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封面图说:哈巴雪山和金沙江——“三江并流”自然景观位于青藏高原南延部分的横断山脉纵谷地区,由怒江、澜沧江、金沙江及其流域内的山脉组成。它地处东亚、南亚和青藏高原三大地理区域的交汇处,是世界上罕见的高山地貌及其演化的代表地区,也是世界上生物物种最丰富的地区之一。哈巴雪山在金沙江左岸,与玉龙雪山隔江相望。图片反映的是金沙江的云南香格里拉段,远处为哈巴雪山。哈巴雪山主峰海拔 5396 m,而最低江面海拔仅为 1550 m,山脚与山顶的气温差达 22.8℃,巨大的海拔差异形成了明显的高山垂直性气候。

彩图提供:陈建伟教授 北京林业大学 E-mail: cites.chenjw@163.com

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刘洪军, 张振东, 官曙光, 于道德, 郑永允. 海洋酸化效应对海水鱼类的综合影响评述. 生态学报, 2012, 32(10): 3233-3239.

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海洋酸化效应对海水鱼类的综合影响评述

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摘要:人类活动引起的大气 CO₂浓度的升高,除了使全球温度升高外,导致的另一个严重生态问题——海洋酸化(Ocean acidification, OA),受到社会各界包括科研界的高度重视,该领域的大部分研究结果都是在近十年才发表出来的,目前还有很多需要解决的问题。海洋酸化的研究涉及到很多学科的交叉包括化学、古生物学、生态学、生物地球化学等等。在生物学领域,海洋酸化主要围绕敏感物种,例如由碳酸钙形成贝壳或外骨骼的贝类,珊瑚礁群体等。

鱼类作为海洋脊椎动物的代表生物类群,自身具有一定的酸碱平衡调节能力,但相关海洋酸化方向的研究并不是很多。尽管人们对于海洋酸化对鱼类的影响了解甚少,这并不说明海洋酸化对鱼类没有作用或者效应小,在相关研究逐步展开的同时,发现鱼类同样受到海洋酸化的危害,几乎涉及到鱼类整个生活史和几乎大部分生理过程,尤其是早期生活史的高度敏感。因此就目前国内外对此领域研究结果做综述,以期待业界同行能够对海水鱼类这个大的类群引起重视。

关键词:海洋酸化; 二氧化碳; 海水鱼类

A review of comprehensive effect of ocean acidification on marine fishes

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Abstract: Increasing anthropogenic atmospheric CO₂ is not only increasing global temperature but also rapidly acidifying seawater through the formation of carbonic acid. This results in another serious ecological problem: a process known as ‘ocean acidification’. If the current trajectory of global emissions is maintained, atmospheric CO₂ concentrations will exceed 500 μL/L by mid-century and could reach between 730 and 1020 μL/L at the end of the century. This would cause ocean pH to decline by 0.3—0.4 units compared with current-day levels (8.06), with a rate of change many times faster than at any time during the past 650000 years.

Research of ocean acidification involves many fields, including chemistry, ecology, biogeochemistry, and so on. Ocean acidification is expected to influence marine ecosystems through its effects on marine calcifying organisms (which biomimicrize calcium carbonate into hard parts such as shells and skeletons), such as shelled mollusks and coral reefs. Most papers on ocean acidification have been published in the past decade, and have highlighted effects on marine calcifiers from a range of marine ecosystems including deep-sea and tropical corals. There are still some problems that need to be resolved. These effects are not well understood at the community and ecosystem levels, especially for non-calcifying species such as marine fishes, although the consequences are likely to involve range shifts and population declines. A current focus in ocean acidification research is to understand the resilience that organisms possess to withstand such changes, and to

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extend these investigations beyond calcification, addressing impacts on other vulnerable physiological processes.

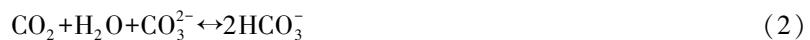
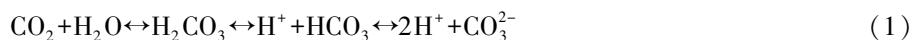
In general, marine fishes appear to be relatively tolerant to mild increases in CO₂ and decreases in pH; however, the research on ocean acidification effects has been very scarce. Although we know little about the impacts of ocean acidification on marine fish, it does not mean that ocean acidification will have little or no effect on them. In fact, there is increasing evidence from laboratory experiments that elevated levels of dissolved CO₂ and reduced seawater pH can affect developmental, metabolic and behavioral processes of some marine species, including some non-calcifying species, with highly significant consequences for population replenishment and sustainability. In general, ocean acidification could affect marine fish at all ontogenetic stages and mostly physiological duration.

Most benthic marine species have a planktonic larval phase that must transition to a benthic existence to join the adult population. This life-history transition is usually associated with high rates of mortality and can be a period of strong sensitivity to environmental factors. Thus, the highest sensitivity of marine fishes is in the early life history stages, during which serious adverse impacts on the whole wild fish populations can arise. This paper summarizes empirical evidence for the impacts of ocean acidification on marine fish, and we hope that special emphasis will be placed on this important area of research.

Key Words: ocean acidification; CO₂; marine fishes

海洋酸化的定义比较简单,也容易理解:由于海洋吸收人类活动排放的一些化学物质,包括碳,氮,硫的化合物而引起的海洋pH值的持续降低^[1]。虽然在某些特定的近岸海域,氮硫的化合物同样对海洋酸化起到很重要的作用^[2],但是主要成因还是海洋对CO₂的吸收所致。由于人类的活动,导致大量CO₂释放到环境中,对于大气来说最显著的就是温室效应,但是事实上,这个效应由于海洋的存在而被延缓,因为大气中CO₂超过30%被海洋吸收^[3-5],也就是说,正是海洋的存在延缓了由CO₂引起的全球变暖速率^[3],但同时也导致了海洋自身的酸化^[6]。根据报道,进入到大气的CO₂浓度已经从280μL/L(1750年),上升到目前的383μL/L,这个水平是65万年内的最高水平,并且在本世纪还会以每年0.5%的速度递增^[7]。对应于大气CO₂浓度的上升,与工业革命前相比海洋的pH值目前已经下降了0.1个单位^[8],并且到本世纪末将再下降0.4个单位,到2250年下降0.7个单位^[4]。

海洋吸收CO₂的直接后果就是增加氢离子的含量,这也是pH值降低的主要原因,另一个后果则是增加了碳酸和碳酸氢根离子的浓度。而作为平衡式1的产物——碳酸根离子,在p(CO₂)增大的情况下,导致平衡式2向右移动,从而降低了CO₃²⁻的浓度^[9],这两个简单的过程影响着几乎所有的海洋生物。



首先,海洋酸化不仅仅使海水pH值下降,同样导致海洋生物组织液pH值降低^[10],这使得多细胞海洋生物面临着环境和细胞外液pH值下降的双重压力。虽然有些生物(包括鱼类)具备一定的酸碱平衡调节能力^[11],但是从能量学的角度来看,对于机体长期处于酸碱平衡的调节机制,势必会导致其他生理功能的下降,尤其是对那些需要高能量的特殊种类和生物的发育时期^[12]。酸化本身就是一种环境胁迫,与极端温度、低溶氧以及其他环境胁迫类似,对生物体发育过程中的各个时期,包括早期发育、成体阶段、性成熟以及繁殖都能产生巨大影响^[13-14]。

其次,碳酸根离子浓度的降低减少了海洋生物利用碳酸钙晶体来合成自身贝壳或者外骨骼的原料^[4-5],也就是钙化过程。钙化其实是生物矿化的一种,其中海洋生物主要将碳酸钙沉积为方解石和文石两种晶体相^[15]。影响最为显著的种类包括钙化藻^[16]、珊瑚礁^[17]、棘皮动物、甲壳类、贝类等^[8, 18]。虽然就目前而言,海洋酸化的程度并不是特别严重,但是对于一些敏感种类(藻类),即使海水pH值仅下降0.1个单位,也会大

大降低其钙化能力以及钙化进程^[19];而且在不久的将来,随着海洋酸化的加剧,当 pH 值低于一些生物的特定阈值时,像海螺、珊瑚这些以碳酸钙为主要发育条件的外骨骼海洋生物就将面临被海水溶解的风险^[8-9, 17]。

海洋酸化除了影响到生物的酸碱平衡以及生物钙化过程外,对海洋生态系统的其他环节同样影响巨大,涉及到很多层面。包括海水的化学特性、很多元素和化合物的地球化学过程的改变,例如降低硝化速度、影响到氮元素的循环^[20]。

从影响的种类来看,海洋酸化效应涉及到从微藻、大型藻类、到贝类、棘皮类、珊瑚虫和低等脊椎动物鱼类等。从而,海洋种质资源量减少或消亡、物种多样性的降低、食物链的断裂、海洋生态平衡破坏等等一系列的连锁反应都有可能或者在某些区域已经出现^[18]。另外,人类活动导致 CO₂ 升高对全球环境的直接后果是温室效应,海洋酸化、海水温度的上升加上近岸水域的富营养化以及 CO₂ 本身对生物的影响,他们之间的协同效应对潮间带和浅海生态系统的影响更为突出和严重^[21-22]。

1 鱼类自身的酸碱调节能力

对于海洋生物来说,pH 值作为海水重要的理化因子,其重要性与温度以及盐度等相似。因此很多海洋生物在长期进化过程中,自身已具有比较完善的酸碱平衡调节系统,像软体动物中的头足纲^[23]、甲壳类中的短足目以及硬骨鱼类^[11]。与其他脊椎动物类似,鱼类必须维持细胞内外的酸碱平衡。CO₂ 导致的海水酸化,使得鱼类体液的 $p(\text{CO}_2)$ 升高,pH 值迅速下降,鱼类体液积累碳酸氢根,鱼类的调节主要通过鳃部(功能细胞为鳃小片上皮氯细胞)进行离子交换,将过多的 H⁺ 排出体外^[11, 24]。其他器官如小肠,肾脏甚至是淡水鱼类的鳔器官在某些情况下也具有一定的酸碱调节能力^[25-26],但是主要的调节器官还是鳃,其上皮进行的酸碱离子交换占总量的 90% 或以上^[27-30]。

由于生活环境的不同,鱼类调节酸碱平衡的机制与陆生动物具有很大的差异^[27],同时,对于鱼类自身,随着生活环境(海水、淡水和半咸水)、发育时期以及生态习性等的不同,不同鱼类、同种鱼类在不同环境、不同发育时期在酸碱平衡的调节能力和机制也存在很大差异。

首先,海水鱼类对于酸碱平衡调节的能力相对地要高于淡水鱼类,其缓冲的速度也相对迅速。这主要是因为海洋环境中碳酸氢根和其他涉及到缓冲过程的相关离子(如 Na⁺、Cl⁻ 等)比较丰富^[21]。

其次,鱼类的活动能力与其耐受 pH 值变化相关,这涉及无氧代谢酶类的存在,尤其是对于高效运动的肌肉组织,类似于人类运动中的乳酸耐受性。耐受性表现为机体细胞内 pH 值变化的幅度小。例如在海水 $p(\text{CO}_2)$ 相同的情况下,导致活动性弱的底栖鱼类 pH 值下降 0.2 个单位,相对地,具有高活动性鱼类(金枪鱼)仅仅下降 0.02 个单位^[31]。

2 海洋酸化与鱼类生物矿化

海洋酸化影响着海洋生物的矿化过程,尤其是对于利用碳酸钙形成方解石或者文石晶体的种类,鱼类的耳石也属于此类范畴。鱼类耳石主要化学成分为碳酸钙^[32],虽然有少量证据表明文石或球文石沉积相的偶然出现^[15, 33],其主要形式还是方解石,这一点类似于其他海洋无脊椎动物^[34]。因此,与鱼类的骨骼、鳞片和牙齿相比,耳石是最容易受到海洋酸化影响的矿化器官^[35-36]。鱼类具有三对耳石,主要用于探测声音,对自身进行定位^[37-38]。2009 年在 Science 上发表的一篇文章,是基于 CO₂ 对于海水化学组成的影响,而考虑到其降低碳酸钙的饱和度而会减缓耳石的形成过程。但是结果却与预测相反。发现提高的 CO₂ 下,同等大小的鲈鱼 (*Atractoscion nobilis*) 仔鱼(7—8 日龄)的耳石会增大,在长度上增大 7%—9%^[39]。Checkley 认为由于鱼类自身所具有的这种酸碱调节能力,通过反馈补偿机制反而增加了耳石内淋巴可获得的碳酸盐含量,因此,会导致耳石在酸性条件下矿化过程的加速^[39]。可惜的是,这个实验没有持续到幼鱼时期。另外,虹鳟鱼 (*Oncorhynchus mykiss*) 的耳石在环境胁迫的情况下,也具有变大的趋势^[40]。因为酸化本身就是一种环境胁迫,因此两者导致耳石变大的可能性都是存在的。在头足类—欧洲横纹乌贼(*Sepia officinalis*)的实验中,也发现环境胁迫下骨骼钙化速度存在加快的现象^[41]。无论钙化过程如何变化,其对钙化生物(包括鱼类)钙化器官形态学的影响必然导致钙化器官功能的衰退、丧失或紊乱,依据程度的不同对钙化生物生存、发育、生长以

及繁殖的负面作用,更让人们感到担忧。

然而,鱼类的骨骼系统、牙齿和鳞片在矿化的过程中与低等的海洋无脊椎动物有着本质的区别,这些器官和组织主要是沉积磷酸钙来代替碳酸钙^[42-43]。其中磷作为鱼类体内 pH 值缓冲系统的重要组成部分,在应对外界 pH 值变化过程中起到重要的作用。鱼类其他矿化器官和组织主要沉积磷酸钙也是鱼类对酸化不敏感的原因之一,但是随着海洋酸化的加剧,对于海洋酸化对鱼类矿化的长期效应目前还知之甚少,亟待进一步研究。

3 海洋酸化与鱼类性别

大部分鱼类的性别分化过程发生在变态期前后,由于鱼类性别的可塑性较大,容易受到外界环境因子的影响,因此,在性别分化的关键期,鱼类所处的环境状态能够很大程度上影响到其个体的性别。从群体来看,会使性别比例发生偏倚,在研究中发现温度、和溶解氧等能够影响到鱼类的性别分化和决定过程^[44-45]。Rubin 早在 1985 年发现 pH 值能够影响到鱼类的性别分化和性别决定过程^[46],在极端条件下(例如在较高 pH 值)慈鲷科—凯氏隐带丽鱼(*Apistogramma caetei*)繁殖后代的雄性比例降低到 10% 以下^[44]。在其他慈鲷科鱼类,如 *Pelvicachromis* 属、*Apistogramma* 属等中也发现类似的现象。总的来说,低 pH 值和高 pH 值分别产生偏向于雄性比例高和雌性比例高的后代^[44-45]。虽然 pH 值对鱼类性别影响的广度和深度不如温度那么明显,涉及到的种类也不多,但是,这种影响对于单一物种来说却是不容忽视的,抛开 pH 值影响鱼类性别的机制不谈,也不管其究竟偏向于哪个性别,这些实例给人们最为重要的启示是:在海洋酸化条件下,低 pH 值会导致一些敏感鱼类种群雌雄比例的失调,虽然在短期内不会影响种群的繁殖,但是长期持续发展的海洋酸化,即使是变化很小,在经历过几代的繁殖后,这种较小的失衡会被无限的放大,最极端和悲观的预测是导致该种群单一性别的缺失。由于该条件是人为造成,在鱼类还来不及调整自身、进化出特殊的繁殖策略的情况下,例如鱼类的天然雌核发育现象^[47],很有可能导致某些鱼类的灭绝。

4 海洋酸化与鱼类早期发育

类似于其他海洋生物,海洋酸化对于鱼类早期阶段(仔、稚、幼鱼的发育)以及鱼类的配子(精子和卵子)的负面影响更为明显。鱼类的早期发育阶段应对 pH 的变化更为敏感,调节能力较差,主要原因有二:(1)、鱼类的离子调节能力(包括 pH 值)与鳃器官的发育完善密切相关^[48],在鱼类早期阶段鳃器官发育不完善,因此还不具备成体那样较强的调节能力;(2)、即使鳃器官及其功能发育完善,与成体相比,鱼类早期阶段具有更大的鳃表面积,其维持自稳态需要更多的能量,也就更容易受到环境因子的影响^[11]。

值得一提的是,部分鱼类胚胎发育过程对海洋酸化具有较高的耐受性,在一种小丑鱼(*Amphiprion percula*)中的实验已经证实,即使在最大的 $p(\text{CO}_2)$ (和/或 pH 值)条件下,小丑鱼的胚胎孵化的时间、孵化率以及孵化后仔鱼的长度都与对照组相同^[49]。Munday 将该现象解释为,小丑鱼的胚胎已经发育出完善的酸碱调节能力。实际上,在胚胎发育时期,很少鱼类能够完善鳃器官的发育,这样的解释明显缺乏证据。另外,有报道证实,在鱼类胚胎卵裂开始后,卵膜上发育和存在一定数量的氯细胞,能够进行离子交换功能,似乎是胚胎调节能力的根本所在。不可否认的是,鱼类卵子的形态(包括大小、形状、卵壳的厚度)和组成的多样性(黏性、浮性、油球多寡)、受精后胚胎孵化的时程,孵化后所处的发育时期等等差异,都可能会成为鱼类耐受酸化的物理或者化学因素,但直接的证据仍需进一步研究。

海洋酸化同样影响到鱼类的感官系统的发育,例如破坏鱼类的嗅觉系统,从而改变化学信号介导的仔鱼行为。同样在小丑鱼实验发现,CO₂ 浓度提高到 700 μmol/mol 时,4 d 后其仔鱼行为学和对照组出现明显差异,将近 50% 的仔鱼失去判断能力(主要包括摄食和躲避敌害);而在 850 μmol/mol 下,所有仔鱼从第 2 天就其失去躲避捕食的能力^[50]。

Munday 最近又发表了一篇题目为《Ocean acidification does not affect the early life history development of a tropical marine fish》的文章,通过设定不同梯度的 $p(\text{CO}_2)$,对橙线雀鲷(*Acanthochromis polyacanthus*)早期发育过程进行实验。结果发现生长、存活率以及耳石的大小,对称性和骨骼等都不受 $p(\text{CO}_2)$ 的影响^[51],这是因为

橙线雀鲷为一种比较特殊的珊瑚鱼类,缺乏浮游的仔鱼阶段,而且具有典型的亲本护巢行为。因此,该实验是基于幼鱼阶段,而此时除了性腺外,所有器官组织业已发育成熟,功能完善,表现出对酸碱紊乱的适应性是比较合理的^[51]。

除了上述关于鱼类早期的经典实验外,另外还有一些关于CO₂碳效应对鱼类的影响。例如,将金头鲷(*Pagrus major*)的鱼卵和仔鱼分别暴露在由HCl和CO₂调制的海水中(pH值相同)水体,结果发现与HCl组(1%—4%)相比,CO₂组表现为更高的(60%——100%)死亡率^[52],这个实验很好地说明了不是酸化(海水pH值的降低),而是CO₂产生了其他的生物学效应,导致了金头鲷仔鱼的大量死亡。这又回到了酸化的起因,超出了本文讨论的范畴,属于碳效应范围,这里不再赘述。

5 研究展望

总之,海洋酸化的趋势带给整个海洋系统太多不确定的负面影响,鱼类作为海洋脊椎动物,在整个海洋生态系统中具有重要地位,同时海洋鱼类也是人类目前蛋白重要来源,研究和预测海洋酸化对海洋鱼类影响的重要性不言而喻。虽然在短期和一定的p(CO₂)(和/或pH值)条件下,鱼类对于酸碱平衡具有一定的调节能力。但是超出鱼类的耐受范围,即使是短期效应,同样会导致鱼类的酸碱平衡紊乱,导致代谢抑制、呼吸、循环、生长、繁殖等其他生理过程异常,严重的则导致死亡。目前海洋鱼类已经开始或早已开始生活在导致的酸化海水中,海洋酸化的长期效应有待深入研究。

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