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国家重点研发计划课题 中期执行情况报告

项目名称：海洋生态系统储碳过程的多尺度调控
及其对全球变化的响应

项目牵头单位：厦门大学

课题名称：海洋酸化对固碳、储碳过程的影响及其机制

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编报要求

一、内容说明

课题中期执行情况报告着重围绕课题任务书的内容，报告课题中期重要进展情况，具体包括课题的总体目标及考核指标实现程度，人员、资金等支撑条件落实情况，课题经费使用情况等，并报告中期执行过程中的重大事项及突出进展。

二、格式要求

文字简练；报告的密级一般与任务书规定的密级相同；报告文本统一用 A4 幅面纸，文字内容一律通过“国家科技管理信息系统公共服务平台”在线填报；报告文本第一次出现外文名称时要写清全称和缩写，再出现时可以使用缩写。

三、编制程序及时间要求

项目中期总结前，由课题承担单位组织课题参与单位编制课题中期执行情况报告，经课题负责人及课题牵头单位审核后，提交项目牵头单位。

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一、总体进展情况

1. 课题中期总体进展情况

对照课题任务书的计划目标和各项主要指标要求，简要阐明课题中期进展情况，评述课题中期任务的实施进展状态。

课题自 2016 年 7 月启动实施以来，总体进展良好，按照课题计划顺利进行，完成了中期计划目标和各项主要指标，迄今已发表 SCI 论文 14 篇（其中课题号为第一标注的 SCI 论文 11 篇，第二标注 3 篇）。

1.1 研究进展

1) 系统开展了海洋酸化对海洋优势固氮蓝藻束毛藻 (*Trichodesmium*) 影响的研究，结合室内受控培养和南海北部的现场培养实验，采用生理、生化和蛋白质组学相结合研究手段，分析了海水 pCO₂ 上升和 pH 下降对束毛藻生长、固碳、固氮、碳浓缩机制等的影响及其机理。

2) 以代表性硅藻威氏海链藻 (*Thalassiosira weissflogii*)、假微海链藻 (*Thalassiosira pseudonana*)、三角褐指藻 (*Phaeodactylum tricornerutum*) 为研究对象，通过室内受控培养实验，比较研究了氮营养盐充分和缺乏条件下三种藻类的光能捕获、固碳、光呼吸、氮同化等关键代谢过程及其能量收支对海洋酸化响应的差异。

3) 以束毛藻 (*Trichodesmium*) 为研究对象，采用生理、生化结合转录组学的实验手段，系统研究了磷营养盐限制条件下海洋酸化对束毛藻生长、固氮以及磷的吸收、利用和代谢的影响。

4) 以中尺度围格 (mesocosms) 为实验平台，开展了海洋酸化对近海富营养环境下浮游植物群落及其附着态细菌的影响的研究，探讨了藻华过程中植物和异养细菌代谢速率如何变化，进而评估其对近岸生态系统的影响。

5) 开展了对珠江口及其附近南海北部海域的溶解和颗粒态有机碳中的不饱和脂肪醛类 (PUA) 的调查，研究了 PUA 的空间分布、物理和生物控制因素以及其在海洋生物地球化学循环中的应用。

6) 通过对珠江口及南海北部区域溶解和颗粒氨基酸的浓度、组成及其手性化合物的分析，研究了从河流到海洋混合过程中溶解有机物 (DOM) 的来源、原位生产和微生物降解活性的转化过程。

7) 开展了珠江口不同形态磷含量的时空变化调查,研究了珠江径流变化对珠江口水体中不同形态磷动态变化的调节机制。

8) 比较研究了夏季南海近岸区、陆架区及海盆区的浮游植物分级生长与摄食死亡动力学。

9) 开展了南海西沙站的初级生产力和输出生产力的物理-生物地球化学耦合模拟研究。

10) 开展了海洋酸化在低磷条件下对硅藻储碳的影响研究,通过室内培养实验测定浮游植物生长对海洋酸化的响应,探讨了海洋酸化及河口低磷环境对浮游植生长及储碳的影响机制。

11) 通过对台湾海峡近岸上升流区域的观测,发现了营养盐相对丰富的上升流区域也存在显著的固氮作用。开展了近岸上升流区域固氮生物群落结构的研究,探讨了近岸上升流营养盐结构对固氮生物生长、固氮的影响机制。

1.2 航次进展

1) 搭载“2017年基金委南海东北部-吕宋海峡综合航次”,课题成员李骁麟任航次首席科学家:

- 在23个大面站位开展了真光层以浅的浮游植物群落结构、固碳速率和固氮速率的调查,采集了约420个叶绿素、POC、PON、DNA、RNA等样品;在5个重点站位开展了海洋酸化对浮游植物群落结构及其固氮和固碳能力影响的甲板受控培养实验,并在其中一个重点站位开展了海洋酸化对浮游植物释放溶解有机碳(DOC)、生物可降解溶解有机碳(BDOC)、氨基酸影响的研究。现已完成了大面站位及重点站位酸化培养实验的叶绿素分析,其余样品和参数的分析工作正在进行中。

- 开展了南海和黑潮溶解有机碳的交换和转化研究,采集南海及吕宋海峡附近的40个站位全水柱共约600个DOC、氨基酸,尿素和BDOC样品,并与6个重点站位采集固相萃取DOM(SPE-DOM)样品用于质谱解析。对黑潮表层和南海表层样品进行微生物降解实验。现已完成重点站位的DOC分析以及所有SPE-DOM的回收率测定,其他样品和参数的分析工作正在进行。

- 开展南海浮游植物不同粒径结构分布及组成的观测。通过CTD采集水样,对南海及吕宋海峡附近的重点站位(N1、F2、E1、D3、C3、B1、B4、A9、SEATS、

DC2、DC4、DC6、DC9、BL15、A14) 进行浮游植物群落粒径分级样品采集, 并开展微型浮游动物对浮游植物摄食压力的影响研究等。样品及参数的初步分析已完成。

2) 搭载“2017 年基金委珠江口-南海西部共享航次”, 课题成员徐杰任航次首席科学家, 研究了异养细菌代谢过程对珠江冲淡水的响应机制, 以及细菌下行控制随环境梯度的变化规律。

3) 搭载“2017 年基金委台湾海峡春季、夏季、秋季三个共享航次”, 针对南海北部进行了常规监测, 开展了水文、海洋生物、生态、化学、海洋地质的综合调查, 通过多学科交叉与综合研究, 推进南海北部动力环境演变及生态响应研究。

4) 与国家自然科学基金创新群体项目“海洋氮循环与全球变化”联合组织“2017 年秋季南海 SEATS 时间序列站观测航次”, 课题负责人史大林任航次首席科学家, 通过对南海北部典型站位的观测, 研究南海微小型蓝藻和固氮蓝藻的分布特征及其受海洋酸化的影响。

5) 搭载“2018 年基金委共享“南海东北部—吕宋海峡”综合航次”, 针对课题主要科学问题“海洋酸化对南海固氮浮游植物群落结构的影响”展开多学科综合调查:

- 厘清南海北部和黑潮固氮速率及固氮生物分布特征, 解析影响该分布的主要环境因子;
- 通过现场痕量洁净条件下添加铁、磷等营养盐, 探究南海和黑潮固氮作用的营养盐限制特征, 从限制性营养盐层面上解析南海和黑潮固氮的差异;
- 探究不同营养盐条件下南海原核浮游植物群落对海洋酸化的响应及其分子机理。

2. 课题调整情况

如课题出现超前/迟滞等情况, 请详细说明原因、措施及履行相关审批管理制度的情况。

无。

二、取得的重要进展及成果

1 课题中期重要进展及成果

简要介绍课题研究工作的重要进展、阶段性成果（一般不超过3项）及前景。

1.1 揭示了海洋酸化抑制束毛藻的固氮和生长及其机理

常量营养元素氮是全球中低纬度大面积寡营养海区初级生产力的主要限制因子。广泛分布于热带、亚热带寡营养海域的自养固氮蓝藻束毛藻，是海洋生态系统中“新氮”的主要输入者，可贡献高达50%的全球海洋总固氮量，其对全球变化的响应将对海洋初级生产力和生物泵效率产生重要的影响，是近年来海洋酸化研究的热点。围绕该重大科学问题，国际上开展了一系列的研究，但报道的研究发现却截然相反，且原因不明。针对这一备受关注却悬而未决的科学问题，我们开展了系统性的实验室和现场研究工作，发现海洋酸化降低了束毛藻的生长和固氮速率，这是由于海水pH下降干扰了胞内pH稳态，从而导致束毛藻为维持正常生理状态所需消耗的能量显著增加而引起的。此外，通过对海水培养基水化学的系统分析，我们揭示了先前报道的酸化对束毛藻固氮的促进作用，很可能是由于相关室内实验使用的人工海水培养基误受金属和氨的污染所导致的假象。该成果不仅揭示了酸化对束毛藻的影响及其机理，而且解决了关于酸化对束毛藻影响的争议。论文发表后在国内外产生广泛影响，Almetric统计显示其受关注度位列全球同期发表论文的前2%，被美国化学学会 *Chemical & Engineering News* 作“科学聚焦”介绍，被新华社、美国科学促进协会、*Science News* 等国内外媒体报道，并被国家自然科学基金委在头版介绍。

Hong H.Z., Shen R., Zhang F.T., Wen Z.Z., Chang S.W., Lin W.F., Kranz S.A., Luo Y.-W., Kao S.-J., Morel F.M.M., Shi D.L.* 2017. The complex effects of ocean acidification on the prominent N₂-fixing cyanobacterium *Trichodesmium*. *Science* 356: 527-531.

Shi D.L.*, Shen R., Kranz S.A., Morel F.M.M., Hong H.Z. 2017. Response to Comment on “The complex effects of ocean acidification on the prominent N₂-fixing cyanobacterium *Trichodesmium*”. *Science* 357: eaao0428.

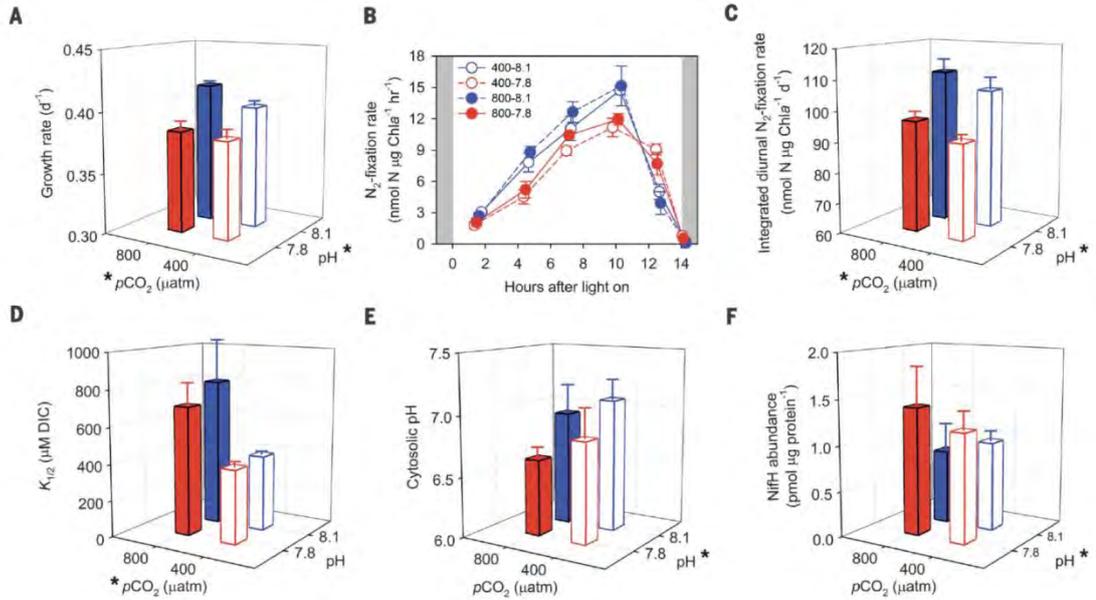


图 1. 海洋酸化 $p\text{CO}_2$ 升高和 pH 下降对束毛藻 (A) 生长速率、(B) 和 (C) 固氮速率、(D) 光合作用无机碳半饱和参数、(E) 胞质 pH、(F) 固氮酶丰度的影响。

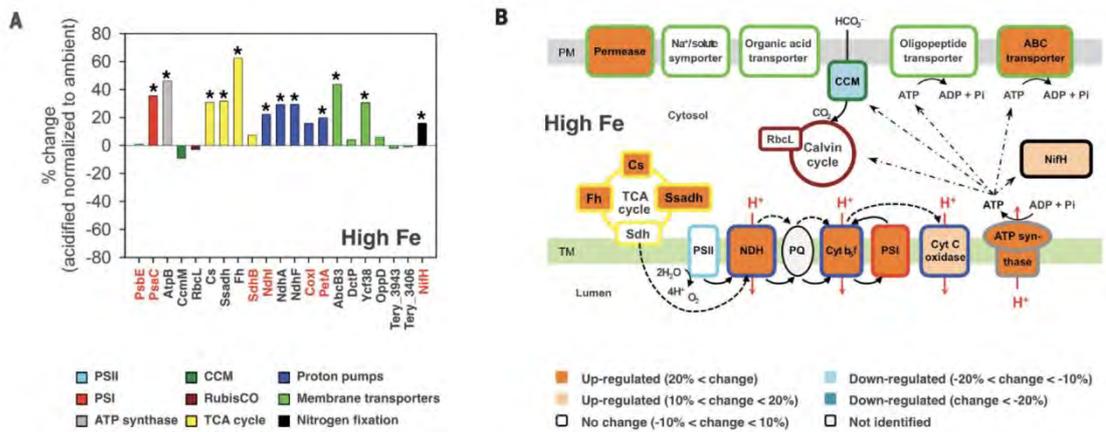


图 2. 海洋酸化对 (A) 束毛藻参与光合作用、能量生产、固碳、胞质 pH 稳态以及固氮等关键细胞过程的蛋白表达的影响及其 (B) 概念图。

1.2 阐明了氮营养盐水平对硅藻细胞能量代谢响应海洋酸化的影响及机理

在全球变化下的海洋生态系统中，浮游植物受海水酸化、营养盐供给改变等多环境因子变化的联合胁迫。准确阐明并预测复杂且相互关联的多环境因子的耦合效应及其机制，对了解全球变化对海洋生态系统的影响具有重要意义，也是重大的科学挑战，因为生物多样性等各种因素可能对准确预测造成影响。我们抓住能量的捕获、固定、消耗及储存这一初级生产过程的本质核心，将宏观生态学系统水平上的能量收支概念创新性的

运用于细胞水平上，以评估全球变化多环境因子协同作用对浮游植物的影响。以海洋初级生产力的重要贡献者硅藻为研究对象，我们从生理、生化、分子等多个水平上，系统解析了威氏海链藻、假威海链藻、三角褐指藻的光合效率、CO₂浓缩机制、光呼吸等关键能量代谢过程对海水酸化的响应受氮营养盐水平（充分或限制）的影响以及机理。在上述实验基础上，我们运用前期工作中创新性建立的细胞能量收支模型，有效的预测了三种硅藻在氮限制和氮充分条件下对酸化响应的差异及其机理。此外，在上述研究中，为了定量评估藻类光呼吸重要产物——乙醇酸，我们建立了一个崭新的液相色谱-四级杆质谱（LC-MS）测定方法，其灵敏度比现有方法提高了至少5倍、且需要的样品量仅为25毫升，可用于精确定量寡营养海区海水中的乙醇酸。

Hong H.Z., Li D.M., Lin W.F., Li W.Y., **Shi D.L.*** 2017. Nitrogen nutritional condition affects the response of energy metabolism in diatoms to elevated carbon dioxide. *Marine Ecology Progress Series* 567: 41-56.

Hong H.Z., Li W.Y., **Li X.L.**, Huang B.Q., **Shi D.L.*** 2017. Determination of glycolic acid in natural seawater by liquid chromatography coupled with triple quadrupole mass spectrometry. *Limnology and Oceanography: Methods* 15: 631-641.

	<i>T. pseudonana</i>		<i>P. tricornutum</i>		<i>T. weissflogii</i>	
	N rep.	N lim.	N rep.	N lim.	N rep.	N lim.
Relative change in PSII photon flux rate ^a	-3	-14	0	-24	-2	3
Contribution to photosynthetic rate by down-regulation of CCM	2 to 10	2 to 10	2 to 10	2 to 10	2 to 10	2 to 10
Contribution to photosynthetic rate by down-regulation of photorespiration ^b	1	3	0	1	1	4
Contribution to photosynthetic rate by change in nitrate reduction ^c	1	1	2	1	0	0
Predicted relative change of photosynthetic rate ^d	1 to 8	-9 to 0	4 to 12	-20 to -12	1 to 9	9 to 17
Contribution to net carbon fixation by change in respiration ^e	0	8	4	9	-1	16
Predicted relative change of net carbon fixation ^f	1 to 8	-1 to 8	8 to 16	-11 to -3	0 to 10	25 to 33

^aCalculated as the percentage change in rETR150 × PsbA at 750 μatm relative to 400 μatm CO₂. The values of rETR150 and PsbA are from Table 5 and Fig. 2, respectively. Doubling pCO₂ down-regulates CCM and the energy saved will contribute to the photosynthetic rate by 2 to 10% (Hopkinson et al. 2011)

^bCalculated as relative change of the expression of *PGP/GDCT* genes × (872 kJ mol C⁻¹ × 7%)/590 kJ mol C⁻¹ (Shi et al. 2015). The transcription levels of *PGP/GDCT* genes are from Fig. 3

^cCalculated as relative change of NR expression × (288 kJ mol N⁻¹/C:N ratio)/590 kJ mol C⁻¹ (Shi et al. 2015). The relative change of NR expression was calculated using the values in Fig. 4

^dSum of relative change in photon flux rate, contribution to the photosynthetic rate by down-regulation of CCM, photorespiration and nitrate reduction

^eAssuming one-third of the carbon fixed by photosynthesis is respired (Losh et al. 2013), contribution to net carbon fixation by decrease in respiration was calculated as relative change of the *COX1* gene expression divided by 3

^fPredicted relative change of net carbon assimilation is the sum of relative change of the photosynthetic rate and respiration

表 1. 海洋酸化对氮充分和氮限制条件下假威海链藻、三角褐指藻、威氏海链藻的光能捕获、CO₂浓缩机制、光呼吸、硝酸盐还原等能量代谢过程影响的实验观测与细胞能量模型预测。

1.3 海洋酸化对近海富营养环境下浮游植物群落以及自养和异养微生物代谢的影响

大气 CO₂ 水平不断增加会导致海洋浮游植物生长和生态系统的各种影响。受人类活动影响严重的近海富营养水域海洋酸化的影响可能超过预期，然而这个过程与富营养化发展耦合在一起，形成复杂动态过程和机制。因此，我们在厦门五缘湾开展了中尺度围格实验，通过向近岸海水添加人工浮游植物群落（硅藻和定鞭藻）和其附着态细菌，模拟 100 年后大气 CO₂ 的浓度，探索在大气 CO₂ 提升的全球变化背景下，植物藻华过程中浮游植物的固碳和生长以及异养细菌代谢速率将如何变化，进而评估其对近岸生态系统的影响。我们的实验结果表明，在人为形成的近海水华过程中，所有的体系中都是硅藻为绝对优势种类，但是，在高 CO₂ 加富处理组中发现了显著提高的有机碳生产速率和叶绿素 a 浓度。相对于溶解无机磷和硅，溶解态无机氮的吸收效率在高 CO₂ 环境下显著增加。对于异养细菌代谢，附着态和浮游态细菌的呼吸速率在平台期段显著下调，而细菌生产力无显著变化，表明在 CO₂ 加富条件下，细菌碳同化的效率发生改变，总需碳量下调，更多吸收的碳用于自身生长而用于呼吸消耗比例减少。自养和异养类群代谢速率的同时变化，促进整个生物群落净群落生产力升高，说明 CO₂ 加富效应将会对近岸碳循环产生深远的影响。同时，近岸区域由于还受到包括升温，富营养，缺氧等一些列环节问题交互影响，将导致研究观测到结果变化更加复杂难以预测。

Liu X., Li Y., Wu Y.P., Huang B.Q., Dai M.H., Fu F.X., Hutchins D.A., Gao K.S. 2017. Effects of elevated CO₂ on phytoplankton during a mesocosm experiment in the southern eutrophicated coastal water of China. *Scientific Reports* DOI: 10.1038/s41598-017-07195-8.

Huang, Y., X. Liu, E. A. Laws, C. Bingzhang, Y. Li, Y. Xie, Y. Wu, K. Gao, and B. Huang. 2018. Effects of increasing atmospheric CO₂ on the marine phytoplankton and bacterial metabolism during a bloom: A coastal mesocosm study. *Science of The Total Environment* 633:618-629. doi:10.1016/j.scitotenv.2018.03.222

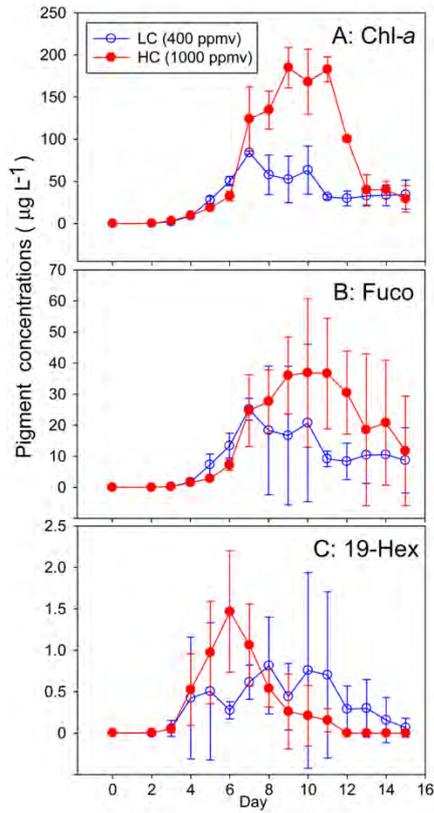


图 3.高 CO₂ 和低 CO₂ 加富环境中叶绿素 a 浓度(A), 硅藻 (B) 和定鞭藻(C)特征色素浓度的时间变化

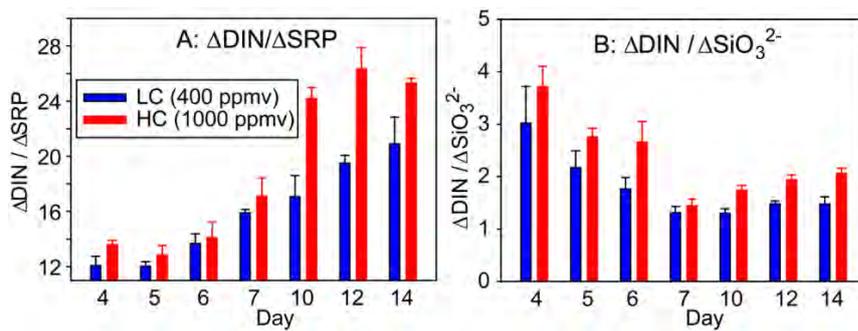


图 4. 高、低 CO₂ 加富环境中溶解无机氮与活性磷 (A) 和硅酸盐 (B) 比值的时间变化

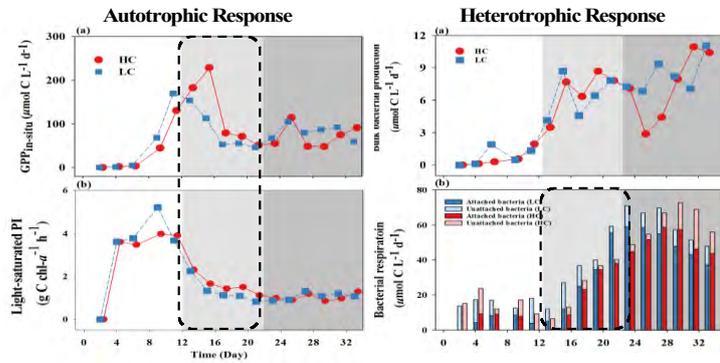
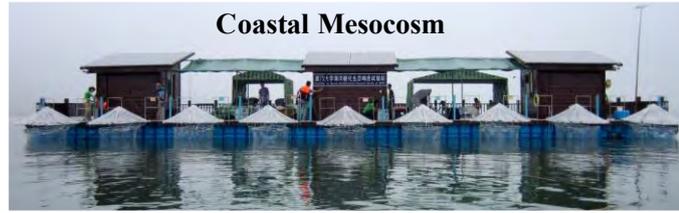


图 5. 厦门近岸中尺度围隔实验和自养和异养生物的代谢变化

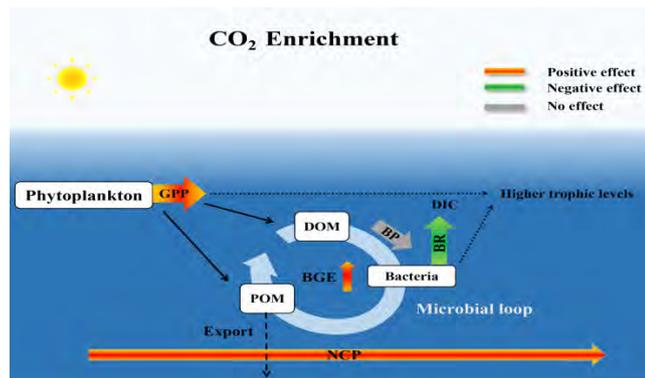


图 6. 大气 CO₂ 升高条件下近岸生态系统的变化示意图

2 预期社会经济效益

重点阐明对学科/行业产生的重要影响，对社会民生、生态环境、国家安全等的作用，以及研究成果的合作交流、转移转化和示范推广情况，人才、专利、技术标准战略在课题中的实施情况等。

通过课题实施，项目中期获得的经济社会效益如下：

2.1 科学研究和学术交流

课题的实施显著提升我国在海洋全球变化研究，特别是海洋酸化对生态系统固碳、

储碳的影响这一前沿领域的基础研究水平。课题的成果以撰写、发表学术研究报告、论著、论文和参加学术会议交流等形式呈现：

1) **科学研究**：发表 SCI 论文 14 篇，详见附件清单；

2) **学术交流**：组织和参加学术会议 10 余次。

- 2017 年 2 月，徐杰参加了由国家自然科学基金委员会和香港研究资助局主题研究计划共同组织的“2017 年度海洋环流、生态系统、缺氧及生态后果研讨会”，并做口头报告

- 2017 年 2 月，柳欣参加在夏威夷举办的 ASLO 2017 meeting，并做口头报告

- 2017 年 4 月，史大林作为发起人之一参加了厦门大学香山论坛之“陆地-河口-近海生态系统储碳和碳循环”，并做口头报告

- 2017 年 8 月，徐杰参加了在新加坡举办的第 14 届亚洲大洋洲地球科学学会年会，并做口头报告

- 2017 年 8 月，史大林参加了在山东泰安举办的第十一届海峡两岸海洋科学研讨会，并做大会特邀报告

- 2017 年 8 月，李骁麟参加了在山东泰安举办的第十一届海峡两岸海洋科学研讨会，并做口头报告

- 2018 年 5 月，史大林参加了在南京举办的第十七届中国生态学会

- 2018 年 5 月，史大林参加了在杭州举办的“全球变化下海洋有害藻华与缺氧研讨会”

- 2018 年 6 月，柳欣参加了在美国夏威夷举办的 AOGS 2018 meeting，并做口头报告

- 2018 年 7 月，史大林、李骁麟、柳欣参加了在上海举办的第五届地球系统学大会，李骁麟做口头报告

2.2 队伍建设和人才培养

1) 2017 年 6 月，柳欣于受聘为近海海洋环境科学国家重点实验室（厦门大学）、厦门大学环境与生态学院副教授

2) 2017 年 11 月，史大林于获第二十四届福建运盛青年科技奖

3) 2018 年 1 月，史大林团队研究成果“海洋酸化对束毛藻的影响及其机理”入选“2017 年度中国海洋与湖沼十大科技进展”

4)2018 年 5 月，史大林获得第五届中国生态学学会青年科技奖

5)课题培养毕业博士生 0 名、研究生 6（史大林 4 名，李骁麟 2 名）名

2.3 公众科普传播

1)史大林课题组参与 2017 年 11 月由近海海洋环境科学国家重点实验室（厦门大学）等单位主办的大型海洋知识科普活动——“第六届厦门大学海洋开放日”。本次活动吸引了 5000 余市民朋友前来参观。课题组结合自身优势，准备了丰富多彩又引人深思的趣味小实验，通过观察实验现象、讲解实验原理与市民朋友们一起探索海洋奥秘，并倡导大家爱护海洋、保护生态环境，共同关注我们的海洋和未来。



图 7. 史大林课题组组织的海洋开放日活动。

2)李芊课题组 2017 年 9 月在广州举办融知识性、科学性、趣味性为一体的“海洋环境与人类健康”的科普讲座，总受众达到 100 多人次。通过海洋科学家故事、海洋科普电影和海洋科普游戏，鼓励青少年认识海洋、保护海洋，体验海洋科学探险的乐趣。



图 8. 李芊课题组举办的海洋环境与人类健康讲座。

3) 史大林课题组参与 2018 年 4 月 2 日至 4 月 10 日由近海海洋环境国家重点实验室、法国塔拉基金会等单位联合举办的名为“知遇鹭岛，共话蓝海——法国 Tara 科考帆船与厦门大学嘉庚号科考船联合活动周”大型公益活动，开展中小學生及公众开放、海洋科普展览、中法海洋科学研讨会、公众大讲堂等系列活动，旨在激发公众探索海洋知识、参与海洋保护的热情，唤起公众对海洋事业更多的兴趣和关注，促进中法两国科教文化领域的交流。此次活动吸引近万名观众在线直播观看，余千名市民朋友现场参与。



图 9. 史大林课题组参与 TARA 号与嘉庚号联合活动周。

三、课题人员及经费投入使用情况

1. 人员及经费投入情况

对照课题任务书阐述课题及课题资金（包括专项经费、自筹经费等）到位情况、课题资金单独核算情况、预算调剂情况、支出情况和经费使用监督管理情况、人员投入情况等。

1) 经费收支情况：

课题三收到项目拨款 115.80 万元，其中直接费 97.48 万元，间接费 18.32 万元。外拨给合作单位中国科学院南海海洋研究所 48.00 万元。

截止 2018 年 6 月 30 日，课题三总支出 73.18 万元。直接费用支出共 58.75 万元，其中设备费 4.20 万元，材料费 17.28 万元，测试化验加工费 11.62 万元，差旅费 10.38 万元，出版等事务费 0.31 万元，劳务费 14.96 万元；间接费用支出共 14.43 万元，其中绩效支出 2.65 万元。

课题三经费支出中，厦门大学共支出 49.93 万元，占课题三经费总支出的 68.23%。直接费用支出共 39.34 万元，其中材料费 16.71 万元，测试化验加工费 6.97 万元，差旅费 6.69 万元，出版等事务费 0.08 万元，劳务费 8.89 万元；间接费用支出共 10.59 万元，其中绩效支出 2.65 万元。中国科学院南海海洋研究所共支出 23.25 万元，占课题三经费总支出的 31.77%。直接费用支出共 19.41 万元，其中设备费 4.20 万元，材料费 0.57 万元，测试化验加工费 4.65 万元，差旅费 3.69 万元，出版等事务费 0.23 万元，劳务费 6.07 万元；间接费用支出共 3.84 万元。

2) 经费使用监督管理情况：

厦门大学对科研经费通过项目预算化管理，确保专款专用和科目额度控制：每个项目需要进行在科技系统进行立项登记，审批无误后在科研预算申报系统进行预算申报，之后写入财务系统，经费支出额度直接在网上受财务系统控制，进行预算调整时必须在网上提交修改申请，审批通过后才能在财务系统改写。每个项目独立核算，设计并建设了一系列核算办法及管理制度，主要包括《厦门大学纵向科研项目资金管理办法》、《厦门大学纵向科研项目劳务费管理办法》、《厦门大学国内差旅费管理办法》、《厦门大学出国（出境）差旅费管理办法》、《厦门大学物资管理制度》、《厦门大学预算程序与预算管理》、《厦门大学科研经费管理办法》等。

4) 人员投入情况:

截至 2018 年 6 月 30 日, 课题三共计人员投入 24 人。其中高级职称 5 人, 中级职称 6 人, 博士 13 人, 硕士 11 人。

2. 课题经费拨付情况

课题牵头单位向课题承担单位、课题承担单位向课题参与单位拨付中央财政资金情况。

课题三于 2016 年收到项目拨款 115.80 万元, 外拨给合作单位中国科学院南海海洋研究所 48.00 万元。

3. 人员及经费实际调整情况

如出现课题人员的调整, 以及经费未及时到位、停拨、迟拨等特殊情况, 请详细说明原因、措施、履行相关审批管理制度以及整改等情况。

无。

四、课题配套支撑条件情况

阐述各主要研究任务的配套支撑条件落实及调整变化情况。如有调整变化, 请说明调整变化对完成课题目标的影响和作用。

课题依托于课题牵头单位厦门大学和参加单位中国科学院南海研究所, 厦门大学主要承担浮游植物群落结构、固碳、储碳及有机物表征、转化、生物利用等研究任务, 中国科学院南海海洋研究所主要承担细菌群落组成、代谢活性以及有机物生物利用, 数值模型等研究任务。

厦门大学是国家“985 工程”、“211 工程”、“双一流”重点建设高校, 也是国内海洋科学领域的传统优势学校, 厦门大学拥有国家级科研平台——近海海洋环境科学国家重点实验室, 拥有一系列先进的生物海洋学、化学海洋学研究平台, 包括亚洲最大的海洋酸

化影响研究中水量试验平台、液质联用仪、电感耦合等离子质谱仪、流式分选性细胞仪、基因组测序系统、双光子激光共聚焦显微镜系统等，以上平台仪器已全部投入使用。新建的科考船“嘉庚号”（排水量，3600吨）于2017年4月1日抵达厦门交付使用。课题利用“嘉庚号”在2017年10月与国家自然科学基金创新群体项目“海洋氮循环与全球变化”联合组织“2017年秋季南海 SEATS 时间序列站观测航次”，课题负责人史大林任航次首席科学家，通过对南海北部典型站位的观测，研究南海微小型蓝藻和固氮蓝藻的分布特征及其受海洋酸化的影响；在2018年6月搭载“基金委共享‘南海东北部—吕宋海峡’综合航次”，针对课题主要科学问题“海洋酸化对南海固氮浮游植物群落结构的影响”展开多学科综合调查。“嘉庚号”科考船是课题收集现场数据、开展过程机理研究的关键配套支撑平台。

中国科学院南海海洋研究所是中国科学院创新系列研究所，是我国综合型海洋科学研究的主力单位，拥有三艘大型海洋科考船，为本课题提供航次保障和海上观测支持；拥有浪潮天梭高性能计算群集，为本课题数值模拟提供可靠的超算平台。

五、组织实施风险及应对情况

阐述课题在组织实施过程中，面对外部政策、组织管理、研发变化和知识产权等方面的风险以及应对措施。

在组织管理方面，课题总体由负责人承担组织和管理工作，并指定一名联系人协助负责人，其主要职责包括：课题内部信息和数据的收集与整理、与项目办公室联络以及和其它课题组之间的信息互通与交流等。在项目组的统筹管理下，通过邮件交流、参与项目定期协调会和专题研讨会等，保障课题和项目组间的充分协调和沟通。在课题内部，通过举办小型论坛保证课题成员的定期会面，加强课题成员之间的学术交流，实现数据在课题内部的共享和课题成员在具体科学问题上的合作等，保障课题科研活动的顺利进行和获得高质量的研究成果。

在科学研究方面，依托项目组聘请的领域专家咨询组、国际专家顾问组和项目实施专家组获取专家指导意见，推动课题研究工作的实施。

在知识产权方面，课题组对知识产权保护、成果管理及合作权益分配等相关内容上进行协调和监督管理，包括：

- 1)相关研究人员和项目办公室签署《学术规范承诺书》;
- 2)学术成果的发表必须通过正规渠道;
- 3)必须如实记录并报告实验结果和统计资料;
- 4)在作品中引用已发表的成果必须注明出处;
- 5)鼓励人员协作与数据共享,学术成果按照贡献大小原则确定署名先后;

对违背学术道德规范者,一经查实,依情节、后果严重程度,将给与项目内警告和通报相关依托管理单位等。

六、课题组织实施中的重大问题及建议

无。

七、任务书中有特殊约定或其他需要说明的事项

无。

附件：发表论文清单和首页

截止2018年6月30日,课题三共发表论文14篇,SCI收录14篇,其中第一标注11篇,第二标注3篇。

第一标注:

- 1) Hong Haizheng, Shen Rong, Zhang Futing, Wen Zuozhu, Chang Siwei, Lin Wenfang, Kranz Sven A., Luo Ya-wei, Kao Shuh-Ji, Morel Francois M.M., **Shi Dalin***, 2017, The complex effects of ocean acidification on the prominent N₂-fixing cyanobacterium *Trichodesmium*, *Science* 356: 527-531. 1区, 41.058 (第一标注)
- 2) **Dalin Shi ***, Rong Shen, Sven A Kranz., Francois M.M. Morel, Haizheng Hong, 2017, Response to Comment on “The complex effects of ocean acidification on the prominent N₂-fixing cyanobacterium *Trichodesmium*”, *Science* 357: eaao0428. 1区, 41.058 (第一标注)

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OCEAN ACIDIFICATION

The complex effects of ocean acidification on the prominent N₂-fixing cyanobacterium *Trichodesmium*

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Acidification of seawater caused by anthropogenic carbon dioxide (CO₂) is anticipated to influence the growth of dinitrogen (N₂)-fixing phytoplankton, which contribute a large fraction of primary production in the tropical and subtropical ocean. We found that growth and N₂-fixation of the ubiquitous cyanobacterium *Trichodesmium* decreased under acidified conditions, notwithstanding a beneficial effect of high CO₂. Acidification resulted in low cytosolic pH and reduced N₂-fixation rates despite elevated nitrogenase concentrations. Low cytosolic pH required increased proton pumping across the thylakoid membrane and elevated adenosine triphosphate production. These requirements were not satisfied under field or experimental iron-limiting conditions, which greatly amplified the negative effect of acidification.

The ongoing increase in dissolved carbon dioxide (CO₂) in the surface ocean caused by anthropogenic emissions is expected to affect the growth of marine phytoplankton because CO₂ is the substrate for photosynthetic carbon fixation (1). However, the concomitant decrease in seawater pH can also affect phytoplankton intracellular pH homeostasis (2), as well as the bioavailability of major and trace nutrients (3, 4). Many recent laboratory and field experiments have examined this question and evinced generally modest effects of “ocean acidification” on phytoplankton (5). Organisms that have received particular attention are the ubiquitous cyanobacteria *Trichodesmium* spp., prominent dinitrogen (N₂) fixers in oligotrophic oceans (6), whose growth is often limited by iron (Fe) (7). Paradoxically, some studies have reported considerable increases in the rates of N₂-fixation, photosynthesis, and/or growth under acidified conditions (8–11), whereas others have documented significant decreases in the same rates under similar conditions in the same isolate of *Trichodesmium erythraeum* IMS101 (*T. erythraeum*) (12). In view of the key ecological role played by diazotrophs in the large regions of the oceans that are N-limited, it is important to resolve this discrepancy. In this study, we revisited the question of the effect of acidification on *T. erythraeum*: duplicating the methods used in previous experiments that yielded contrary results, examining the individual effects of high CO₂ and low pH, probing the biochemical

basis for the observed effects under Fe-sufficient and Fe-limited conditions, and assessing the response to acidification of naturally occurring *Trichodesmium* populations in the South China Sea.

The growth rates previously observed in cultures of *T. erythraeum* under ambient partial pressure of CO₂ (P_{CO_2}) vary widely, from <0.2 day⁻¹ to >0.5 day⁻¹, without a clear understanding of the underlying reasons (8–13). Like previous investigators, we observed slow growth and N₂-fixation rates in YBCII medium prepared according to the published method (14), and these rates increased under acidified conditions (high P_{CO_2} /low pH) as reported (Fig. 1A). Experiments with systematic modifications of the medium revealed contamination by a toxic metal (likely copper) (supplementary text) and by ammonium (NH₄⁺), which we found at a concentration of 20 μM (supplementary text). Ammonia (NH₃) crosses biological membranes and is thought to inhibit the oxygen-evolving complex of photosystem II (15). Increasing the EDTA concentration to control metal toxicity and using an ultrapure source for MgCl₂, which was identified as the source of NH₄⁺ contamination, we observed markedly increased growth rates (Fig. 1, A and B). Metal and NH₄⁺ toxicity thus likely explains the low and highly variable growth rates of *T. erythraeum* observed by previous investigators in YBCII or similar media (0.16 to 0.41 day⁻¹) (table S1).

Metal and NH₄⁺ toxicity also explains the positive effect of acidification on *T. erythraeum* in YBCII (Fig. 1A). Low pH shifts the NH₃/NH₄⁺ equilibrium ($pK_a = -9.5$ in seawater, where K_a is the acid dissociation constant) toward a lower concentration of NH₃ and changes the bioavailable concentration of metals (supplementary text) (16). When NH₄⁺ was minimized and high EDTA

used, the positive effect of acidification seen in YBCII medium was reversed (Fig. 1, A and B). *T. erythraeum* then reached a growth rate of >0.5 day⁻¹ (Fig. 1B), which is nearly the same as in a natural seawater medium with free trace metal concentrations buffered with 20 μM EDTA (“Aquil-tricho”) (Fig. 1C and table S2) (17). In Aquil-tricho, the growth and N₂-fixation rates of *T. erythraeum* also decreased at high P_{CO_2} /low pH (Fig. 1C). As previously observed (12), these adverse effects were enhanced under Fe-limiting conditions despite increasing the total Fe concentration at low pH to maintain constant the biologically available free iron, Fe’ (table S3) (4).

One complication in the response of phytoplankton to ocean acidification is that the increase in P_{CO_2} and the decrease in pH may have opposite effects on physiology and growth. Hence, we varied P_{CO_2} and pH independently by adjusting the alkalinity in Aquil-tricho medium prepared with synthetic ocean water (table S4) (17). Both the growth and the N₂-fixation rates of *T. erythraeum* at high Fe dropped at low pH (pH 7.8 versus 8.1) but increased slightly at high P_{CO_2} (800 versus 400 μatm) (Fig. 2, A to C, and supplementary text). Overall, the inhibitory effect of low pH overwhelmed the stimulatory effect of high P_{CO_2} , reducing growth and N₂-fixation under high CO₂/low pH conditions (Fig. 2, A and C). The positive effects of increasing P_{CO_2} (at constant pH) can be attributed to the down-regulation of the carbon-concentrating mechanisms (CCMs) that saturate the carboxylating enzyme, Rubisco (18). This is evidenced by the lower apparent affinities [higher half saturation concentrations ($K_{1/2}$)] for dissolved inorganic carbon at high P_{CO_2} (Fig. 2D) (19). This down-regulation allows energy and resources to be reallocated to other cellular processes, including N₂-fixation (Fig. 2, A to C) (18).

A key question regarding the effect of ocean acidification on *Trichodesmium* is whether the pH in the cytosol, where nitrogenase is located, decreases along with seawater pH. Using a fluorescent membrane-permeable probe (20), we measured a substantially lower cytosolic pH at a seawater pH of 7.8 compared with 8.1 (Fig. 2E). Symmetrically, the nitrogenase concentration increased at low pH (Fig. 2F), in opposite direction to the daily N₂-fixation (contrast Fig. 2, C and F). This indicates a lower efficiency of the nitrogenase enzyme of *T. erythraeum* at low pH, which may be due to a greater allocation of electrons to protons (H⁺) instead of N₂, as evidenced by an enhanced production of H₂ (12, 21).

To probe at the molecular level how acidification affects the biochemistry of *T. erythraeum*, we quantified a number of key proteins under ambient and acidified conditions with either sufficient or limiting Fe supply (Fig. 3). At high Fe, acidification resulted in an up-regulation of several proteins involved in energy generation and pH homeostasis, in addition to nitrogenase (Fig. 3, A and B). This includes the proteins involved in translocation of H⁺ across the thylakoid membrane, reflecting the need to maintain cytosolic pH homeostasis and the H⁺ gradient necessary for the function of adenosine triphosphate (ATP)

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TECHNICAL RESPONSE

OCEAN ACIDIFICATION

Response to Comment on “The complex effects of ocean acidification on the prominent N₂-fixing cyanobacterium *Trichodesmium*”

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Hutchins *et al.* question the validity of our results showing that under fast growth conditions, the beneficial effect of high CO₂ on *Trichodesmium* is overwhelmed by the deleterious effect of the concomitant decrease in ambient and cellular pH. The positive effect of acidification reported by Hutchins and co-workers is likely caused by culture conditions that support suboptimal growth rates.

The effects of ocean acidification on *Trichodesmium* spp., a globally important N₂-fixing cyanobacterium in oligotrophic oceans, have received considerable attention over the past decade. Paradoxically, both beneficial and deleterious effects of acidification on the rates of growth and N₂ fixation in this organism have been reported, without a mechanistic understanding of the underlying reasons. In our experiments, acidification of the medium had a clear detrimental effect on growth and N₂ fixation in *Trichodesmium erythraeum* strain IMS101 (hereafter *T. erythraeum*) (1). Cellular and molecular data show that this inhibition, which is amplified at low Fe concentrations, is caused by a decrease in cytosolic pH and the resulting biochemical cost of proton pumping across the thylakoid and plasma membranes.

Hutchins *et al.*, who have reported a beneficial effect of acidification on *T. erythraeum* (2, 3), question the validity of our results (4). They marshal three principal arguments: (i) They question our ability to measure growth rates and the validity of our results that show higher growth rates than in their experiments; (ii) they argue that their experiments were carried out under conditions that were essentially identical to ours; and (iii) they contend that their observation of a systematic nutrient-like response to increasing CO₂ establishes the validity of their data and conclusions. We respond to these points in order.

i) In our hands, *T. erythraeum* grows at a maximum rate of $0.56 \pm 0.02 \text{ day}^{-1}$ at 27°C and $80 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ (Fig. 1A) (1). This growth rate is based on chlorophyll a (Chl a)

measurements made every day at the same time because of the strong diel cycle exhibited by the organism. At the low biomass used in our study, Chl a and particulate organic carbon (POC) are proportional to each other (5). The growth rate we observed is within the range reported by several authors ($\mu_{\text{max}} = 0.46$ to 0.7 day^{-1}) (6–9). The significantly slower growth rates [$\mu_{\text{max}} = 0.33 \pm 0.04 \text{ day}^{-1}$ (2, 3)] obtained by Hutchins *et al.* do not militate in support of their results and interpretation.

ii) It is impossible for us to really know why Hutchins *et al.* obtained slow maximum growth rates in their experiments. Those may have been caused by some contaminant or by a component of the experimental medium. In our laboratory, *T. erythraeum* growth is strongly inhibited in the presence of $1 \mu\text{M}$ ammonium ($\mu_{\text{max}} = 0.37 \pm 0.04 \text{ day}^{-1}$) (Fig. 1B), a concentration often encountered in artificial seawater (10). Under these conditions, acidification indeed improves rather

than impairs growth and N₂ fixation, owing to the lower concentration and toxicity of membrane-permeable ammonia as the $[\text{NH}_3]/[\text{NH}_4^+]$ ratio decreases. At a concentration of $\sim 0.5 \mu\text{M}$ ammonium, the background reported by Hutchins *et al.* for their artificial seawater, we measured no significant effect of acidification on growth or N₂ fixation (1). It is tempting to interpret this lack of effect as a balance between a lessening of NH₃ toxicity and the detrimental effect of low cellular pH documented in our study. The growth rate is also highly affected by low or high concentrations of the chelating agent EDTA (and hence presumably also by the background concentrations of metals that are introduced as contaminants in artificial seawater). We observed a slow maximum growth rate at $2 \mu\text{M}$ EDTA (1), the concentration in the YBCII recipe used by Hutchins *et al.* (2). And we have not been able to grow *T. erythraeum* at $100 \mu\text{M}$ EDTA, the concentration apparently used by Hutchins *et al.* (3) in their experiments with the Aquil medium (11, 12). *T. erythraeum* is clearly quite sensitive to the chemistry of its growth medium—a situation that can easily lead to misinterpretation of experimental results.

iii) We agree with Hutchins *et al.* that high CO₂ concentrations are beneficial to *T. erythraeum*. We observed higher growth and N₂ fixation rates at high CO₂ when pH was held constant (1). This effect is explained by the lower material and energetic requirements to concentrate CO₂ at the site of fixation by Rubisco, as seen in the physiological and molecular data (1). Under conditions that promote fast growth rates, the positive effect of higher CO₂ is, however, overwhelmed by the negative effect of the lower pH when both parameters are allowed to covary as they do in natural seawater. Why the positive effect of high CO₂ may be dominant under the experimental conditions used by Hutchins *et al.* will only be understood when the reasons why they obtain slow maximum growth rates are also known.

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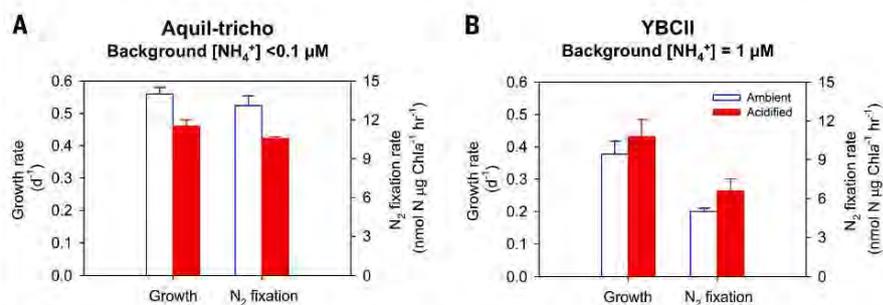


Fig. 1. The effect of ocean acidification on growth and short-term N₂ fixation of *T. erythraeum*. (A and B) Specific growth rates and short-term N₂ fixation rates of *T. erythraeum* in natural seawater Aquil-tricho medium (background [NH₄⁺] < 0.1 μM) (A) and in the artificial medium YBCII (background [NH₄⁺] = 1 μM) (B) under ambient conditions (400 μatm CO₂, pH 8.1) and acidified conditions (800 μatm CO₂, pH 7.8). Error bars denote SD of biological replicates (*n* = 3).

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Effects of increasing atmospheric CO₂ on the marine phytoplankton and bacterial metabolism during a bloom: A coastal mesocosm study

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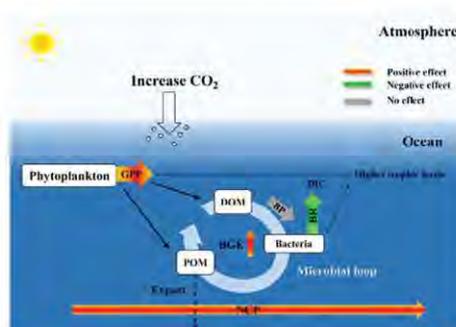
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HIGHLIGHTS

- The effects of increasing atmospheric CO₂ were assessed in a coastal mesocosm.
- CO₂ enrichment enhanced primary production and photosynthesis efficiency.
- Elevation of atmospheric CO₂ decreased bacterial respiration.
- CO₂ enrichment enhanced carbon transfer efficiency through the microbial loop.
- The contemporaneous responses have profound implications on carbon cycle.

GRAPHICAL ABSTRACT



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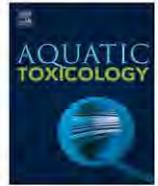
Net community production

ABSTRACT

Increases of atmospheric CO₂ concentrations due to human activity and associated effects on aquatic ecosystems are recognized as an environmental issue at a global scale. Growing attention is being paid to CO₂ enrichment effects under multiple stresses or fluctuating environmental conditions in order to extrapolate from laboratory-scale experiments to natural systems. We carried out a mesocosm experiment in coastal water with an assemblage of three model phytoplankton species and their associated bacteria under the influence of elevated CO₂ concentrations. Net community production and the metabolic characteristics of the phytoplankton and bacteria were monitored to elucidate how these organisms responded to CO₂ enrichment during the course of the algal bloom. We found that CO₂ enrichment (1000 μatm) significantly enhanced gross primary production and the ratio of photosynthesis to chlorophyll *a* by approximately 38% and 39%, respectively, during the early stationary phase of the algal bloom. Although there were few effects on bulk bacterial production, a significant decrease of bulk bacterial respiration (up to 31%) at elevated CO₂ resulted in an increase of bacterial growth efficiency. The implication is that an elevation of CO₂ concentrations leads to a reduction of bacterial carbon demand and enhances carbon transfer efficiency through the microbial loop, with a greater proportion of fixed carbon being allocated to bacterial biomass and less being lost as CO₂. The contemporaneous responses of phytoplankton and bacterial

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Effects of ocean acidification on copepods

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ABSTRACT

Ocean acidification (OA) leads to significant changes in seawater carbon chemistry, broadly affects marine organisms, and considered as a global threat to the fitness of marine ecosystems. Due to the crucial role of copepods in marine food webs of transferring energy from primary producers to higher trophic levels, numerous studies have been conducted to examine the impacts of OA on biological traits of copepods such as growth and reproduction. Under OA stress, the copepods demonstrated species-specific and stage-dependent responses. Notably, different populations of the same copepod species demonstrated different sensitivities to the increased pCO₂. In copepods, the deleterious effects of OA are also reinforced by other naturally occurring co-stressors (e.g., thermal stress, food deprivation, and metal pollution). Given that most OA stress studies have focused on the effects of short-term exposure (shorter than a single generation), experiments using adults might have underestimated the damaging effects of OA and the long-term multigenerational exposure to multiple stressors (e.g., increased pCO₂ and food shortage) will be required. Particularly, omics-based technologies (e.g., genomics, proteomics, and metabolomics) will be helpful to better understand the underlying processes behind biological responses (e.g., survival, development, and offspring production) at the mechanistic level which will improve our predictions of the responses of copepods to climate change stressors including OA.

1. Introduction

Due to anthropogenic activities, atmospheric CO₂ has steadily increased from a pre-industrial level of ~280 μatm to a present-day concentration of ~400 μatm (Siegenthaler et al., 2005). As the atmospheric CO₂ increases, significant changes in the seawater carbonate chemistry occur as a result of higher CO₂ absorption by the ocean, ultimately leading to continuous reduction in pH and carbonate concentration (Orr et al., 2005). Moreover, average surface pH of ocean has decreased by 0.1 units (a 26% increase in hydrogen ion concentration) since the industrial revolution (Orr et al., 2005). Also atmospheric CO₂ level will reach 1000 μatm by the end of this century and 1900 μatm in the year 2300, leading to a decline of 0.3–0.4 units and 0.77 units in the atmosphere and the seawater surface pH, respectively (Caldeira and Wickett, 2003). Decrease in seawater pH can be attributed to multiple factors; for example, upwelling of deeper acidified water into continental shelves (Feely et al., 2008), high levels of heterotrophic respiration (Wootton et al., 2008), and CO₂ leakage from sub-seabed carbon capture and storage sources (Shitashima et al., 2013). Organisms inhabiting in these zones will be subjected to lower pH values than those predicted for the global sea surface, which can potentially confer on their acclimatory plasticity and/or adaptive responses to pCO₂

stress. In addition, carbon fixation and storage in sub-seabed geological formations have been proposed as a potential strategy to reduce the marked accumulation of anthropogenic CO₂ in the atmosphere (Reguera et al., 2009).

Ocean acidification (OA) is also known to modulate calcification as a result of reduction in the carbonate ion concentration, which can elicit profound impact on many calcifying organisms (Langdon et al., 2000; Orr et al., 2005). Moreover, organisms exposed to high pCO₂ are vulnerable to hypercapnia and acidosis (Melzner et al., 2009) and tend to endure the adverse outcome of the reduced pH by energy reallocation from fitness-priority traits (growth and reduction) to mobilization of energy-consuming acid-base regulatory processes.

Thus, OA has been reported to perturb a multitude of physiological processes including but not limited to calcification (Langdon et al., 2000), metabolism (Lannig et al., 2010), survival (Talmage and Gobler, 2010), development (Kurihara et al., 2004a), and reproduction (Havenhand et al., 2008) in calcified and non-calcified species and is considered a major global threat to the fitness of marine ecosystems.

Copepods are abundant small crustaceans and often comprise the majority of the biomass of zooplankton in marine ecosystems. They play a crucial role in the marine food web by transferring energy from primary producers to higher trophic levels. As a result, accurate

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Effects of elevated CO₂ on phytoplankton during a mesocosm experiment in the southern eutrophicated coastal water of China

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There is a growing consensus that the ongoing increase in atmospheric CO₂ level will lead to a variety of effects on marine phytoplankton and ecosystems. However, the effects of CO₂ enrichment on eutrophic coastal waters are still unclear, as are the complex mechanisms coupled to the development of eutrophication. Here, we report the first mesocosm CO₂ perturbation study in a eutrophic subtropical bay during summer by investigating the effect of rising CO₂ on a model artificial community consisting of well-characterized cultured diatoms (*Phaeodactylum tricornutum* and *Thalassiosira weissflogii*) and prymnesiophytes (*Emiliania huxleyi* and *Gephyrocapsa oceanica*). These species were inoculated into triplicate 4 m³ enclosures with equivalent chlorophyll *a* (Chl-*a*) under present and higher partial pressures of atmospheric CO₂ ($p\text{CO}_2 = 400$ and 1000 ppmv). Diatom bloom events were observed in all enclosures, with enhanced organic carbon production and Chl-*a* concentrations under high CO₂ treatments. Relative to the low CO₂ treatments, the consumption of the dissolved inorganic nitrogen and uptake ratios of N/P and N/Si increased significantly during the bloom. These observed responses suggest more extensive and complex effects of higher CO₂ concentrations on phytoplankton communities in coastal eutrophic environments.

At present, one of the most far-reaching global perturbations of the marine environment is caused by the massive invasion of fossil fuel CO₂ into the ocean, making it the second largest sink for anthropogenic carbon dioxide after the atmosphere itself¹. CO₂ dissolved in seawater forms free H⁺ ions, lowering ocean pH and shifting dissolved inorganic carbon away from carbonate (CO₃²⁻) towards more bicarbonate (HCO₃⁻) and CO₂. This global effect of anthropogenic CO₂ emissions on ocean carbonate chemistry is of concern because it is already lowering the pH of the oceans, which may have ramifications for the growth, productivity and dominance of individual organisms or whole marine ecosystems².

It has been suggested that the consequences of global ocean acidification will become more acute in the coastal zone, due to the decomposition of organic matter produced in eutrophic waters³. Coastal areas are complex and dynamic places in which environmental factors typically exhibit great spatial and temporal variability. For example, CO₂ partial pressures ($p\text{CO}_2$) in the inner estuary of the highly eutrophic Pearl River was found to range from 3380 to 4785 μatm in the summer, with a pH of 7.0–7.2⁴. Meanwhile, in a concurrent bloom in the outer estuary of the Pearl River $p\text{CO}_2$ dropped rapidly to ~200 μatm , and pH rose to as high as 8.6⁵. This is mainly due to a variety of biogeochemical processes in coastal water, not from changes of CO₂ in atmospheric concentrations. Terrigenous inputs, upwelling effects and biological activities (algal blooms, bacterial respiration) play important roles on the variations of $p\text{CO}_2$ and pH in the water. The coastal acidification has been predicted to be over 10%

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Spatiotemporal Variability in Phosphorus Species in the Pearl River Estuary: Influence of the River Discharge

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Phosphorus was the stoichiometrically limiting nutrient in the Pearl River Estuary (PRE). In order to examine how the river discharge regulates phosphorus dynamics in the PRE, the concentrations of dissolved inorganic phosphorus (DIP) and organic phosphorus (DOP), particulate inorganic phosphorus (PIP) and organic phosphorus (POP) in the water column were determined in May 2015 (spring), August 2015 (summer) and January 2016 (winter). Our results showed that all types of phosphorus were significantly lower in spring and summer than in winter. The Pearl River discharge input played an important role in regulating phosphorus dynamics. Strong vertical mixing in winter resulted in high levels of total particulate phosphorus ($1.50 \pm 0.97 \mu\text{M}$) and dissolved phosphate (DIP: $1.44 \pm 0.57 \mu\text{M}$, DOP: $0.58 \pm 0.42 \mu\text{M}$) at the surface. On the other hand, the river discharge input created stratification in spring and summer, favoring the settlement of suspended particulate matter and enhancing light levels. This promoted phytoplankton growth, which was responsible for a DIP drawdown of $0.43 \pm 0.37 \mu\text{M}$ in May and $0.56 \pm 0.42 \mu\text{M}$ in August at the surface. Additionally, stratification restricted the bottom phosphorus replenishment. Our findings provided an insight into processes causing stoichiometric P limitation in the PRE.

Phosphorus (P) is an important nutrient for all living organisms and plays an essential role in regulating the primary production in estuarine and marine environments¹. Primary production is frequently limited by P in estuaries and marine systems^{2–4}.

Phosphorus is present in both dissolved and particulate organic or inorganic forms in aquatic environments. The various P species differ in bioavailability and geochemical cycling in the water column. Dissolved inorganic P (DIP) is preferentially utilized by living organisms^{5,6}. Dissolved organic P (DOP) represents an intermediate state during the mineralization of particulate organic matter and is a potential P source for plankton⁷. Marine organisms not only uptake inorganic phosphate but also utilize part of DOP under specific ecological conditions, especially when the supply of DIP is not sufficient^{8–11}. For example, 55–65% of DOP was found to be bioavailable in the productive surface layer of the central Baltic Sea¹², up to 88% in Loch Creran (Scotland)¹³, 7–25% in the North Pacific Subtropical Gyre³ and 8% in Bothnian Bay⁹.

It has been reported that more than 90% of phosphorus carried by rivers to estuaries and coastal waters is associated with suspended solids^{14,15}. As a result, particle-bound phosphorus is expected to be an important fraction of phosphorus in estuaries. Particulate phosphorus (PP) consists of living and dead plankton, precipitates of P minerals, P adsorbed to particles, and amorphous P phases¹⁶. Riverine PP exists as particulate inorganic phosphorus (PIP) and particulate organic phosphorus (POP). POP originates from the living or detrital organic matter. However, the components of PIP are very complex. It encompasses DIP adsorbed onto particles and phosphorus co-precipitated with calcite or iron oxyhydroxides⁶. Approximately 20% of PP in estuaries is DIP adsorbed onto particles¹⁷, which is desorbed to water through biogeochemical processes. Furthermore, increasing salinity improves the desorption of DIP adsorbed onto particles¹⁵. Additionally, PP that is bound to oxidized iron

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Nitrogen nutritional condition affects the response of energy metabolism in diatoms to elevated carbon dioxide

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ABSTRACT: Marine phytoplankton are expected to benefit from enhanced carbon dioxide (CO₂), attributable largely to down-regulation of the CO₂ concentrating mechanism (CCM) which saves energy resources for other cellular processes. However, the nitrogen (N) nutritional condition (N-replete vs. N-limiting) of phytoplankton may affect the responses of their intracellular metabolic processes to elevated CO₂. We cultured the model diatoms *Thalassiosira pseudonana*, *Phaeodactylum tricornerutum*, and *Thalassiosira weissflogii* at ambient and elevated CO₂ levels under N-replete and N-limiting conditions. Key metabolic processes, including light harvesting, C fixation, photorespiration, respiration, and N assimilation, were assessed systematically and then incorporated into an energy budget to compare the effects of CO₂ on the metabolic pathways and the consequent changes in photosynthesis and C fixation as a result of energy reallocation under the different N nutritional conditions. Under the N-replete condition, down-regulation of the CCM at high CO₂ was the primary contributor to increased photosynthesis rates of the diatoms. Under N-limiting conditions, elevated CO₂ significantly affected the photosynthetic photon flux and respiration, in addition to CCM down-regulation and declines in photorespiration, resulting in an increase of the C:N ratio in all 3 diatom species. In *T. pseudonana* and *T. weissflogii*, the elevated C:N ratio was driven largely by an increased cellular C quota, whereas in *P. tricornerutum* it resulted primarily from a decreased cellular N quota. The N-limited diatoms therefore could fix more C per unit of N in response to elevated CO₂, which could potentially provide a negative feedback to the ongoing increase in atmospheric CO₂.

KEY WORDS: Ocean acidification · N-limitation · Energy budget · C:N ratio · Diatoms

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INTRODUCTION

Human activities such as fossil fuel combustion, cement production, and deforestation have caused atmospheric carbon dioxide (CO₂) levels to increase by nearly 40% over the past 250 yr (Feely et al. 2009). If this anthropogenic emission continues unabated, atmospheric CO₂ concentrations will reach 800 μatm by the end of this century (Orr et al. 2005). The oceans have tempered the rapid rise in atmos-

pheric CO₂ by absorbing about a third of the anthropogenic CO₂ released (Sabine et al. 2004, Sabine & Feely 2007). However, the dissolution of anthropogenic CO₂ in the surface ocean leads to substantial perturbations in seawater dissolved inorganic C chemistry. As a result, the concentrations of dissolved CO₂ and bicarbonate (HCO₃⁻) increase, whereas seawater pH and the concentration of carbonate (CO₃²⁻) decrease. Collectively, these chemical changes are commonly referred to as ocean

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Determination of glycolic acid in natural seawater by liquid chromatography coupled with triple quadrupole mass spectrometry

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Abstract

Glycolic acid, which is produced during photorespiration, is one of the major components of dissolved organic matter released by phytoplankton, comprising up to 40% of their daily primary productivity. However, the sensitivity of existing methods does not allow for accurate measurement of glycolic acid levels in oligotrophic seawater. In this study, we present a straightforward, robust, and sensitive liquid chromatography-mass spectrometry (LC-MS) method to quantify glycolic acid in natural seawater following liquid-liquid extraction, requiring only a small sample size (25 mL seawater). The method has a highly sensitive detection limit of 9 nM, at least fivefold lower than existing methods. This approach was successfully applied to the analysis of seawater samples collected from both eutrophic and oligotrophic marine environments. The results showed that glycolic acid concentrations in natural seawater are positively correlated with chlorophyll *a* concentrations, indicating that phytoplankton contribute significantly to glycolic acid production in marine environments. As glycolic acid is an important carbon and energy source for marine bacteria, the method developed within this study allows further investigation into the rates of its release and uptake by phytoplankton and heterotrophic bacteria, respectively, as well as the role it plays in phytoplankton-bacteria interactions.

Photorespiration, which is important and prevalent in marine phytoplankton (Beardall 1989), occurs when O₂ outcompetes CO₂ for binding with RubisCO (ribulose-1,5-bisphosphate carboxylase/oxygenase), a Calvin Cycle enzyme. The fixation of O₂ rather than CO₂ by RubisCO results in the formation of 2-P-glycolate, which is then further metabolized to form various small organic compounds, such as glycolic acid, glycine, and serine (Beardall 1989; Fig. 1). Increases in levels of photorespiration, due to factors such as high irradiance, high temperature, or high O₂ concentrations, can stimulate the release of fixed carbon, of which glycolic acid is one of the major components (Al-Hasan and Fogg 1987; Parker et al. 2004).

Previous culture experiments have demonstrated that glycolic acid can constitute a substantial proportion of algal excreted dissolved organic matter (DOM) in the media of a variety of marine species including *Chrysophyceae*, *Bacillariophyceae*, *Chlorophyceae*, *Cyanophyceae*, etc., with high values observed in *Chaetoceros pelagicus*, *Skeletonema costatum*, and *Chlorococcum* sp. (Hellebust 1965). Field measurements have also showed that glycolic acid is a significant component (10–50%) of phytoplankton excreted DOM in marine environments (Wright and Shah 1975; Edenborn and Litchfield

1987). Excreted glycolic acid and other phytoplankton extracellular products have been estimated to account for 5–40% of the total fixed carbon, with levels reported to be in the same order of magnitude as net primary production in oligotrophic tropical oceans (Fogg 1983; Edenborn and Litchfield 1987; Leboulanger et al. 1997).

Excreted glycolic acid is taken up and utilized rapidly as an energy source by marine heterotrophic microorganisms, thereby playing a significant role in phytoplankton-bacteria interactions, which are important for the cycling of marine organic matters (Fogg 1983; Leboulanger et al. 1997; Lau and Armbrust 2006). Due to the essential role of glycolic acid in marine ecosystems, it is critical to investigate the dynamics of glycolic acid in the seawater environment. Leboulanger et al. (1997) observed that the concentration of glycolic acid in seawater increased during day time due to phytoplankton photorespiration and decreased rapidly to very low concentrations at night time due to fast uptake by bacteria. The quantification of glycolic acid in seawater during a diel cycle could thus be used to estimate its release and uptake rates by phytoplankton and heterotrophic bacteria, respectively (Leboulanger et al. 1997). Other studies, however, have reported that in situ glycolic acid concentrations often remain at very low and constant levels (Billen et al. 1980; Lau et al. 2007). Assuming steady-state conditions, the release rate of glycolic

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Alleviation of mercury toxicity to a marine copepod under multigenerational exposure by ocean acidification

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Ocean acidification (OA) may potentially modify the responses of aquatic organisms to other environmental stressors including metals. In this study, we investigated the effects of near-future OA ($p\text{CO}_2$ 1000 μatm) and mercury (Hg) on the development and reproduction of marine copepod *Tigriopus japonicus* under multigenerational life-cycle exposure. Metal accumulation as well as seven life history traits (survival rate, sex ratio, developmental time from nauplius to copepodite, developmental time from nauplius to adult, number of clutches, number of nauplii/clutch and fecundity) was quantified for each generation. Hg exposure alone evidently suppressed the number of nauplii/clutch, whereas single OA exposure negligibly affected the seven traits of copepods. However, OA exposure significantly alleviated the Hg inhibitory effects on number of nauplii/clutch and fecundity, which could be explained by the reduced Hg accumulation under OA. Such combined exposure also significantly shortened the development time. Thus, in contrast to earlier findings for other toxic metals, this study demonstrated that OA potentially mitigated the Hg toxicity to some important life traits in marine copepods during multigenerational exposure.

Ocean acidification (OA) caused by absorption of increasing anthropogenic CO_2 , with a continuous decline in pH^1 is now widely regarded as a major threat to global marine biodiversity. The atmospheric CO_2 increased steadily from a preindustrial level ($\sim 280 \mu\text{atm}$) to a contemporary concentration with about $400 \mu\text{atm}^{2,3}$. Average ocean surface pH has dropped by 0.1 units (a 26% increase in the hydrogen ion concentration) since the industrial revolution^{4–6}. It is predicted that the atmospheric $p\text{CO}_2$ will break the barrier of 1000 μatm by the end of 2100, resulting in a decrease in seawater surface pH of 0.3–0.5 units (pH 7.6–7.9)⁷. Increased seawater $p\text{CO}_2$ can result in hypercapnia and acidosis⁸ which may cause re-allocation of energy into growth and reproduction due to mobilization of energy costly acid-base regulatory processes to fight against internal pH reduction. Accordingly, OA has been shown to perturb a range of physiological processes including calcification⁹, survival¹⁰, fertilization¹¹, embryonic development¹², metabolism¹³, and reproduction¹⁴ in calcifying and non-calcifying organisms.

In addition to the increase in global atmospheric CO_2 levels, anthropogenic activities also significantly promote the mercury (Hg) emission to the atmosphere¹⁵, which will finally enter into marine environments^{16,17}. Thus, OA and Hg pollution may co-occur in marine environments. Indeed, Hg pollution has been a serious environmental concern for marine environments in China^{18–20}, which contributed approximately 28% to the global Hg emissions in the atmosphere. For example, the maximum level of total Hg (T-Hg) was reported to be 2.7 $\mu\text{g/L}$ in the seawater in Jinzhou Bay, about three orders of magnitude higher than the background level²⁰. Hg toxicity is often ascribed to its high affinity for the SH groups in endogenous biomolecules including proteins and enzymes, hence resulting in their dysfunctions (e.g., oxidative damage) and subsequently producing multi-toxicities in the organisms^{21,22}. To our knowledge, only one study examined the impacts of elevated $p\text{CO}_2$ (i.e., 380, 850 and 1500 μatm with equal pH values of 8.10, 7.85 and 7.60, respectively) on Hg accumulation in the early stages of the squid *Loligo vulgaris*²³. The results demonstrated that, in the whole egg strand and paralarvae, OA enhanced Hg

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Nitrogen fixation in two coastal upwelling regions of the Taiwan Strait

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Recent studies have demonstrated that dinitrogen fixation can be important in nutrient-rich coastal upwelling regions. During a cruise to the Taiwan Strait in summer 2015, we found that the nitrogen fixation rate in surface waters ranged from below detection limits to $7.51 \text{ nmol N L}^{-1} \text{ d}^{-1}$. Higher rates accompanied by low N:P ratios (1–10.4:1) associated with low temperatures occurred in the surface water where the Pingtan and the Dongshan upwelling regions met (the NE area). In contrast, insignificant rates were observed in the southwest area of the Dongshan upwelling region (the SW area) with sufficient N and deficient P, and therefore high N:P ratios (e.g., >43 at station C2) due largely to the influence of the Pearl River plume. Diatom-associated symbionts (het-1 ; 10^4 – 10^6 copies L^{-1}) that are efficient in organic matter export were found to dominate the other diazotrophic groups that were surveyed, which may represent a direct relationship between new nitrogen input and export in the upwelling regions. Our results suggest a hydrographical influence on the diazotroph community and N_2 fixation in coastal upwelling regions.

Marine dinitrogen (N_2) fixers are able to convert dissolved nitrogen gas into bioavailable nitrogen (N), providing new nitrogen to the photic zone for the net sequestration of atmospheric carbon dioxide (CO_2)^{1,2}. For more than two decades there have been attempts to estimate oceanic N_2 fixation, but most work has focused on the warm and oligotrophic open ocean waters^{3–5}. Recent studies have shown that oceanic regions that are traditionally regarded as unfavorable for N_2 fixation could also be important^{6–14}. For example, nutrient-replete coastal upwelling regions in the tropical and sub-tropical oceans, which play a disproportionately important role in nutrient cycling¹⁵, have been demonstrated to have significant N_2 fixation potential^{6,8,9,11,12,16}.

It has been shown that active N_2 fixation may occur in an upwelling region with enriched nutrients [e.g., N, phosphorus (P), silicon (Si) and potentially iron (Fe)] sourced from the subsurface where high rates of water column denitrification are often observed^{6,8,11}. In such cases, a high nitrate (NO_3^-) concentration does not inhibit N_2 fixation, and factors such as the N:P ratios of the upwelled water, the level of oxygen deficiency in the water column, and temperature may be responsible for the relatively high levels of N_2 fixation observed^{6,11}. In contrast, in the upwelling region off Vietnam and in the Northwest African upwelling region, high diazotrophic activity has been recorded in areas bordering instead of in the actual upwelling region^{9,12}. External factors, such as dust input and river plume intrusion that may provide micronutrients and enhance the stability of the water column, could have promoted N_2 fixation in such adjacent zones of coastal upwelling regions^{9,12}. Unlike the two scenarios described above, Zhang, *et al.* recently proposed a “transition zone” scenario where coastal upwelling regions may induce coupled physical and biological effects, consequently modulating N_2 fixation¹⁶. These previous studies therefore suggest that the response of diazotrophs to upwelling events and the underlying mechanisms are not likely uniform across coastal upwelling systems that have different hydrographic and biogeochemical characteristics (e.g., shelf width, bathymetry, benthic environment, seasonal upwelling intensity, and extent of external nutrient inputs), which clearly warrants further investigation.

Located between Taiwan Island and the southeastern Chinese mainland, the Taiwan Strait (TWS) is approximately 180 km wide and 350 km long, with an average depth of 60 m (Fig. 1). Water circulation and the formation of upwelling regions in the TWS are driven by complex bottom topography coupled with strong monsoon forcing^{17–22}. Upwelling regions in the TWS have been well defined and studied previously^{17,22–25}. Among them, the Dongshan upwelling (DSU) and the Pingtan upwelling (PTU) regions are wind-driven, topographically-forced coastal upwelling systems, which form in the western TWS during the summer monsoon period.

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Size-dependent phytoplankton growth and grazing in the northern South China Sea

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ABSTRACT: Field surveys of the northern South China Sea (NSCS) were conducted during the summer of 2015 and 2016 with size-fractionated chlorophyll *a* (chl *a*) measurements and size-specific dilution experiments for 3 phytoplankton size classes, including micro- (20 to 200 μm), nano- (2 to 20 μm), and picophytoplankton (<2 μm). Our results suggest that phytoplankton size structure and size-specific rates of growth and grazing mortality could vary substantially along the coastal, transition, and oceanic zones of the NSCS. There was an elevated microphytoplankton concentration in the inner shelf, in contrast to the dominance of nanophytoplankton over the middle and outer shelves. However, the phytoplankton community was mostly dominated by pico-cells in the oligotrophic oceanic regions. We found a nonlinear relationship between nanophytoplankton and total chl *a*, which is different from both pico-cells (a linear decrease) and micro-cells (a linear increase). By assessing the functional responses of the size-specific growth rates to nitrate concentrations, we found a higher nitrate-saturated maximal growth rate and a larger half-saturation constant for microphytoplankton, whereas nano- and picophytoplankton showed similar lower maximal rates and smaller half-saturation constants. There was also much higher grazing mortality of microphytoplankton in response to the increase in total chl *a*. These findings are important for understanding plankton dynamics and the associated biogeochemical fluxes in contrasting marine ecosystems, as well as for future size-structure modeling of the NSCS.

KEY WORDS: Size-fractionated chlorophyll · Size-specific phytoplankton growth · Microzooplankton grazing · South China Sea

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INTRODUCTION

The size of plankton is crucial in many ecological processes, including regulating phytoplankton community compositions, determining energy flow of plankton food webs, and controlling biogeochemical cycles in the ocean (Ward et al. 2012). The size structure of the phytoplankton community also affects a variety of phytoplankton metabolic processes, such as growth, nutrient uptake, and respiration (Nielsen 2006, Marañón et al. 2007). In contrast to phytoplankton communities dominated by larger size classes in nutrient-replete coastal regions, primary production in oligotrophic regions is largely contributed by

smaller-sized picoplankton (Chisholm 1992, Ciotti et al. 2002, Liu et al. 2007). This discrepancy may be due to the competitive advantage of large phytoplankton for growing in highly fluctuating nutrient environments (Malone 1980) and the advantage of small phytoplankton in acquiring sparse nutrients in low-nutrient environments (Sherr et al. 2005). Field investigations concerning size-specific phytoplankton growth in contrasting marine ecosystems are thus important for understanding the spatial and temporal variations of phytoplankton assemblages and associated biogeochemical transformations (Marañón 2015).

Microzooplankton grazing on average accounts for >60 % of the phytoplankton loss in the ocean (Calbet

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Global Proteome Profiling of a Marine Copepod and the Mitigating Effect of Ocean Acidification on Mercury Toxicity after Multigenerational Exposure

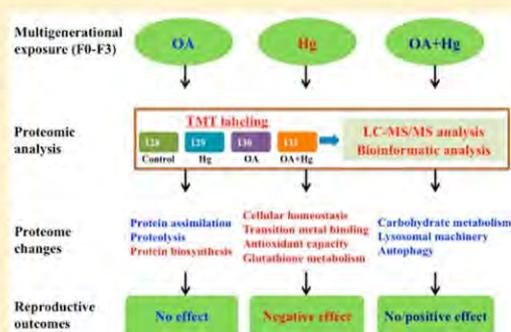
Minghua Wang,^{*,†,‡,§} Jae-Seong Lee,^{†,§} and Yan Li[†]

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Supporting Information

ABSTRACT: Previously, we found that ocean acidification (OA) mitigates mercury (Hg) toxicity to marine copepod *Tigriopus japonicus* under multigenerational exposure (four generations, F0–F3). To determine the response mechanisms of *T. japonicus* against long-term exposure to OA and Hg pollution, we investigated the proteome of F3 copepods after multigenerational exposure to four conditions: pCO₂ 400 μatm + control; pCO₂ 1000 μatm + control; pCO₂ 400 μatm + 1.0 μg/L Hg; and pCO₂ 1000 μatm + 1.0 μg/L Hg. Functional enrichment analysis indicated that OA enhanced the copepod's energy production mainly by increasing protein assimilation and proteolysis as a compensatory strategy, which explained its physiological resilience to reduced pH. Conversely, Hg treatment decreased many critical processes, including ferric iron binding, antioxidant activity, cellular homeostasis, and glutathione metabolism, and these toxic events could translate into higher-level responses, i.e., restrained reproduction in copepods. Importantly, the mediation of Hg toxicity in *T. japonicus* by OA could be explained by the enhanced lysosome-autophagy pathway proteomes that are responsible for repairing and removing damaged proteins and enzymes under stress. Overall, this study provided molecular insights into the response of *T. japonicus* to long-term exposure of OA and Hg, with a particular emphasis on the mitigating impact of the CO₂-driven acidification on Hg toxicity.



INTRODUCTION

Ocean acidification (OA), a continuous decrease in pH resulting from the absorption of increased anthropogenic CO₂, has become a major global threat to the fitness of marine ecosystems. Atmospheric pCO₂ has steadily increased from a preindustrial level (i.e., approximately 280 μatm) to a present-day concentration of ~400 μatm.¹ Average ocean surface pH has been reduced by 0.1 units (a 26% increase in the hydrogen ion concentration) in comparison with levels during the industrial revolution,^{2,3} and the atmospheric CO₂ level is projected to reach 1000 μatm by the end of 2100, leading to a decline of 0.3–0.5 units in seawater surface pH (7.6–7.9).⁴ Also, some low-pH “hot spots” in coastal zones may already have experienced the pH values forecasted for the end of 2100 as a result of a multitude of drivers, e.g., upwelling of deeper acidified water along continental shelves⁵ and high levels of heterotrophic respiration,^{6,7} thereby subjecting the organisms in these zones to lower pH values than projected for the global sea surface. For instance, in the northwestern-northern near-shore areas of Bohai Sea, China, seawater pH values were 7.64–7.68 equal to that predicted for the end of 2100.⁷ Elevated pCO₂ in seawater can cause hypercapnia and acidosis⁸ and may

subsequently result in redistribution of energy into growth and reproduction caused by the mobilization of energy-costly acid–base regulatory processes to counteract reduced pH. Accordingly, OA disturbs a multitude of physiological processes including calcification,⁹ metabolism,¹⁰ survival,¹¹ development,¹² and reproduction¹³ in calcifying and noncalcifying organisms.

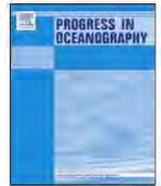
In addition to increasing global atmospheric CO₂ levels, human activities have also led to a mass of mercury (Hg) emission into the atmosphere, which is eventually deposited in marine environments especially coastal zones. Thus, OA and Hg pollution may co-occur in these environments. Indeed, Hg pollution is a severe problem for marine environments in China^{14,15} because it contributes approximately 28% to the global Hg emission into the atmosphere. The maximum total Hg (T-Hg) has reached 2.7 μg/L in the seawater of Jinzhou Bay, Bohai Sea, about 3 orders of magnitude higher than the

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Spatial distributions of polyunsaturated aldehydes and their biogeochemical implications in the Pearl River Estuary and the adjacent northern South China Sea



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ABSTRACT

This study reports the first comprehensive exploration of the spatial patterns of dissolved and particulate polyunsaturated aldehydes (PUAs), their physical and biological controlling factors, and their potential biogeochemical influences in the Pearl River Estuary (PRE) of the northern South China Sea (NSCS). High levels of total particulate PUAs (0–41 nM) and dissolved PUAs (0.10–0.37 nM) were observed with substantial spatial variation during an intense summer phytoplankton bloom outside the PRE mouth. We found the particulate PUAs strongly correlated with temperature within the high chlorophyll bloom, while showing a generally positive correlation with chlorophyll-*a* for the entire region. Additionally, the Si/N ratio significantly correlated with the particulate PUAs along the estuary suggesting the important role of silica on PUA production in this region. The dissolved PUAs counterparts exhibited a positive correlation with chlorophyll-*a* within the high chlorophyll bloom, but a negatively one with temperature outside, reflecting the essential bio-physical coupling effects on the dissolved PUAs distributions in the ocean. Biogeochemical implications of PUAs on the coastal ecosystem include not only the deleterious restriction of high PUAs-producing diatom bloom on copepod population, but also the profound influence of particulate PUAs on the microbial cycling of organic carbon in the NSCS.

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1. Introduction

In recent decades, polyunsaturated aldehydes (PUAs) have attracted increasing attention as these metabolites may play an important role in chemically mediated planktonic interactions and thus regulators of phytoplankton bloom dynamics in the ocean (Miralto et al., 1999; Frost, 2005). The presence of PUAs in seawater, mostly derived from oxidation of fatty acids of phytoplankton cells, may affect a number of processes over various trophic levels, including bacteria production (Edwards et al., 2015), phytoplankton growth (Ribalet et al., 2007a), zooplankton grazing (Jüttner, 2005), as well as fertilization, embryonic development, and larval survival of marine invertebrates (Tosti et al., 2003; Caldwell, 2009). Marine diatoms are believed to be the major phytoplankton producing PUAs in response to their physiological stresses, including growth limitation, competition, and predation (Ivanora and Miralto, 2010). Diatom PUA production, however, would depend not only on the organism's physiological state, but also on the species and strains of diatoms, with only 36% of the major diatom species capable of producing PUAs (Wichard et al., 2005a).

While results from culture and laboratory experiments have been criticized for using PUA concentrations orders of magnitude higher than their natural levels in the seawater (Ribalet et al., 2007a; Wichard et al., 2008), there are still few attempts to address the influence of PUAs on various levels of food webs in natural marine ecosystems (Balestra et al., 2011). Until recently, there are very few field PUA measurements available to understand the actual variations of PUAs under in situ conditions (Vidoudez et al., 2011a; Bartual et al., 2014; Morillo-Garcia et al., 2014; Ribalet et al., 2014). It is now recognized that nanomolar and sub-nanomolar concentrations of PUAs are released as particulate and dissolved fractions in the ocean after diatom cell disruption due to zooplankton feeding or cell lysis during phytoplankton blooms (Vidoudez et al., 2011a; Ribalet et al., 2014). The dissolved PUAs (*d*PUA) in seawater would be important for shaping community structure and function of the planktonic ecosystem (Ribalet et al., 2014), whereas the particulate PUAs (*p*PUA) could affect the ocean carbon cycle by stimulating the remineralization of sinking organic matter, decreasing the efficiency of carbon export, and shoaling the depth of nutrient regeneration (Edwards et al., 2015).

The Pearl River Estuary (PRE), one of the largest estuaries in the northern South China Sea (NSCS), is strongly influenced by coastal outflows and seawater intrusion (Mao et al., 2004). As the river

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Variability in sinking fluxes and composition of particle-bound phosphorus in the Xisha area of the northern South China Sea

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Northern South China Sea

ABSTRACT

Export fluxes of phosphorus (P) by sinking particles are important in studying ocean biogeochemical dynamics, whereas their composition and temporal variability are still inadequately understood in the global oceans, including the northern South China Sea (NSCS). A time-series study of particle fluxes was conducted at a mooring station adjacent to the Xisha Trough in the NSCS from September 2012 to September 2014, with sinking particles collected every two weeks by two sediment traps deployed at 500 m and 1500 m depths. Five operationally defined particulate P classes of sinking particles including loosely-bound P, Fe-bound P, CaCO₃-bound P, detrital apatite P, and refractory organic P were quantified by a sequential extraction method (SEDEX). Our results revealed substantial variability in sinking particulate P composition at the Xisha over two years of samplings. Particulate inorganic P was largely contributed from Fe-bound P in the upper trap, but detrital P in the lower trap. Particulate organic P, including exchangeable organic P, CaCO₃-bound organic P, and refractory organic P, contributed up to 50–55% of total sinking particulate P. Increase of CaCO₃-bound P in the upper trap during 2014 could be related to a strong El Niño event with enhanced CaCO₃ deposition. We also found sediment resuspension responsible for the unusual high particles fluxes at the lower trap based on analyses of a two-component mixing model. There was on average a total mass flux of $78 \pm 50 \text{ mg m}^{-2} \text{ d}^{-1}$ at the upper trap during the study period. A significant correlation between integrated primary productivity in the region and particle fluxes at 500 m of the station suggested the important role of biological production in controlling the concentration, composition, and export fluxes of sinking particulate P in the NSCS.

1. Introduction

Phosphorus (P), an essential element for phytoplankton growth, plays an important role in marine ecosystem dynamics and eventually controls the productivity of the ocean over geological time scales (Tyrrell, 1999). Being a particle active species in seawater, dissolved inorganic phosphorus (DIP) is readily scavenged out of seawater by settling particles in the coastal environments (Ruttenberg and Berner, 1993). In the open ocean, DIP is incorporated into organic matter by phytoplankton and the fixed organic phosphorus is subsequently exported out of the euphotic zone by particles sinking to the deep ocean (Benitez-Nelson et al., 2007). As concentration of DIP is often very low in the surface ocean, remineralization of sinking particulate organic phosphorus (POP) and subsequent upwelling of the regenerated phosphate in the thermocline are thus important mechanisms for sustaining phytoplankton production and the associated biological carbon pump (Bjorkman and Karl, 2003; Honjo et al., 2008).

Particulate phosphorus can be partitioned into organic and inorganic forms in the ocean due to their different consumption pathways. In the North Pacific Ocean, a large fraction of the settling particulate P was actually found in the sinking biogenic organic matter (e.g., Yoshimura et al., 2007), which is in contrast to the coastal waters where particulate inorganic phosphorus (PIP) often dominated sinking P fluxes (Faul et al., 2005; Lyons et al., 2011). The predominance of compounds derived from phytoplankton and zooplankton affects phosphorus composition of sinking particles, as the amount of sinking particulate materials below the euphotic zone would be constrained by primary productivity above (Benitez-Nelson and Buesseler, 1999; Francois et al., 2001). Variations in the inorganic-to-organic ratios of sinking particulate P should reflect the change of water column biogeochemistry (Sekula-Wood et al., 2012). It is therefore crucial to identify and quantify the various forms of inorganic and organic P in sinking particles and their associated export fluxes in order to fully understand the dynamic of P cycle in the ocean.

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附表 2

国家重点研发计划课题中期执行情况信息表

一、课题基本情况

课题名称	海洋酸化对固碳、储碳过程的影响及其机制		
课题编号	2016YFA0601203		
密级	■公开 □秘密 □机密 □绝密		
课题承担单位	厦门大学	单位性质	大专院校
课题负责人	史大林	参加单位数	2
课题类型	■基础前沿 □重大共性关键技术 □应用示范 □其他		
课题进展情况	■按计划进行 □进度超前 □进度拖延 □进度停顿 □申请调整或撤消		
与项目内其他课题/ 应用单位/企业合作情况	□信息交流 □技术咨询 ■研发合作 □成果转化 □实现产业化		
课题实施情况	■达到预期指标 □超过预期指标 □未达到预期指标		

二、课题中期经费及人员投入情况（经费单位：万元）

总经费			专项经费					自筹经费		
预算数	到位数		预算数	到位数	是否按计划拨付课题承担单位	执行数	预算数	到位数	执行数	
386.00	115.80		386.00	115.80	是	73.18	0.00	0.00	0.00	
总人数	其中女性	高级职称	中级职称	初职称级	其他人员	博士	硕士	学士	其他学历	总人年
24	10	5	6	0	0	13	11	0	0	12.25
人才情况	院士	千人计划	万人计划	百人计划	长江学者	青年长江学者	杰青	优青	海外引进人才数	
	0	2	0	1	0	0	0	1	0	

三、课题中期目标及考核指标完成情况

课题目标	成果名称	成果类型	考核指标				考核方式(方法)及评价手段	中期实际完成指标状态
			指标名称	立项时已有指标值/状态	中期指标值/状态	完成时指标值/状态		
以南海北部陆架、海盆和珊瑚礁浮游生态系统为研究对象, 阐明海洋酸化对浮游植物群落结构的影响, 定量解析群落结构变化与初级生产力、颗粒有机碳输出以及溶解有机碳释放之间的关系; 研究海洋酸化对珊瑚礁固碳、钙化效率的影响, 阐明其分子机理; 揭示海洋酸化背景下细菌群落结构和代谢活动的变化, 定性探讨溶解有机碳降解、利用和转化以及微食物环中的碳流受海洋酸化的影响及其机理; 构建具有生物泵和微型生物碳泵结构的海洋生物地球化学模型, 并与一维物理海洋模型耦合, 模拟现代海洋生态系统固碳-储碳过程及其对海洋酸化的响应	2: 海洋酸化对生态系统固碳和储碳的影响及其机制	<ul style="list-style-type: none"> ■新理论 □新原理 □新产品 □新技术 □新方法 □关键部件 □数据库 □软件 □应用解决方案 □实验装置/系统 □临床指南/规范 □工程工艺 □标准 ■论文 □发明专利 □其他 	指标 2.1 海洋酸化对生态系统固碳和储碳的影响及其数值模拟	1.海洋酸化对浮游植物群落结构和固碳影响的研究仍然较少且缺乏机制性的理解, 对微型生物群落组成及其有机碳代谢影响的研究也非常有限, 对溶解有机碳生物可利用性的影响及其机制尚不清晰; 2.对珊瑚礁固碳和钙化效率的影响及其机理仍需进一步的研究。	1.阐明海洋酸化对南海浮游植物代表种光合固碳和利用关键氮营养盐的影响及其机理; 2.揭示南海北部有机物的来源、组成、矿化过程及其对细菌代谢过程的调控, 评估有机物的转化和输出与环境变化的关系以及对储碳的潜在影响; 3.发表论文 7-9 篇。	1.提升对浮游植物群落组成和固碳受海洋酸化影响及其机制的认识; 2.提升对海洋酸化影响下细菌群落组成和代谢活性的认识; 3.提升对海洋酸化影响下珊瑚礁固碳和钙化效率的认识; 4.定性探讨海洋酸化对溶解有机碳生物可利用性的影响; 5.构建具有生物泵和微型生物碳泵结构的海洋生物地球化学模型; 6.发表论文 15-20 篇。	论文	<p>1.系统揭示了海洋酸化对南海代表性固氮蓝藻束毛藻固氮作用和生长的影响及其机理;</p> <p>2.阐明了氮营养状况对代表性硅藻的光合固碳、光呼吸、氮同化等关键过程响应海洋酸化的调控;</p> <p>3.利用中尺度围隔系统, 揭示了海洋酸化对近海富营养环境中浮游植物群落固碳以及自养和异养微生物代谢的影响;</p> <p>4.初步揭示了珠江口及南海北部海域中溶解和颗粒态有机碳的来源、组成、分布、控制因素及转化过程</p> <p>5.发表论文 15 篇, 其中 SCI 收录 15 篇, 第一标注 12 篇。</p>
科技报告 考核指标	序号	报告类型	数量	提交时间		公开类别及时限	是否按计划提交科技报告	
	1	年度科技报告	2	2016-2017 年每年 12 月		延期 3 年公开	是	
	2	中期科技报告	1	2018 年 6 月		延期 3 年公开	是	
其他目标与考核指标完成情况								

四、课题中期实现经济社会效益情况

获得企业标准数		获得行业标准数	
获得国家标准数		获得国际标准数	
申请发明专利项数		获得授权发明专利项数	
其中国外		其中国外	
申请其他各类专利项数		获得授权其他各类专利项数	
其中国外		其中国外	
毕业研究生数	6	发表科技论文数	14
其中博士生		其中 SCI、EI 收录数	14
取得软件著作权数		出版专著数	
取得的新理论、新原理数		取得的新技术、新工艺、新方法数	
取得的新产品、新品种、新装置 数		示范、推广面积数（亩）	
获得新药（医疗器械）证书数、临床批件数		获得临床指南、规范数	
新建生产线数		新建示范工程数	
培训农民数		培训技术人员数	
获得国家级科技奖励数		获得省部级科技奖励数	
成果转化数（项）		成果创产值(万)	成果创税收(万)
成果转化收入(万)		成果创利润(万)	成果创出口额(万)