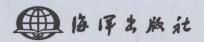
渔业环境评价与 生态修复

Fishery Environmental Evaluation and Ecological Rehabilitation

主 编: 刘 晴 徐 跑



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主编:刘 晴 徐 跑 副主编:杨 健 李应仁 李继龙

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目 次

.

Controlling harmful cyanobacterial blooms in a world experiencing anthropogenic and climat-
ically-induced change ····· Hans W. Paerl et al(1)
Contamination by legacy and emerging Pops in the Asia-Pacific region
Shinsuke Tanabe(13)
Chemical and biological environmental agents and quality relegation of fishery products
The ACIAR-BFAR Rinconada Lakes project: improving fish culture practices for sustaina-
bility and profitability Maria Lourdes Cuvin-Aralar et al(51)
渔业遥感应用研究 … 李继龙等(66)
西北印度洋大眼金枪鱼环境因子空间叠加渔场预报模型与模块开发 杨胜龙等(74)
Immobilized microorganism method purifying the harmful substances to fish
海洋、海岸工程对海洋渔业生物资源影响及其损害评价有关问题的分析与探讨
2004—2009 年渤海湾(天津区域)鱼虾贝产卵场水质环境综合评价 李宝华等(97)
大型底栖动物污染指数(MPI)评价海岛潮间带环境 章飞军等(106)
我国海洋滩涂贝类养殖产地环境监测和评价研究 黄瑛等(116)
海水滩涂贝类养殖环境质量的评价方法
洄游性鱼类耳石中锶、钙元素的环境"指纹"特征 姜涛等(134)
鱼类软组织中微量元素的生物存在和积累
基于 WebGIS 的大洋渔业信息服务系统 · · · · · · · · · · · · · · · · · · ·
杭州湾滩涂湿地鱼类种类组成和多样性的季节变化 张 衡(162)
黄河干流甘肃段渔业资源现状与保护研究 张彬等(173)
象山港养殖水域光谱特征测量与分析
2009 年莱州湾海域水质营养盐特征及年际变化规律研究 刘义豪等(192)
冬眠期氨暴露对中华鳖幼鳖部分组织学特性的影响 陈欣然等(201)
大肠杆菌和粪肠球菌感染对虾夷扇贝免疫酶活性的影响 李斌等(213)

不同饲料及投喂频率对星斑川鲽幼鱼生长和养殖水环境的影响 孙	丽慧等(223)
环境因子对链状亚历山大藻生长的影响 邵	盛男等(238)
气候变化与渔业:影响和对策 刘	洪波等(249)
大型湖泊对气候变化的响应 苏	彦平等(255)
不同品种的鱼苗对凤眼莲生长影响的试验	胡廷尖(264)
人工鱼礁礁体阻力系数的模型实验研究	刘健等(274)
渤海中国对虾、三疣梭子蟹、海蜇放流状况与效果 杨	文波等(283)
黄浦江上游渔业资源增殖放流效果评价	洪波等(299)
渤海莱洲湾梭子蟹放流海域生态特征研究 黄	经献等(307)
人工湿地处理海水养殖外排水影响因素及其效果分析 张	海耿等(319)
生物操控技术在景观水体生态修复中的应用	朱明等(331)
深水网箱内养殖水环境物理修复研究 张	小明等(337)
Prevention of luminous disease of prawns by Vibro harveyi using ecological technological	gy
CHEN Yue-zhor	ng et al(350)
Correlations between detachment of abalone larvae from plates and the change in co	-
structures of benthic diatoms HUANG Wan-hor	og et al (359)
	ig ci ai (337)
中国银鱼的研究现状及展望 周日	
中国银鱼的研究现状及展望 ······ 周日 月日 月日 月日 月日 月日 月日 日本	昕期等(376)
	昕期等(376) 丽萍等(387)
异育银鲫体外肝细胞损伤模型的建立及甘草多糖的保肝作用 曹	昕期等(376) 丽萍等(387) 明硕等(396)
异育银鲫体外肝细胞损伤模型的建立及甘草多糖的保肝作用 ······ 曹克 淡水蚌体内活性物质的研究进展 ····· 马克	昕期等(376) 丽萍等(387) 明硕等(396)
异育银鲫体外肝细胞损伤模型的建立及甘草多糖的保肝作用 ······ 曹克 淡水蚌体内活性物质的研究进展 ····· 马克 天然海域渔业生物种质资源经济价值评估 ····· 沈	昕期等(376) 丽萍等(387) 明硕等(396) 公铭等(405)
异育银鲫体外肝细胞损伤模型的建立及甘草多糖的保肝作用 ··········· 曹克 淡水蚌体内活性物质的研究进展 ····································	昕期等(376) 丽萍等(387) 明硕等(396) 公铭等(405) 晓莉等(410)
异育银鲫体外肝细胞损伤模型的建立及甘草多糖的保肝作用	斯期等(376) 丽萍等(387) 明硕等(396) 公铭等(405) 烧莉等(410) 文斌等(419)
异育银鲫体外肝细胞损伤模型的建立及甘草多糖的保肝作用	斯期等(376) 丽萍等(387) 明硕等(396) 公铭等(405) 烧莉等(410) 文斌等(419) 曾首英(431)
异育银鲫体外肝细胞损伤模型的建立及甘草多糖的保肝作用	斯期等(376) 丽萍等(387) 明硕等(396) 公铭等(405) 烧莉等(410) 文斌等(419) 曾首等(442)
异育银鲫体外肝细胞损伤模型的建立及甘草多糖的保肝作用	斯期等(376) 丽萍等(387) 明硕等(396) 公铭等(405) 烧莉等(410) 文献等(419) 曾首等(442) 赵颖等(453)

Content

Controlling harmful cyanobacterial blooms in a world experiencing anthropogenic and climatic-
ally-induced change Hans W. Paerl et al. (1)
Contamination by legacy and emerging Pops in the Asia-Pacific region
Chemical and biological environmental agents and quality relegation of fishery products
The ACIAR-BFAR Rinconada Lakes project; improving fish culture practices for sustaina-
bility and profitability
Applications of remote sensing in fishery LI Ji-long et al(66)
Predictive model of fishing ground for bigeye tuna and modulc development in the Northwest
India Ocean
Immobilized microorganism method purifying the harmful substances to fish
ZHAN Pei-rong et al(86)
Analyse the effect and damage assessment of marine coastal engineering on fishery Res-
ources ····· MA Shao-sai(92)
The comprehensive assessment on the water quality status at the fish, shrimp and shellfish
spawning ground in area of Tianjin in the Bohai Bay from 2004 to 2009
LI Bao-hua et al. (97)
Evaluation of the inter-tidal environment of island by macrozoobenthos pollution index(MPI)
ZHANG Fei-jun et al(106)
Monitory and assessment of the culture environment quality of the marine intertidal shellfish
HUANG Ying et al(116)
Evaluating the security of environment in shellfish aquaculture in China
Characteristics of Sr and Ca environmental fingerprint in otolith of diadromous fish
Bioavailability and bioaccumulation of trace element in the soft tissues of fish

WANG Dan-ting et al(144)
Information service system of ocean fisheries based on WebGIS ZHANG Sheng-mao(155)
Seasonal changes of species composition and diversity of fishes in the mudflat wetlands of
the Hangzhou Bay ZHANG Heng(162)
Investigation and research on fishery resources in the upper reaches of the Yellow River
main stream in Gansu province ZHANG Bing et al(173)
Spectrum measurement and analysis of aquaculture area in Xiangshan Bay
ZHOU Wei-feng et al(185)
Distribution features and inter-annual variation of nutrients in Laizhou Bay in 2009
LIU Yi-hao et al(192)
Effect of chronic ammonia exposure on partial physiological and histological characteritic of
juvenile soft-shelled turtle, Pelodiscus sinensis during hiberination
Effect of uptake of Escherichia coli and Enterococcus faecalis on the activities of immunity-
related enzymes of scallop ····· LI Bin et al(213)
Effects of diets with different protein levels, phosphorus levels and feeding frequency on
growth performance and water environment of juvenile starry flounder (Platichthys stellatus)
SUN Li-hui et al(223)
Effects of some ecological factors on the growth of dinoflagellate Alexandrium catenella
Global climate change and fishery: impacts and strategies LIU Hong-bo et al (249)
Response of the large lakes to climate change
Impact of effect of different kinds of fly fish on the growth of water hyacinth (Eichharnia
crassipes) HU Ting-jian et al(264)
Model experiments of the hydraulic resistance coefficient of artificial reefs
LIU Jian et al(274)
Status and effect of releasing and stock enhancement of Penaeus chinensis, Portunus tritub-
erculatus and Rhopilema esculentum in Bohai Sea ······ YANG Wenbo et al (283)
Assessment on releasing and enhancement of fisheries resources in upper reaches of Huangpu
River HONG Bo et al(299)
Research on ecological characteristics of Bohai Lavzhou Bay where Portunus trituberculatus

3

discharged HUANG Jing-xian et al (307
Analysis of the influence factors and effect for constructed wetland treat mariculture effluent
ZHANG Hai-geng(319
Application of bio-manipulation technology on ecological restoration of scenery waters
ZHU Ming et al(331
Physical rehabilitation of the water environment within cage culture
Prevention of luminous disease of prawns by Vibrio harveyi using ecological technology
Correlations between detachment of abalone larvae from plates and the change in community
structures of benthic diatoms HUANG Wan-hong et al (359)
Icefish research in China: current state and prospects ZHOU Xin-qi et al (376)
Establishment of t-BHP injured models of primary hepatocytes in Carassius auratus gibelio
var. Eérqisi and a study on the protective effects of GPS on liver ····· CAO Li-ping et al (387)
Advances of active substances in freshwater mussel MA Ming-shuo et al(396)
Economic value assessment of oceanic natural fishery organisms SHEN Gong-ming et al (405)
Sequence analysis of mitochondrial putative control region gene fragments of Pelodiscus sin-
ensis in four regions in China LI Xiao-li et al(410)
Biology and population discrimination of Chinese mitten crab(Eriocheir sinensis): a review
······ YANG Wen-bing et al(419)
Morphological variations among six population of Procambarus clarkia
ZENG Shou-ying(431)
Measurements of the fish target strength with single and dual-chambered swimbladders by
two acoustic models LIN Dan-qing et al(442)
Method comparison for genetic DNA extraction from Anodonta woodiana elloptica
ZHAO Ying et al(453)
Molecular cloning of propiomelanocortin cDNA and multi-tissue mRNA expression in
Parasilurus asotus DING Wei-dong et al (457)
Stability test of three kinds of prohibited drug solutions MU Ying-chun et al (475)

Controlling harmful cyanobacterial blooms in a world experiencing anthropogenic and climatically-induced change

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Abstract: The proliferation of bloom-forming, harmful (toxic, food web altering) cyanobacteria (CyanoHABs) is attributable to human nutrient over-enrichment. Phosphorus (P) input reductions have been prescribed to control CyanoHABs, because P limitation is widespread and some CyanoHABs can fix atmospheric nitrogen (N₂), thereby satisfying their nitrogen (N) requirements. However, eutrophying systems are increasingly plagued with non-N₂ fixing CyanoHABs that are N and P co-limited or even N limited. Many of these systems are experiencing accelerating N loads, often exceeding rates of P loading. Therefore N and P input constraints are likely needed for long-term CyanoHAB control in such systems. Climatic changes, specifically warming, increased vertical stratification, salinization, and intensification of storms and droughts, play additional, interactive roles in modulating CyanoHAB frequency, intensity, geographic distribution and duration. This has complicated management strategies for control because CyanoHABs are capable of taking advantage of unprecedented levels of nutrient enrichment and regional and global climatic change, including warming and altered hydrology. Future climatic change scenarios, especially temperature increases and their physical-chemical-biological effects, will likely promote CyanoHABs. Management strategies should therefore incorporate climate change scenarios in the development of predictive bloom thresholds based on the interactions of nutrient enrichment, altered thermal and hydrologic properties of aquatic ecosystems.

Key words; cyanobacterial bloom; nutrientenrichment; climatic change; control

Introduction

One of the most troublesome symptoms of nutrient-over-enrichment is the proliferation of toxic, food-web altering and hypoxia-generating harmful cyanobacterial blooms, or CyanoHABs (Chorus and Bartram, 1999; Huisman et al., 2005; Paerl and Fulton, 2006) (Fig. 1). CyanoHABs are expanding geographically and now threaten the ecological integrity and sustainability

of some of the world's largest and most resourceful water bodies, including Lakes Victoria, Africa; Erie, US-Canada; Okeechobee, Florida; Taihu, China; Kasimagaura, Japan; the Baltic Sea in Northern Europe; and the Caspian Sea in west Asia (Larsson et al., 1985; Havens et al., 2001; Elmgren and Larsson, 2001; Qin et al., 2009). Identifying environmental factors driving the rapid rise in CyanoHABs is paramount to developing management strategies aimed at ensuring sustainability of a significant fraction of the world's water resources.

When devising long-term, effective CyanoHAB management strategies, ecologists and managers face two set of "moving targets"; (1) nutrient over-enrichment in human-dominated watersheds (Vitousek et al., 1997; Conley et al., 2009), and (2) changing climatic conditions, including global warming, altered rainfall patterns and droughts, additionally modulate CyanoHABs (Paerl and Huisman, 2008). Understanding and (when possible) manipulating the interactive, and in many instances synergistic, impacts of anthropogenic and climatic drivers of CyanoHABs is a major challenge for ensuring protection and sustainability of affected waters.

Here, we synthesize established and emerging information on environmental factors influencing CyanoHAB growth and bloom potentials, in order to provide an integrative and effective approach to their management in a world experiencing contemporaneous anthropogenic and climatically-induced environmental change.

The Players

Cyanobacteria were the first oxygenic phototrophs on Earth. They are responsible for the formation of an oxygen-rich biosphere in which they have thrived and profoundly affected biogeochemical cycling (Schopf and Walter, 1982). Their long evolutionary history has provided them with many eco-physiological adaptations and mechanism enabling them to take advantage of environmental changes and extremes. They possess high affinity uptake and intracellular storage capabilities for N and P (Syrett 1980; Healy 1982; Padisak 1997; Flores and Herrero, 2005); ideal for exploiting periodic enrichment of these potentially-limiting nutrients. Some genera can convert "inert" atmospheric nitrogen (N_2) into biologically-usable ammonia, via nitrogen fixation (Fogg, 1969); ensuring access to biologically-available N. In addition, CyanoHABs produce secondary metabolites potentially toxic to higher-ranked organisms, including consumers of algae (zooplankton, fish), and mammals (including man) that use affected waters as a habitat, for drinking and recreational purposes (Carmichael, 1997; Chorus and Bertram, 1999).

Nutrient controls: Both N and P are important

CyanoHABs are stimulated by excessive anthropogenic nutrient loading (Fogg 1969; Reynolds, 1987; Paerl, 1988). In freshwater ecosystems, phosphorus (P) availability has traditionally been viewed as a key factor limiting CyanoHAB proliferation (Likens, 1972; Schindler et al.,

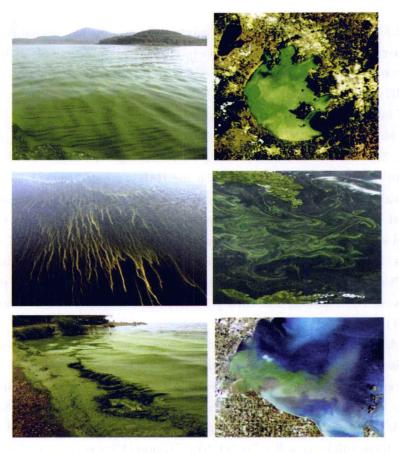


Fig. 1 Examples of large water bodies that have experienced increases in frequencies, magnitudes, and duration of CyanoHABs. Shown (on the left) are photographs of the blooms and (on the right) remote sensing images of each system. Top: Lake Taihu, China (photograph by H. Paerl), and MODIS remote sensing image of the lake and nearby cities (May, 2007) (Courtesy NASA). Middle: Baltic Sea-Gulf of Finland (courtesy of Finnish Border Guard and Institute of Marine Research, Helsinki, Finland), and SeaWiFS image of the same region (June 2005) (Courtesy NASA). Bottom: Lake Erie, southern shore (photograph courtesy NOAA), and LANDSAT image of a bloom in the Western region of the lake, near Maumee Bay during summer 2003 (Courtesy LANDSAT).

2008). Accordingly, controlling P inputs has been the "holy grail" for resource managers. Indeed, controlling P availability has reduced CyanoHAB bloom potentials in numerous freshwater lakes (Schindler, 1977). The emphasis on P reductions for CyanoHAB control is based on knowledge that some CyanoHAB genera conduct N₂ fixation, which can help satisfy cellular N-requirements under P-limited conditions (Paerl and Fulton, 2006). However, at the ecosystem-level, only a fraction, usually far less than 50% of primary and secondary production demands are met by N₂ fixation, even when P supplies are sufficient (Howarth et al., 1988; Paerl, 1990; Lewis and Wurtsbaugh, 2008). This indicates that N₂ fixation is controlled by factors in addition to P availa-

bility.

Nutrient loading dynamics have changed substantially over the past several decades. While P reductions have been actively pursued, human population growth in watersheds has been paralleled by increased N loading, often at higher rates than P (Vitousek et al., 1997; Galloway and Cowling, 2002; Rabalais, 2002). Excessive N loads are now as large a concern as P loads as stimulants of freshwater, estuarine and marine eutrophication and harmful algal (including cyanobacterial) blooms (Nixon 1995; Havens et al., 2001; Boesch et al., 2001; Conley et al., 2009; Paerl, 2009; Hai et al., 2010). In the Baltic Sea region, Elmgren and Larsson (2001) concluded that effective control of eutrophication and HAB outbreaks required considering total amounts and ratios of N and P discharged to nutrient-sensitive river-fjord-sea continuum. Similarly, Paerl et al. (2004) showed that single nutrient input reductions, including a P-detergent ban and improved wastewater treatment for P during the 1980's in North Carolina's (USA) Neuse River System, helped solve one problem (arrest freshwater blooms), but exacerbated blooms in downstream N-sensitive estuarine waters. In both cases, parallel N and P input reductions were required to stem eutrophication and HAB potentials along the freshwater to marine continuum (Paerl, 2009).

In Florida's (USA) freshwater lakes, which supply drinking and irrigation water, excessive N loading, from expanding wastewater and agricultural discharges, was identified (in addition to P) as a key culprit in eutrophication and CyanoHAB expansion (Kratzer and Brezonik, 1981; Havens et al. 2001). In some cases (e. g. Lake Okeechobee), dominance by N_2 fixing Cyano-HABs (which were largely controlled by P input reductions) is now shared with non N_2 fixing genera (e. g. *Microcystis*), as well as "switch hitter" CyanoHAB genera (e. g. *Cylindrospermopsis*, Lyngbya) that effectively compete for reactive N when it is available and then fix N_2 when N is depleted. In these cases, both N and P reductions are needed to control CyanoHABs (Havens et al., 2001; Piehler et al., 2009).

In Lake Erie (USA-Canada), the current CyanoHAB problem is a resurgence of non-N₂ fixing *Microcystis* populations. Since 1995, blooms of *Microcystis* have annually reoccurred throughout Lake Erie (Fig. 1), a lake thought "recovered" from eutrophication due to well-managed P (but not N)-abatement programs. By what means and mechanisms have CyanoHABs re-emerged, despite concerted efforts to control P? Large lakes like Okeechobee, Taihu, Kasumigaura, Japan, deeper systems like Lake Erie and very deep systems like Lake Tahoe, CA – NV, USA tend to be co-limited by N and P (Havens et al., 2001, North et al., 2007; Elser et al., 2007; Hai et al., 2010); largely because previously-loaded P and N are effectively retained and recycled. While N can be "lost" via denitrification, this process does not appear to keep up with "new" N inputs, especially in systems heavily impacted by N over-enrichment (Seitzinger 1988; Havens et al., 2001). Overall, N and P co-limitation appears most common in eutrophic systems (Elser et al., 2007; Sterner, 2008), which are highly susceptible to CyanoHAB outbreaks (Huisman et al., 2005).

The integral role of climate change

In addition to evolving nutrient over-enrichment issues, other environmental changes play integral roles in the recent upsurge of CyanoHABs. Climate change, specifically global warming, favors CyanoHABs in several ways. As a group, cyanobacteria exhibit optimal growth rates at relatively high temperatures, usually in excess of 25°C (Robarts and Zohary, 1987; Paerl and Huisman, 2008). At these elevated temperatures, CyanoHABs compete most effectively with eukaryotic algae (Fig. 2).

Warming of surface waters also intensifies vertical density stratification and thus suppresses vertical mixing. Furthermore, warming lengthens the period of stratification. Some CyanoHABs form gas vesicles, which provide buoyancy (Reynolds,1987). Under strong and persistent vertically stratified conditions, positively buoyant cyanobacteria can form dense surface blooms which shade deeper non-buoyant eukaryotic phytoplankton, enhancing the CyanoHABs' competitive advantage (Huisman et al., 2004; Jöhnk et al., 2008) (Fig. 3). Increased water temperatures also decrease the viscosity of water and therefore the water's resistance to vertical migration of phytoplankton; facilitating upward (optimizing photosynthetic production) and downward (optimizing nutrient acquisition) migration by CyanoHABs. This further enhances their competitive advantages in stratified waters (Reynolds, 1987).

Dense surface blooms of cyanobacteria may locally increase water temperatures, through the intense absorption of light by their photosynthetic and photoprotective pigments. In the Baltic Sea and in Lake IJsselmeer (Netherlands), surface blooms tend to be warmer than ambient waters (Kahru et al., 1993; Ibelings et al., 2003). This represents a potential positive feedback mechanism, whereby CyanoHABs favor their own competitive dominance over eukaryotic phytoplankton (Hense et al., 2007).

A key driver of global warming is the rising level of the atmospheric greenhouse gases, most notably carbon dioxide (CO_2). In nutrient-enriched waters, algal blooms exhibit a strong demand for CO_2 to support photosynthetic growth; to the extent that the rate of CO_2 supply can at times control the rate of algal biomass production (Shapiro, 1990). High rates of photosynthesis and hence high demand for CO_2 will also increase the pH of affected waters, thereby restricting availability of free CO_2 (Ibelings and Maberly, 1998). Under these conditions, buoyant CyanoHABs have a distinct advantage over sub-surface phytoplankton populations, since surface – dwelling taxa can directly intercept CO_2 from the atmosphere, thus minimizing dissolved inorganic carbon (DIC) limitation of photosynthetic growth (Paerl and Ustach, 1982), while subsurface eukaryotic algal populations would be highly dependent on relatively slow diffusion to supply new CO_2 , putting them at a disadvantage.

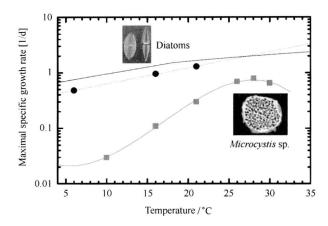


Fig. 2 Temperature dependence of the specific growth rates, a eukaryote (diatom) (Butterwick et al. 2005), and a bloom-forming cyanobacterium *Microcystis* sp. The data are from controlled laboratory experiments using light-saturated and nutrient-saturated conditions.

Summer droughts appear to be increasing in intensity and duration, possibly another symptom of global warming (IPCC, 2007). This, combined with increased use of freshwater for irrigation, has led to rising salinities worldwide. Increased salination is a serious threat to freshwater supplies; it also has major impacts on freshwater plankton composition and possibly CyanoHAB potentials. One impact of salination is increased vertical density stratification, which would benefit buoyant, scum-forming CyanoHABs (Fig. 3). In addition, some species of common CyanoHAB genera such as Anabaena, Microcystis and Nodularia are more salt tolerant than their eukaryotic freshwater algal counterparts (Horne and Galat, 1985; Moisander et al., 2002). Strains of Microcystis aeruginosa can tolerate salinities ranging up to 10 g · L -1, which is 30% of the salinity of seawater (Tonk et al., 2006). Likewise, Anabaena aphanizominoides can withstand salt levels up to 15 g · L -1, while Anabaenopsis spp. and toxic Nodularia spumigena tolerate salinities ranging from 0 g · L⁻¹ to more than 20 g · L⁻¹ (Horne and Galat, 1985; Moisander et al., 2002; Mazur-Marzec et al., 2005). The high salt tolerance of these CyanoHABs allows for expanding blooms in brackish waters, including the Baltic Sea, the Caspian Sea, Patos Lagoon Estuary, Brazil, the Swan River Estuary, Australia, San Francisco Bay Delta, California and Lake Ponchartrain, Louisiana.

Global warming and associated changes in climatic oscillations affect patterns, intensities and duration of precipitation and droughts which may promote CyanoHAB dominance. For example, larger and more intense precipitation events will increase enrichment of water bodies with land – derived nutrients through enhanced erosion, surface runoff and groundwater discharge. Freshwater discharge would also increase, which in the short-term may prevent blooms by promoting flushing. However, as the discharge subsides and water residence time increases, its nutrient load will be captured and cycled by receiving water bodies, promoting bloom potentials. This scenario can be

observed in geographically-distinct places including the Swan River, Australia, Hartbeespoort-dam, South Africa, the Neuse River Estuary, NC, USA, and the Potomac Estuary, MD, USA. In addition, attempts to control fluctuations in the discharge of rivers and lakes by dams and sluices increases residence time, aggravating CyanoHAB problems (Burch et al., 1994).

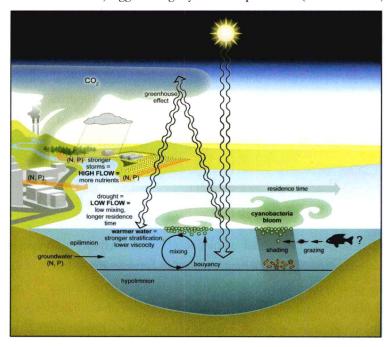


Fig. 3 Conceptual figure, illustrating the environmental processes that control cyanobacterial blooms, including impacts of climate change. Adapted from Paerl and Huisman (2009).

Overall, it appears that increases in hydrologic variability and "extremeness" such as protracted droughts benefit CyanoHABs. If conditions get so extreme as to dry up lakes and reservoirs, most CyanoHAB species can survive such extremeness for long periods (up to many years) as dormant cysts in sediments, soils, or desiccated mats (Potts, 1994).

Some toxin-producing CyanoHABs appear to be particularly successful at exploiting climatic change. The planktonic/benthic filamentous N_2 -fixing genus Lyngbya and the planktonic N_2 fixer Cylindrospermopsis raciborskii have shown remarkable expansion of their geographical ranges, possibly linked to warming and associated hydrodynamic changes. Cylindrospermopsis was originally described as a tropical and subtropical species. However, C raciborskii appeared in southern Europe during the 1930s, and has shown a progressive increase in colonization from Greece and Hungary up to the Netherlands and northern Germany near the end of the 20th century (Padisák, 1997; Wiedner et al., 2007). C raciborskii was first identified in United States Midwest lakes in the 1950s. It probably existed in Florida inland waters for many years, but it wasn't until the 1980s that it began to aggressively proliferate in lake and river systems throughout central Florida (Chapman and Schelske, 1997). More recently, this CyanoHAB has spread throughout US