

DOI: 10.5846/stxb202005131207

于道德, 宋静静, 刘凯凯, 迟雯丹, 盖珊珊, 唐君玮, 袁廷柱, 吴海一. 大型年长鱼类对海洋生态系统生物资源养护的作用. 生态学报, 2021, 41(18): 7432-7439.

Yu D D, Song J J, Liu K K, Chi W D, Ge S S, Tang J W, Yuan T Z, Wu H Y. An ecosystem perspective on fisheries conservation based on the importance of the big old fish. Acta Ecologica Sinica, 2021, 41(18): 7432-7439.

大型年长鱼类对海洋生态系统生物资源养护的作用

于道德¹, 宋静静¹, 刘凯凯¹, 迟雯丹¹, 盖珊珊¹, 唐君玮², 袁廷柱², 吴海一^{1,*}

¹ 山东省海洋科学研究院, 青岛市海洋生物种质资源挖掘与利用工程实验室, 青岛 266104

² 长岛海洋生态文明综合试验区经济促进中心, 烟台 265800

摘要:随着人口增长和渔业资源需求的上升, 人类沿着食物网营养级自上向下捕捞渔业资源的趋势仍在持续, 导致海洋生物多样性丧失及其生态功能与服务价值迅速下降。由捕捞活动造成的渔业诱导进化进一步导致鱼类资源小型化已受到国内外学者的广泛关注。从大型年长鱼类这一独特视角出发, 综述了大型年长鱼类在种群繁衍过程中的作用, 其具备巨大的繁殖能量输出、丰富的亲本繁殖经验以及强大的年龄组繁殖力贡献, 更有利于种群的延续; 大型年长鱼类对于初次性成熟亲鱼生殖洄游具有一定的引领作用, 并在季节性集群繁殖过程中占据主导地位, 可通过抑制小个体同类繁殖维护种群结构的稳定; 大型年长鱼类在生态系统中更是占据了较高营养级和广阔的生态位宽度, 面对生态环境的改变, 具有更强的适应调控能力; 大型年长鱼类在种群基因交流过程中亦起到十分关键的作用。保护大型年长鱼类更有利于鱼类种群的快速恢复, 这为生物资源养护和渔业管理政策制定方面提供了一定的参考。

关键词:大型年长鱼类; 渔业诱导进化; 种群繁殖力; 物种多样性; 生物资源养护

An ecosystem perspective on fisheries conservation based on the importance of the big old fish

YU Daode¹, SONG Jingjing¹, LIU Kaikai¹, CHI Wendan¹, GE Shanshan¹, TANG Junwei², YUAN Tingzhu², WU Haiyi^{1,*}

¹ Marine Biomass Germplasm Resources Mining and Utilization Engineering Laboratory of Qingdao, Marine Science Research Institute of Shandong Province, Qingdao 266104, China

² Marine Economic Promotion Center of Chang Island Marine Ecological Civilization Comprehensive Test Zone, Yantai 265800, China

Abstract: With the increase of population and the demand of fishery resources, the trend of human fishing from high to low trophic level is still continuing, which could threaten the marine biodiversity and benefits. It has been widely concerned that fishery-induced evolution (FIE) caused by overfishing has led to the general miniaturization of fishes. In this paper, we reviewed the role of big old fish in the process of population reproduction. The big old fish has huge reproductive-energy output and rich parental experience, which is more conducive to the continuation of their population. We believe that big old fish has played a leading role in the breeding migration of the first sexual maturation broodstock. The big old fish also can maintain the stability of the population structure by inhibiting the reproduction of small fish. Besides, the big old fish occupies a higher trophic level and expansive niche breadth in the ecosystem, which leads to stronger adaptability to respond to environmental changes. The big old fish also plays a key role in the process of population gene exchange. Therefore, it is indicated that the protection of big old fish would be more conducive to the rapid recovery of fish population, which can

基金项目: 国家重点研发计划(2018YFC1406406); 烟台科技计划(2018SFBF084)

收稿日期: 2020-05-13; 网络出版日期: 2021-06-15

* 通讯作者 Corresponding author. E-mail: wuhaiyi@shandong.cn

provide useful information for biological resources conservation and fishery administration.

Key Words: big old fish; fishery-induced evolution; population fecundity; biodiversity; biological resources conservation

人类对于海洋渔业资源的过度捕捞历史悠久。随着人口增长和渔业资源需求的上升,沿着食物网营养级自上向下捕捞渔业资源的趋势不断加强^[1],引发一系列的级联反应,导致海洋生物多样性及其关联的生态功能与服务价值下降^[2]。越来越多的证据表明,过度捕捞除了导致被捕捞种群数量的下降外,破坏式的捕捞方式还导致其关键生境退化^[3-4]。二者的协同效应与全球环境变化的耦合进一步加快了海洋经济种群的崩溃,最终导致被捕捞物种逐步从局地灭绝、生态灭绝一直到完全灭绝。这在一定程度上助推了第六次物种大灭绝^[5]。

从农业时代开始,人类偏好捕捞海洋大型物种,加速导致了蓝鲸(*Balaenoptera musculus*)、仓门鳐(*Raja laevis*)等众多大型物种灭绝或濒危,其中很多种类早在现代生态研究(20世纪50年代)之前就已灭绝,例如斯特拉海牛(Steller's sea cow)于1741年被发现后仅仅27年就灭绝了^[6-8]。鱼类作为渔业资源重要的物种组成,占有最大的有效份额(优质蛋白供给服务)^[9-11]。随着渔业技术发展,现代化捕捞方式加大了对大型海洋鱼类的捕捞强度。成年大西洋鳕鱼(*Gadus morhua*)每年自然死亡率是10%—20%左右,而每年因捕捞导致的死亡率为50%左右甚至更高^[12]。虽然关于过度捕捞是否会导致鱼类种群灭绝还具有争议,但是目前世界各国主要经济鱼类呈现资源衰退是不争的事实^[13]。

过度捕捞导致大型年长鱼类死亡率居高不下,而渔业捕捞诱导鱼类自然种群快速小型化亦会导致大型鱼类数量日益减少^[14]。人类捕捞活动的非随机性导致目标种群的自然进化方向发生改变,具体可表现为捕捞选择压力下鱼类表型快速转变,这种现象被称为渔业诱导进化,该表型转变主要与鱼类生活史和繁殖相关^[15]。在高捕捞死亡率条件下,鱼类更倾向于小型早熟个体繁殖,这样可以在较短时间内将基因传给下一代^[16]。因此,渔业诱导进化对鱼类的影响主要体现为个体小型化、过早性成熟且繁殖力低下^[17],是经济鱼类表型进化以及普遍小型化的诱因之一^[18],不利于种群结构稳定^[19]。此外,全球变暖导致水生生态系统的三个普遍生态反应,其中就包括多种类物种(含鱼类)的小型化^[20-21]。众多不利因素的协同作用,加快了大型年长鱼类的消失。

本文通过分析大型年长鱼类在种群和生态系统中的主要功能,提出将保护大型年长鱼类作为鱼类资源修复的关键一环,以期为渔业资源恢复和渔业经济可持续发展提供创新思路。

1 大型年长鱼类在种群中的繁衍作用

大型年长鱼类的名称因物种而异,毕竟某些石斑鱼类能活200年,但很少有鲱鱼能活10年以上。早在90年代,就有学者指出“larger/older”鱼类对于种群补充至关重要^[22-23],Field等^[24]和Hixon等^[25]进而提出了“Big Old Fat Fecund Female Fish (BOFFFF)”假说,探讨大型年长雌鱼在鱼类种群(尤其是长寿鱼类种群)中的关键作用。本文中大型年长鱼类主要是指生命史周期中处于鼎盛时期的鱼类,体型或繁殖力在其种群中占据明显优势。

除了一次性产卵鱼类和其他短寿命的小型鱼类外,大部分经济鱼类都属于多次产卵鱼类。渔业理论学家曾认为多次产卵性鱼类的繁殖力与亲鱼体积呈线性关系,而资源生物学家则认为,这一理论远远低估了大型鱼类的繁殖能力。Barneche等^[26]通过分析342种海洋鱼类,发现79.1%的鱼类繁殖能量输出(卵数量×卵体积×卵能量)随着雌鱼体重增加而超比例增加,幂指数可高达1.33。Bohnsack^[27]研究发现一尾成熟的体重12.5 kg(体长61 cm)美国红鱼(*Lutjanus campechanus*)怀卵量为930万粒,相当于212尾1.1 kg(体长42 cm)小个体的总怀卵量。Bobko等^[28]发现,鱼类繁殖力会随年龄呈跨越式增长,如16龄黑睛平鲷(*Sebastes melanops*)相对产卵量为549粒/g,与6龄的374粒/g对比鲜明。Song等^[29]实验发现海洋模式生物海水青鳉(*Oryzias*

melastigma)成熟亲鱼的产卵量是初次性成熟亲鱼的 25 倍。

学者们还发现大型年长鱼类拥有足够丰富的亲本繁殖经验,针对不同环境条件可通过调节产卵季节、产卵期长短、产卵数量和卵径大小来提高幼鱼质量和存活率^[30-32]。用于投入到后代的能量亦随亲鱼个体大小而变化,体型较大的亲鱼在繁殖过程中投入了更多的能量,初孵仔鱼的油球更大或体长更长,成活率相对更高。Berkeley^[33]选择 5—17 龄黑睛平鲈亲鱼作为实验对象,发现大龄亲鱼所产仔鱼的生长速度和饥饿耐受力都远远高于年轻亲鱼所产的仔鱼。在养殖鱼类中,类似现象也很多,3 龄虹鳟的卵质和发眼卵存活率都大大高于 2 龄亲鱼;连续产卵的欧洲鲈(*Dicentrarchus labrax*)^[34]、鳕鱼^[35-36]的卵质和孵化率也随亲鱼年龄增长持续提高,这种母源补充效应意味着大型年长亲鱼的后代具有更强的存活能力。

已有研究指出鱼类种群潜在繁殖力的传统评估方法没有考虑种群年龄结构因素,而是将补充群体(初次达到性成熟的群体)和剩余群体(重复性成熟的群体)的繁殖力同等计算,此类方法很可能大大高估了种群繁殖力,而低估了大型年长鱼类年龄组的贡献值^[30]。例如,许氏平鲈的补充群体在繁殖过程中往往会有难产死亡、流产等现象,所产仔鱼死亡率高、活力差。Hixon 等^[25]研究指出,鱼类的剩余群体会积极参与每一个繁殖季节,而补充群体很可能会错过。Marshall 等^[37]和 Lambert 等^[38]通过分析也发现,具有繁殖能力的生物量并不与种群潜在繁殖力成正比,大型年长鱼类年龄组的繁殖力贡献相对更大。Mehault 等^[31]亦提出,相对于产卵生物量,总产卵量是更适用于种群潜在繁殖力评估的指标,后者同时考虑了亲鱼体型大小与种群年龄结构组成。

2 大型年长鱼类在种群中的主导作用

从物种认知学的角度来看,种群中大个体年长同类的缺失会影响到群体中其余个体行为。大型年长鱼类积累的认知和经验会有效地传递给后代或者年轻的同类,例如很多鱼类具有生殖洄游的特点,初次性成熟的亲鱼可跟随更有经验的年长亲鱼学习洄游路线到达产卵场进行群体的繁殖。人为捕捞去除大个体则会扰乱鱼类生殖洄游过程,不利于特定种群的繁衍和补充^[39]。

大型年长鱼类在季节性繁殖过程中具备主导地位。例如,豹纹喙鲈(*Mycteroperca rosacea*)在进行集群产卵繁殖过程中,都是由大型个体引领带动,小型个体跟随。体型较大的雄性豹纹喙鲈(>50 cm)只与大小相等或较大的雌性交配并产卵,此种选择性交配行为,更利于种群的稳定补充^[40]。另一种具有多种繁殖策略的单鳍多线鱼(*Pleurogrammus monopterygius*),其大型成熟的雄性具有十分鲜明的婚姻色(基于胡萝卜素)用于吸引雌性,并通过建立巢穴、保卫领地,垄断与雌性的交配机会,同时为后期胚胎孵化提供一个安全环境。婚姻色的产生与维持、巢穴的建立与保护能力是大型成熟雄性多线鱼的品质和社会地位象征,不容易被模仿,而较小体型的多线鱼由于同时缺乏上述能力,只能采取偷袭或寄生的繁殖策略^[41]。由此可见,大型年长鱼类是某些鱼类种群(尤其是筑巢鱼类)集群繁殖过程的“启动因子”,无论种群内部的繁殖策略多复杂,均是基于具有筑巢能力的大型年长鱼类基础之上。有证据表明,尽管体长并非是决定鱼类具有此类能力的唯一因素,但体长、年龄以及健康度确实是最关键的影响要素^[42-43]。

大型年长鱼类还会抑制同类小个体的繁殖,这一点在具有社会性的鱼群中达到极限。由单一或几个雄(雌)性带领一群雌(雄)鱼进行种群繁殖的案例在海洋鱼类中较为常见^[44]。进入繁殖季节后,若大型个体缺失,次级大个体鱼类会快速变为大型个体来完成种群繁殖^[45],以此通过迭代作用(鱼类的代时较短),导致个体提前繁殖,进而整个种群小型化趋势加剧。而对雌雄同体鱼类来说,特殊进化的繁殖习性使得大型年长鱼类的种群内作用被放大。以先雌后雄类型的石斑鱼为例,经过几次繁殖季节,大型雌性个体才会自然性逆转为雄性,这是保证种群雌雄比例稳定、维持种群自然补充的重要机制。现如今,人类利用石斑鱼聚集性群体繁殖这一特点,进一步加快了选择性捕捞速度,使得全世界石斑鱼产业岌岌可危^[46]。

大型年长鱼类对于维护种群结构稳定亦起到一定的主导作用^[30,33]。鱼类种群自身就是一个系统构成,具有明显的阈值效应。大型年长鱼类保证种群结构稳定的同时,还有利于保障后代的存活。例如,大型成年

鳕鱼可以有效控制其幼鱼的潜在掠食者和竞争者数量,但当这些大型年长鱼类变得稀缺时,这种控制就消失了^[47]。

3 大型年长鱼类在生态系统中的特殊功能

鱼类发育属于典型的变态发育,在早期发育过程中要经历一次变态过程,且随着体型与年龄的增长,其生态习性也会发生转变^[48]。以鱼类食性变化为例,典型肉食性鱼类的食物变化史为:浮游动植物(仔鱼期)-桡足类、枝角类(稚鱼期)-小型虾蟹类(幼鱼阶段)-小型鱼类或贝类等(成鱼阶段)。随体型和年龄增长,鱼类摄食的营养级逐渐升高。大型年长鱼类可以更好地通过食物链下行作用来调整生态系统中其他物种种群结构、食物网构成以及相关生态过程。

大型年长鱼类对于所处生态系统具有更强的适应调控能力。例如,研究发现不同季节的鱼卵数量与水体环境中浮游动物丰度高度契合^[49],亲鱼所产鱼卵大小亦会发生变化^[50]。Trippel^[35]研究发现,大西洋鳕鱼(*G. morhua*)所产鱼卵卵径具有季节变化性,相比1月份和2月份,当进入浮游动物无节幼体等饵料充足的3月份时,大西洋鳕鱼会减小卵径大小、增加鱼卵数量。这是鱼类为保证后代高存活率而进行的适应性调整,同时亦是鱼类为了生态系统稳定而发挥的调控作用。相较于小型或初次性成熟的鱼类,只有经历过多次繁殖过程的大型年长鱼类,才能具备此类经验与能力。

大型年长鱼类还在某些典型生态系统中发挥着独特作用。尤其是珊瑚礁生态系统中的鱼类功能群,后者在前者的发育过程中扮演着十分重要的角色(生物侵蚀、沉积物的产生和运输),而该角色功能高度依赖于摄食方式和体型大小^[51]。例如,加勒比海域珊瑚礁系统中两种鹦嘴鱼科的王后鹦嘴鱼(*Scarus vetula*)和绿鹦鲷(*Sparisoma viride*)随年龄增长,对于维持珊瑚礁正常生长的生态作用会越发明显,大个体鱼类平均每年可移除7 kg 珊瑚礁,而小个体的作用可以忽略^[52]。且只有体长超过20 cm的鹦嘴鱼才具有足够长的嘴(颌部)来对珊瑚基质(而非珊瑚表面)进行干预,这是维持珊瑚礁物理生境、保护珊瑚礁正常发育的必要条件之一^[51]。

4 大型年长鱼类更有利于物种多样性的维持

物种水平的多样性是生物多样性的核心基础。一个物种的活动范围与它的体型大小有关,体型较大的物种比体型较小的物种活动范围更广^[53-54]。同一物种的鱼类(也包括其他海洋生物)在自然界存在多个地理种群,它们之间的联系构成了集合种群,这也是鱼类种群扩散和资源自我补充的机制之一。不同种群之间的基因交流或基因连通性对于维持该鱼类物种水平上的生物多样性具有重要的作用,有助于鱼类抵抗各种不同程度的干扰,维持较高的地理种群弹性^[55-57]。

诸多大洋性鱼类会同时存在坐地种群和迁徙种群^[58-59],其中迁徙种群负责不同地理种群之间的基因交流,这一角色是由大型或者年长鱼类来充当。面对不利环境,存在抗性耐受基因的个体,尤其是大型年长鱼类的持续存在意味着种群恢复率可能更高,而这样的适应性基因可以存在于长期的遗传变异中,尤其是在较大规模的有效种群中更有可能出现。反之,则可能导致局地灭绝,甚至是生态灭绝。

年长鱼类通过食性转变拓展生态位空间的能力相对更强,提高自身生存能力和抵抗力的同时增加了种内或种间的基因交流^[60]。例如:较年长的南非无须鳕(*Merluccius capensis*)会占据更深的水域,从而与南非深水无须鳕(*Merluccius paradoxus*)的空间分布发生重叠^[61];类似的还有六线鱼科中的大泷六线鱼和斑头鱼,二者的营养生态位、空间生态位亦有重叠^[62-63]。这为鱼类种间杂交提供了可能性^[64]。

此外,大型年长鱼类本身就是鱼类种群稳定的组成部分,能够有效维持鱼类种群和群落生物的生活史多样性、生产力稳定性,在应对短暂的不利环境波动时,起到重要的缓冲和过滤作用,这对于维持种群稳定意义重大,同样也是生态化渔业管理应当关注的核心问题^[65]。

5 结语

在全球变暖等环境问题日益凸显、大型海洋脊椎动物快速消失的今天^[66],世界渔业资源能否持续^[67],尚

存的渔业资源和重要的海洋生态环境能否得到有效保护是各国学者普遍关心的问题^[68]。人类上千年的“大型全球海洋捕捞实验”即使终止,其引发的渔业诱导进化作用仍然会持续一段时间,这是海洋生态系统阈值效应和延迟效应的结果。在特定海域保护或投放大型或年长鱼类来快速恢复鱼类资源的策略^[39],在自然保护区中起到了关键作用,能够减缓由渔业捕捞引起的鱼类小型化进程^[69]。

然而,实际情况远非如此简单^[70]。除了渔业诱导进化外,其他环境因素,如全球变暖、海洋酸化、缺氧胁迫等诸多气候改变的诱导进化作用亦在持续^[71]。Barneche 等^[26]提出,鱼类体型大小会随着全球水温增高而减小。据估计,地中海区域海面温度每升高 1.5℃,鱼类体长会减少约 15%,这将导致大西洋鲭鱼(*Scomber scombrus*)的个体平均繁殖力降低 50%^[26,72]。鱼类栖息地、产卵场、生物扩散通道等变迁^[73],食物网结构缺失,共生关系解耦联等诸多问题的耦合作用,进一步加剧了渔业资源的衰退^[71]。如北海鳕鱼种群补充失败源于产卵场水温长期变化改变了桡足类种群结构,从而导致仔鱼无法得到充足的饵料保障而大量死亡。又如鳎资源量衰退与厄尔尼诺影响黑潮水系密切相关^[74]。可见,鱼类种群有效补充过程、驱动机理及其对环境变化的响应机制等问题均会影响到鱼类资源恢复的最终成效^[75]。

人类为经济社会发展牺牲生态环境所付出的惨痛代价比比皆是,渔业资源衰退仅仅是其中一例。2020 年新冠肺炎席卷全球,人们更应当深刻思考地球生命共同体。无论我们的认知如何,未来走向何处,坚信生态学家 Aldo Leopold 的这句话“当事物倾向于保持生物群落的完整性、稳定性和美感时,它就是对的,反之则是错的”。

参考文献 (References):

- [1] Jackson J B C, Kirby M X, Berger W H, Bjorndal K A, Botsford L W, Bourque B J, Bradbury R H, Cooke R, Erlandson J, Estes J A, Hughes T P, Kidwell S, Lange C B, Lenihan H S, Pandolfi J M, Peterson C H, Steneck R S, Tegner M J, Warner R R. Historical overfishing and the recent collapse of coastal ecosystems. *Science*, 2001, 293(5530):629-637.
- [2] Worm B, Barbier E B, Beaumont N, Duffy J E, Folke C, Halpern B S, Jackson J B C, Lotze H K, Micheli F, Palumbi S R, Sala E, Selkoe K A, Stachowicz J J, Watson R. Impacts of biodiversity loss on ocean ecosystem services. *Science*, 2007, 314(5800):787-790.
- [3] Coleman F C, Williams S L. Overexploiting marine ecosystem engineers: potential consequences for biodiversity. *Trends in Ecology & Evolution*, 2002, 17(1):40-44.
- [4] Demestre M, Sartor P, Garcia-De-Vinuesa A, Sbrana M, Maynou F, Massaro A. Ecological importance of survival of unwanted invertebrates discarded in different NW Mediterranean trawl fisheries. *Scientia Marina*, 2018, 82(S1):189-198.
- [5] Barnosky A D, Matzke N, Tomiya S, Wogan G O U, Swartz B, Quental T B, Marshall C, McGuire J L, Lindsey E L, Maguire K C, Mersey B, Ferrer E A. Has the Earth's sixth mass extinction already arrived? *Nature*, 2011, 471(7336):51-57.
- [6] Estes J A, Duggins D O, Rathbun G B. The ecology of extinctions in kelp forest communities. *Conservation Biology*, 1989, 3(3):252-264.
- [7] Casey J M, Myers R A. Near extinction of a large, widely distributed fish. *Science*, 1998, 281(5377):690-692.
- [8] Myers R A, Boris W. Extinction, survival or recovery of large predatory fishes. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 2005, 360(1453):13-20.
- [9] Larsen T, Thilsted S H, Kongsbak K, Hansen M. Whole small fish as a rich calcium source. *British Journal of Nutrition*, 2000, 83(2):191-196.
- [10] Dey M M, Rab M A, Paraguas F J, Piumsombun S, Bhatta R, Alam M F, Ahmed M. Fish consumption and food security: a disaggregated analysis by types of fish and classes of consumers in selected Asian countries. *Aquaculture Economics & Management*, 2005, 9(1/2):89-111.
- [11] Food & Agriculture Organization (FAO). The State of World Fisheries and Aquaculture: Meeting the Sustainable Development Goals. Rome: FAO, 2018:1-227.
- [12] Darimont C T, Carlson S M, Kinnison M T, Paquet P C, Reimchen T E, Wilmers C C. Human predators outpace other agents of trait change in the wild. *Proceedings of the National Academy of Sciences of the United States of America*, 2009, 106(3):952-954.
- [13] 赵淑江, 吕宝强, 李汝伟, 朱爱意, 吴常文. 物种灭绝背景下东海渔业资源衰退原因分析. *中国科学: 地球科学*, 2015, 45(11):1628-1640.
- [14] Zhou S J, Smith A D M, Punt A E, Richardson A J, Gibbs M, Fulton E A, Pascoe S, Bulman C, Bayliss P, Sainsbury K. Ecosystem-based fisheries management requires a change to the selective fishing philosophy. *Proceedings of the National Academy of Sciences of the United States of America*, 2010, 107(21):9485-9489.

- [15] Hard J J, Gross M R, Heino M, Hilborn R, Kope R G, Law R, Reynolds J D. Evolutionary consequences of fishing and their implications for salmon. *Evolutionary Applications*, 2008, 1(2):388-408.
- [16] Uusi-Heikkilä S, Kuparinen A, Wolter C, Meinelt T, O'Toole A C, Arlinghaus R. Experimental assessment of the probabilistic maturation reaction norm; condition matters. *Proceedings of the Royal Society B: Biological Sciences*, 2011, 278(1706):709-717.
- [17] Olsen E M, Heino M, Lilly G R, Morgan M J, Brattey J, Ernande B, Dieckmann U. Maturation trends indicative of rapid evolution preceded the collapse of northern cod. *Nature*, 2004, 428(6986):932-935.
- [18] Law R. Fishing, selection, and phenotypic evolution. *ICES Journal of Marine Science*, 2000, 57(3):659-668.
- [19] Anderson C N K, Hsieh C H, Sandin S A, Hewitt R, Hollowed A, Beddington J, May R M, Sugihara G. Why fishing magnifies fluctuations in fish abundance. *Nature*, 2008, 452(7189):835-839.
- [20] Daufresne M, Lengfellner K, Sommer U, Carpenter S R. Global warming benefits the small in aquatic ecosystems. *Proceedings of the National Academy of Sciences of the United States of America*, 2009, 106(31):12788-12793.
- [21] Cheung W W L, Sarmiento J L, Dunne J, Frölicher T L, Lam V W Y, Deng Palomares M L, Watson R, Pauly D. Shrinking of fishes exacerbates impacts of global ocean changes on marine ecosystems. *Nature Climate Change*, 2013, 3(3):254-258.
- [22] Marteinsdottir G, Steinarsson A. Maternal influence on the size and viability of Iceland cod *Gadus morhua* eggs and larvae. *Journal of Fish Biology*, 1998, 52(6):1241-1258.
- [23] Scott B, Marteinsdottir G, Wright P J. Potential effects of maternal factors on spawning stock-recruitment relationships under varying fishing pressure. *Canadian Journal of Fisheries and Aquatic Sciences*, 1999, 56(10):1882-1890.
- [24] Field J G, Moloney C L, du Buisson L, Jarre A, Stroemme T, Lipinski M R, Kainge P. Exploring the BOFFFF Hypothesis Using a Model of Southern African Deepwater Hake (*Merluccius paradoxus*)/Tsukamoto K, Kawamura T, Takeuchi T Jr, Beard T D, Kaiser M J, eds. *Fisheries for Global Welfare and Environment*, 5th World Fisheries Congress. Tokyo:Terrapub, 2008:17-26.
- [25] Hixon M A, Johnson D W, Sogard S M. BOFFFFs: on the importance of conserving old-growth age structure in fishery populations. *ICES Journal of Marine Science*, 2014, 71(8):2171-2185.
- [26] Barneche D R, Robertson D R, White C R, Marshall D J. Fish reproductive-energy output increases disproportionately with body size. *Science*, 2018, 360(6389):642-645.
- [27] Bohnsack J A. The Potential of Marine Fishery Reserves for Reef Fish Management in the US Southern Atlantic. NOAA Technical Memorandum NMFS-SEFRC-261. 1990.
- [28] Bobko S J, Berkeley S A. Maturity, ovarian cycle, fecundity, and age-specific parturition of black rockfish (*Sebastes melanops*). *Fishery Bulletin*, 2004, 102(3):418-429.
- [29] Song J J, Wu H Y, Liu K K, Chi W D, Ge S S, Zhang Z P, Wang M Q, Yu Y, Yu D D. Observation and analysis of morphology abnormalities in development of *Oryzias melastigma* embryos. *Journal of Oceanology and Limnology*, 2021, DOI:https://doi.org/10.1007/s00343-020-0227-y.
- [30] Trippel E A, Kjesbu O S, Solemdal P. Effects of adult age and size structure on reproductive output in marine fishes//Chambers R C, Trippel E A, eds. *Early Life History and Recruitment in Fish Populations*. Dordrecht:Springer, 1997:31-62.
- [31] Mehault S, Domínguez-Petit R, Cerviño S, Saborido-Rey F. Variability in total egg production and implications for management of the southern stock of European hake. *Fisheries Research*, 2010, 104(1/3):111-122.
- [32] Döring J, Hauss H, Haslob H. Spatial and seasonal variability in reproductive investment of Baltic sprat. *Fisheries Research*, 2018, 204:49-60.
- [33] Berkeley S A, Chapman C, Sogard S M. Maternal age as a determinant of larval growth and survival in a marine fish, *Sebastes melanops*. *Ecology*, 2004, 85(5):1258-1264.
- [34] Brooks S, Tyler C R, Sumpter J P. Egg quality in fish: what makes a good egg? *Reviews in Fish Biology and Fisheries*, 1997, 7(4):387-416.
- [35] Trippel E A. Egg size and viability and seasonal offspring production of young Atlantic cod. *Transactions of the American Fisheries Society*, 1998, 127(3):339-359.
- [36] Carr J P, Kaufman L. Estimating the importance of maternal age, size, and spawning experience to recruitment of Atlantic cod (*Gadus morhua*). *Biological Conservation*, 2009, 142(3):477-487.
- [37] Marshall C T, O'Brien L, Tomkiewicz J, Köster F W, Kraus G, Marteinsdottir G, Morgan M J, Saborido-Rey F, Blanchard J L, Secor D H, Wright P J, Mukhina N V, Björnsson H. Developing alternative indices of reproductive potential for use in fisheries management: Case studies for stocks spanning an information gradient. *Journal of Northwest Atlantic Fishery Science*, 2003, 33:161-190.
- [38] Lambert Y. Why should we closely monitor fecundity in marine fish populations? *Journal of Northwest Atlantic Fishery Science*, 2008, 41:93-106.
- [39] Birkeland C, Dayton P K. The importance in fishery management of leaving the big ones. *Trends in Ecology & Evolution*, 2005, 20(7):356-358.
- [40] Erisman B E, Buckhorn M L, Hastings P A. Spawning patterns in the leopard grouper, *Mycteroperca rosacea*, in comparison with other aggregating groupers. *Marine Biology*, 2007, 151(5):1849-1861.

- [41] Lauth R R, Guthridge J L, Cooper D W, McEntire S W. Behavioral ecology of color patterns in Atka mackerel. *Marine and Coastal Fisheries Dynamics, Management, and Ecosystem Science*, 2010, 2(1):399-411.
- [42] Lauth R R, Guthridge J, Nichol D, McEntire S W, Hillgruber N. Timing and duration of mating and brooding periods of Atka mackerel (*Pleurogrammus monopterygius*) in the North Pacific Ocean. *Fishery Bulletin*, 2007, 105(4):560-570.
- [43] Lauth R R, McEntire S W, Zenger Jr H H. Geographic distribution, depth range, and description of Atka mackerel *Pleurogrammus monopterygius* Nesting Habitat in Alaska. *Alaska Fishery Research Bulletin*, 2007, 12(2):165-186.
- [44] Devlin R H, Nagahama Y. Sex determination and sex differentiation in fish: an overview of genetic, physiological, and environmental influences. *Aquaculture*, 2002, 208(3/4):191-364.
- [45] Fishelson L. Protogynous sex reversal in the fish *Anthias squamipinnis* (Teleostei, Anthiidae) regulated by the presence or absence of a male fish. *Nature*, 1970, 227(5253):90-91.
- [46] de Mitcheson Y S, Craig M T, Bertoncini A A, Carpenter K E, Cheung W W L, Choat J H, Cornish A S, Fennessy S T, Ferreira B P, Heemstra P C, Liu M, Myers R F, Pollard D A, Rhodes K L, Rocha L A, Russell B C, Samoilys M A, Sancianco J. Fishing groupers towards extinction: a global assessment of threats and extinction risks in a billion dollar fishery. *Fish and Fisheries*, 2013, 14(2):119-136.
- [47] Scheffer M, Carpenter S, Foley J A, Folke C, Walker B. Catastrophic shifts in ecosystems. *Nature*, 2001, 413(6856):591-596.
- [48] McMenamin S K, Parichy D M. Metamorphosis in teleosts. *Current Topics in Developmental Biology*, 2013, 103:127-165.
- [49] 阙江龙, 徐兆礼, 孙鲁峰. 北部湾西北部饵料浮游动物季节变化及其与鱼卵、仔稚鱼的关系. *中国水产科学*, 2015, 22(5):1027-1035.
- [50] Bagenal T B. The interrelation of the size of fish eggs, the date of spawning and the production cycle. *Journal of Fish Biology*, 1971, 3(2):207-219.
- [51] Bonaldo R M, Hoey A S, Bellwood D R. The ecosystem roles of parrotfishes on tropical reefs//Hughes R N, Hughes D J, Smith I P, eds. *Oceanography and Marine Biology: An Annual Review*, Volume 52. Boca Raton: CRC Press, 2014:81-132.
- [52] Bruggemann J H, Van Kessel A M, Van Rooij J M, Breeman A M. Bioerosion and sediment ingestion by the Caribbean parrotfish *Scarus vetula* and *Sparisoma viride*: implications of fish size, feeding mode and habitat use. *Marine Ecology Progress Series*, 1996, 134:59-71.
- [53] Gaston K J, Blackburn T M. Range size-body size relationships: evidence of scale dependence. *Oikos*, 1996, 75(3):479-485.
- [54] Luiz O J, Allen A P, Robertson D R, Floeter S R, Kulbicki M, Vigliola L, Becheler R, Madin J S. Adult and larval traits as determinants of geographic range size among tropical reef fishes. *Proceedings of the National Academy of Sciences of the United States of America*, 2013, 110(41):16498-16502.
- [55] Roberts C M. Connectivity and management of Caribbean coral reefs. *Science*, 1997, 278(5342):1454-1457.
- [56] Saenz-Agudelo P, Jones G P, Thorrold S R, Planes S. Connectivity dominates larval replenishment in a coastal reef fish metapopulation. *Proceedings of the Royal Society B: Biological Sciences*, 2011, 278(1720):2954-2961.
- [57] Saenz-Agudelo P, Jones G P, Thorrold S R, Planes S. Patterns and persistence of larval retention and connectivity in a marine fish metapopulation. *Molecular Ecology*, 2012, 21(19):4695-4705.
- [58] Jonsson B, Jonsson N. Partial migration: niche shift versus sexual maturation in fishes. *Reviews in Fish Biology and Fisheries*, 1993, 3(4):348-365.
- [59] Chapman B B, Skov C, Hulthén K, Brodersen J, Nilsson P A, Hansson L A, Brönmark C. Partial migration in fishes: definitions, methodologies and taxonomic distribution. *Journal of Fish Biology*, 2012, 81(2):479-499.
- [60] Sgrò C M, Lowe A J, Hoffmann A A. Building evolutionary resilience for conserving biodiversity under climate change. *Evolutionary Applications*, 2011, 4(2):326-337.
- [61] Gordoa A, Duarte C M. Size-dependent spatial distribution of hake (*Merluccius capensis* and *Merluccius paradoxus*) in Namibian Waters. *Canadian Journal of Fisheries and Aquatic Sciences*, 1991, 48(11):2095-2099.
- [62] Kwak S N, Baek G W, Klumpp D W. Comparative feeding ecology of two sympatric greenling species, *Hexagrammos otakii* and *Hexagrammos agrammus* in Eelgrass *Zostera marina* Beds. *Environmental Biology of Fishes*, 2005, 74(2):129-140.
- [63] 纪东平. 荣成俚岛斑头鱼和大泷六线鱼的渔业资源生物学研究[D]. 青岛: 中国海洋大学, 2014.
- [64] Munehara H, Kanamoto Z, Miura T. Spawning behavior and interspecific breeding in three Japanese greenlings (hexagrammidae). *Ichthyological Research*, 2000, 47(3/4):287-292.
- [65] Rouyer T, Sadykov A, Ohlberger J, Stenseth N C. Does increasing mortality change the response of fish populations to environmental fluctuations? *Ecology Letters*, 2012, 15(7):658-665.
- [66] Walther G R, Post E, Convey P, Menzel A, Parmesan C, Beebee T J C, Fromentin J M, Hoegh-Guldberg O, Bairlein F. Ecological responses to recent climate change. *Nature*, 2002, 416(6879):389-395.
- [67] Pauly D, Christensen V, Guénette S, Pitcher T J, Sumaila U R, Walters C J, Watson R, Zeller D. Towards sustainability in world fisheries.

- Nature, 2002, 418(6898):689-695.
- [68] Pimm S L, Ayres M, Balmford A, Branch G, Brandon K, Brooks T, Bustamante R, Costanza R, Cowling R, Curran L M, Dobson A, Farber S, da Fonseca G A B, Gascon C, Kitching R, McNeely J, Lovejoy T, Mittermeier R A, Myers N, Patz J A, Raffle B, Rapport D, Raven P, Roberts C, Rodríguez J P, Rylands A B, Tucker C, Safina C, Samper C, Stiassny M L J, Supriatna J, Wall D H, Wilcove D. Can we defy nature's end? Science, 2001, 293(5538):2207-2208.
- [69] Gaines S D, White C, Carr M H, Palumbi S R. Designing marine reserve networks for both conservation and fisheries management. Proceedings of the National Academy of Sciences of the United States of America, 2010, 107(43):18286-18293.
- [70] Edwards C T T, Plagányi É E. Protecting old fish through spatial management: is there a benefit for sustainable exploitation? Journal of Applied Ecology, 2011, 48(4):853-863.
- [71] Waples R S, Audzijonyte A. Fishery-induced evolution provides insights into adaptive responses of marine species to climate change. Frontiers in Ecology and the Environment, 2016, 14(4):217-224.
- [72] van Rijn I, Buba Y, DeLong J, Kiflawi M, Belmaker J. Large but uneven reduction in fish size across species in relation to changing sea temperatures. Global Change Biology, 2017, 23(9):3667-3674.
- [73] Lacroix G, Barbut L, Volckaert F A M. Complex effect of projected sea temperature and wind change on flatfish dispersal. Global Change Biology, 2018, 24(1):85-100.
- [74] Tsukamoto K. Oceanic biology: spawning of eels near a seamount. Nature, 2006, 439(7079):929.
- [75] 金显仕, 窦硕增, 单秀娟, 王震宇, 万瑞景, 卞晓东. 我国近海渔业资源可持续产出基础研究的热点问题. 渔业科学进展, 2015, 36(1): 124-131.