Nielsen, T.G., Kiorboe, T., Bjornsen, P.K., 1990. Effect of *Chrysochromulina polylepis* sub surface bloom on the plankton community. Mar. Ecol. Prog. Ser. 62, 21–35.

Petrovskii, S.V., Li, B.-L., Malchow, H., 2003. Quantification of the spatial aspect of chaotic dynamics in biological and chemical systems. Bull. Math. Biol. 65, 425–446.

Paine, R.T., 1966. Food web complexity and species diversity. Am. Nat. 100, 65–75.

Paine, R.T., 1980. Food webs: linkage, interaction strength, and community infrastructure. J. Anim. Ecol. 49, 667–685.

Pianka, E.R., 1972. r and K selection or b and d selection? Am. Nat. 106, 581–589.

Powell, T., Richerson, P.J., 1985. Temporal variation, spatial heterogeneity, and competition for resources in plankton system: a theoretical model. Am. Nat. 125, 431–464.

Rhee, G.Y., Gotham, I.J., 1981. The effect of environmental factors on phytoplankton growth-temperature and the interactions of temperature with nutrient limitation. Limnol. Oceanogr. 26, 635–648.

Richerson, P.J., Armstrong, R., Goldman, C.R., 1970. Contemporaneous disequilibrium: a new hypothesis to explain the paradox of plankton. Proc. Natl. Acad. Sci. U.S.A. 67, 1710–1714.

Richardson, T.L., Gibson, C.E., Heaney, S.I., 2000. Temperature, growth and seasonal succession of phytoplankton in Lake Baikal. Siberia. Fres. Biol. 44, 431–440.

Rothhaupt, K.O., 1988. Mechanistic resource competition theory applied to laboratory experiments with zooplankton. Nature 333, 660–662.

Rothhaupt, K.O., 1996. Laboratory experiments with a mixotrophic and phototrophic competitors. Ecology 77, 716–724.

Roy, S., Chattopadhyay, J., 2007. Toxin-alleopathy among phytoplankton species prevents competition exclusion. J. Biol. Syst. 15 (1), 1–21.

Roy, S., Alam, S., Chattopadhyay, J., 2006. Competing effects of toxin-producing phytoplankton on the overall plankton population in the Bay of Bengal. Bull. Math. Biol. 68 (8), 2303–2320.

Roy, S., Bhattacharya, S., Das, P., Chattopadhyay, J. Interaction among nontoxic phytoplankton, toxic phytoplankton and zooplankton: inferences from field observations. Revised version in J. Biol. Phys., submitted for publication.

Sarkar, R.R., Chattopadhyay, J., 2003. Occurence of planktonic blooms under environmental fluctuations and its possible control mechanism—mathematical models and experimental observations. J. Theor. Biol. 224, 501–516.

Scheffer, M., Rinaldi, S., Gragnani, Mur, L.R., van Nes, E.H., 1997. On the dominance of filamentous cyanobacteria in shallow, turbid lakes. Ecology 78, 272–282.

Scheffer, M., Rinaldi, S., Huisman, J., Weissing, F.J., 2003. Why phytoplankton communities have no equilibrium: solutions to the paradox. Hydrobiologia 491, 9–18.

Solé, J., García-Ladona, E., Ruardij, P., Estrada, M., 2005. Modelling allelopathy among marine algae. Ecol. Modell. 183, 373–384.

Sommer, U., 1985. Comparison between steady state and non-steady state competition: experiments with natural phytoplankton. Limnol. Oceanogr. 30, 335–346.

Sommer, U., 1986. Nitrate- and silicate-competition among Antarctic phytoplankton. Mar. Biol. 91, 345–351.

Steidinger, K.A., et al., 1996. *Pfiesteria Piscicida*, a new toxic dinoflagelate genus and species of the order Dinamoebales. J. Phycol. 32, 157–164.

Tilman, D., 1977. Resource competition between planktonic algae: an experimental and theoritical approach. Ecology 58, 338–348.

Tilman, D., 1981. Test of resource competition theory using four species ok Lake Michigan algae. Ecology 62, 802–815.

Tilman, D., 1982. Resource Competition and Community Structure. Princeton University Press, Princeton, NJ.

Tilman, D., 1994. Competition and biodiversity in spatially structured habitats. Ecology 75, 2–16.

Weissing, F., Huisman, J., 1994. Growth and competition in a light gradient. J. Theor. Biol. 168, 323–336.

Wilson, J.B., 1990. Mechanisms of species coexistence: twelve explanations for Hutchinson's 'paradox of the plankton': Evidence from New Zealand plant communities. N.J. Ecol. 13, 17–42.