

DOI: 10.5846/stxb201309082232

王少琴, 许柳雄, 王学昉, 朱国平. 人工集鱼装置对热带金枪鱼类摄食模式的影响研究进展. 生态学报, 2014, 34(13): 3490-3498.  
Wang S Q, Xu L X, Wang X F, Zhu G P. A review of impacts of fish aggregation devices (FADs) on feeding patterns for tropical tunas. Acta Ecologica Sinica, 2014, 34(13): 3490-3498.

## 人工集鱼装置对热带金枪鱼类摄食模式的影响研究进展

王少琴<sup>1</sup>, 许柳雄<sup>1,2,3,4,\*</sup>, 王学昉<sup>1,2,3,4</sup>, 朱国平<sup>1,2,3,4</sup>

(1. 上海海洋大学海洋科学学院, 上海 201306; 2. 国家远洋渔业工程技术研究中心, 上海 201306;  
3. 大洋渔业资源可持续开发省部共建教育部重点实验室, 上海 201306; 4. 远洋渔业协同创新中心, 上海 201306)

**摘要:** 热带金枪鱼类具有聚集在漂浮物体周围的行为特性, 形成的集群表现稳定, 可捕性较高。以此特性, 金枪鱼围网渔业研制并投放了大量的人工集鱼装置(Fish Aggregation Device, FAD)用于聚集并捕捞金枪鱼。然而, 大规模出现的 FAD 会使某些海域海面漂浮物的密度迅速增加, 从而在一定程度上人为地改变了金枪鱼的表层栖息环境, 对金枪鱼种群具有一系列可能的潜在负面影响, 摄食模式的改变就是其中之一。归纳并综合了近年来国内外关于 FAD 对金枪鱼类摄食模式影响的相关研究, 从摄食行为、日摄食量、饵料种类与组成以及生态位宽度 4 个方面对比了随附于 FAD 的金枪鱼和自由状态下同类的不同, 发现大多情况下 FAD 的存在会使金枪鱼的摄食模式发生一定的改变。最后, 归纳了过往实验存在的不足, 对今后研究的发展方向进行了展望。

**关键词:** 金枪鱼围网; 人工集鱼装置; 金枪鱼类; 摄食模式; 生态影响

## A review of impacts of fish aggregation devices (FADs) on feeding patterns for tropical tunas

WANG Shaoqin<sup>1</sup>, XU Liuxiong<sup>1,2,3,4,\*</sup>, WANG Xuefang<sup>1,2,3,4</sup>, ZHU Guoping<sup>1,2,3,4</sup>

1 College of Marine Sciences, Shanghai Ocean University, Shanghai 201306, China

2 National Engineering Research Center for Oceanic Fisheries, Ministry of Education, Shanghai 201306, China

3 Ministry of Education Key Laboratory of Sustainable Exploitation of Oceanic Fisheries Resources, Shanghai 201306, China

4 Collaborative Innovation Center for National Distant-water Fisheries, Shanghai 201306, China

**Abstract:** Tropical tunas are a kind of highly migratory oceanic fishes whose food organisms in perched waters are relatively scarce and are distributed as patches. The tunas are obliged to swim quickly in response to dynamic changes of its prey because of hardly lasting aggregation of food organisms. Tropical tunas are inclined to form natural aggregations which are usually referred to as free swimming schools. In early days, however, the artisanal fisherman noted that the tropical tunas have the habit of gathering around natural floating objects such as logs, seaweed mats, branches and palm leaves, forming stable aggregations, termed as floating-objects-associated schools. They found that fishing was much efficient near these objects than in an open ocean. Tuna purse seine fisheries utilized this type of behavior to develop a great number of fish aggregation devices (FADs) for aggregating tuna and thus improve harvest efficiency. Two types of FADs are often used: drifting FADs (dFADs) and anchored FADs (aFADs). Since the first FAD deployments, FADs-based fishing technology had developed rapidly throughout the early 1990s, and FADs have been generally accepted as an effective mean to increase catch rates and reduce the energy consumption of purse seiners. The large-scale use of FADs, however, considerably

**基金项目:** 国家高技术研究发展计划(2012AA092302); 国家自然科学基金(41006106); 上海市青年科技启明星计划(11QA1403000); 上海海洋大学科技发展专项基金

收稿日期: 2013-09-08; 修订日期: 2014-04-18

\* 通讯作者 Corresponding author. E-mail: lxxu@shou.edu.cn

increases the density of floating objects in some waters, and in turn, to some extent, artificially changes the surface habitat of the tuna. This may impose a series of potentially negative effects on tuna populations, such as changes in patterns of aggregation, feeding pattern and migratory movement and the decline of physical conditions for the population. Of those mentioned-above side effects, changes in the feeding pattern may have more profound impacts on fish populations as it exerts a direct effect on key life history processes, such as growth and reproduction. In the past 30 years, many studies have been conducted to evaluate whether and how FADs affect the feeding pattern. However, the results from these studies are still inconclusive and contradictory.

This review summarizes recent studies in regard to the tuna feeding patterns as influenced by FADs. We compare differences of feeding behavior, daily rations, the types of prey and ecological niche width between FAD-associated and free swimming tuna schools. It implies that, FADs tend to alter the large-scale migratory movements to some extents, but not the local and small-scale migratory movements. FADs may also influence the stomach contains and the rates of empty stomach. Thus, FADs, in most cases, do in fact change feeding pattern and behavior. This review also identifies shortcomings in previous studies in their research methods and contents, and accordingly proposes new research approaches, such as the use of underwater video camera to observe the feeding behavior of tunas directly, take advantage of remaining stomach contents to rebuild diet composition for the estimation of the daily rations. Stable isotope analysis (SIA) can also help improve our understanding of trophic ecology for tunas. We also include a discussion on possible future research direction in evaluating impacts of FADs on feeding behavior for tunas.

**Key Words:** tuna purse seine fishery; fish aggregation devices (FADs); tunas; feeding pattern; ecological impact

热带金枪鱼类栖息的大洋水域,具有饵料生物相对稀少且呈“斑块”状分布及促使饵料聚集的环境条件无法持久等特点,因此金枪鱼类需要根据饵料对象的动态变化快速游动<sup>[1]</sup>。在游动过程中,除因海域生物环境因素自然集结,形成所谓的“自由鱼群”形式外,也如某些中上层鱼类一样,金枪鱼会被漂浮物体吸引而聚集成“漂浮物随附群”<sup>[2-3]</sup>。

漂浮物随附群被围捕时基本处于稳定状态,因此可捕性较高<sup>[4]</sup>。但由于自然界中天然漂浮物数量不足及分布不均,因此金枪鱼围网渔业制造并投放了大量的“人工集鱼装置(FAD)”用于聚集捕捞金枪鱼<sup>[5]</sup>。依水深限制,FAD 又分为漂流 FAD 和锚泊 FAD。这些短时间内大量出现的 FAD 增加了海面漂浮物的密度,被认为人为改变了金枪鱼类的表层栖息环境,并给金枪鱼种群带来了潜在的生态影响<sup>[2,6]</sup>,如集群形式的改变<sup>[7-8]</sup>、摄食模式的变化<sup>[9-11]</sup>、种群健康状况的衰退以及洄游路径的变动<sup>[12]</sup>等。

在诸多可能的潜在影响中,FAD 是否改变金枪鱼的摄食活动将直接影响到其某些生活史过程,如生长、繁殖等,因此在系列研究中应优先考虑该问题<sup>[6]</sup>。在过去的 30 多年中,科学界针对这一问题开

展了大量的研究,但由于种种限制,迄今尚未得出一个各方均能接受或认可的研究结论。本文旨在对历年来的相关研究进行整理,归纳确定的结论,梳理存在的不足,展望改进的方向,从而为量化评估 FAD 对于金枪鱼摄食模式的生态影响提供参考。

## 1 FAD 对金枪鱼摄食行为的影响

### 1.1 水平移动行为

#### 1.1.1 大尺度洄游

金枪鱼类的水平洄游活动根据距离的长短可以分成不同的级别,其中索饵洄游规模最大,饵料丰度就是这个级别重要的限制因素,如西太平洋的沙丁鱼(*Sardina pilchardus*)丰度能够影响到东太平洋向西洄游的金枪鱼比例<sup>[13]</sup>。然而,许多个体行为学实验和捕捞经验均表明,金枪鱼有时可聚集在 FAD 周围长达数天至数十天之久<sup>[14-17]</sup>。虽然这些文献尚无法证明这些鱼群是否从未离开过 FAD,但至少表明它们在这一时期内放弃了大洋尺度上的洄游<sup>[15]</sup>。此外,有研究发现,和自由鱼群中的同类相比,随附于 FAD 的金枪鱼在洄游方向和位移率方面均存在明显的差异<sup>[16]</sup>。这些发现均倾向于支持 FAD 的存在会潜在影响金枪鱼的索饵洄游,而这种大尺度的

迁徙模式正是它们适应大洋生境的行为表现之一。

### 1.1.2 局部洄游

在小尺度级别上,FAD 的出现会使金枪鱼的行为发生更加细微的变化,而这些行为往往又与摄食活动紧密相关:在移动方向方面,Dagorn 等<sup>[18]</sup>对大洋水域中 4 尾自由状态的大眼金枪鱼(*Thunnus obesus*)进行不间断的跟踪,发现其中 3 尾始终朝着一个方向水平游动,从未改变方向;当 FAD 存在时,金枪鱼则会不断改变方向,重复着游向和离开 FAD 的过程。这个反复过程可能正是因为 FAD 周围并不能提供足够的饵料保障,所以迫使鱼群为觅食开展更大范围的搜索。鱼群的聚散模式似乎证实了这个猜测,大部分资料表明自由集群的金枪鱼昼间分散摄食,夜间重新聚集成群<sup>[19-21]</sup>。在 FAD 附近,许多研究<sup>[10,22-24]</sup>观察到金枪鱼变为昼间聚集在 FAD 周围,夜晚离开进行觅食,直到次日白昼再度返回 FAD 的行为规律<sup>[25-26]</sup>。Schaefer 和 Fuller<sup>[27]</sup>监测了锚泊浮标周围的大眼金枪鱼和鲣鱼(*Katsuwonus pelamis*)的行动轨迹,其结果较为详细地表现了这一聚散过程:金枪鱼在午后朝顺流方向,聚集在浮标之下;傍晚以后,金枪鱼开始分散在浮标周围,以逆流方向捕食深海散射层中的生物,直到次日黎明前才停止摄食,并重新聚集到浮标周围。Holland 等<sup>[10]</sup>对这种现象进行了解释,认为随附于 FAD 的金枪鱼的摄食活动与它们的最佳觅食策略密切相关,白昼间 FAD 周围会聚集中上层鱼类及其它小型生物,促使金枪鱼处于食物密度增强的水域,而夜晚金枪鱼离

开 FAD 游向较深水层则是为了摄食在夜间进行垂直移动的种类。

针对这个观点,另一些研究则认为 FAD 随附群的摄食活动和自由鱼群并不存在任何差异<sup>[28-30]</sup>。Mitsunaga 等<sup>[31]</sup>通过标志放流黄鳍金枪鱼(*Thunnus albacores*)幼鱼发现,被标记的幼鱼白天会围绕着 FAD 进行短距离的水平运动,在夜间则聚集在 FAD 周围;Schaefer 和 Fuller<sup>[27]</sup>对东太平洋随附于 FAD 的大眼金枪鱼和鲣鱼进行观察后发现,昼间两种金枪鱼均四处分散,离开 FAD 进行短程的水平移动(大眼金枪鱼维持在 FAD 附近 2 km 以内),而在夜间则与其它金枪鱼一起重新返回 FAD 之下。这些研究普遍支持金枪鱼不会在夜间进行捕食,倾向认为 FAD 并不会影响金枪鱼小范围内的摄食活动。

### 1.2 垂直移动行为

FAD 附近的水域有时并不存在足够的饵料生物以满足大型金枪鱼集群的摄食需要,这就可能迫使它们离开 FAD,下潜到较深的水层进行觅食<sup>[14]</sup>,因此一些个体行为学研究开始聚焦 FAD 的存在是否会使金枪鱼的垂直移动深度发生改变。如表 1 所示<sup>[10, 22, 27, 31-33]</sup>,自由集群的金枪鱼通常栖息在较深的水层<sup>[10, 32-33]</sup>,有时甚至下潜到数 km 水深栖息<sup>[34-35]</sup>,而 FAD 随附群分布的垂直水深则相对较浅,一般在近表水域活动<sup>[22, 31]</sup>。从这一角度来说,FAD 的存在可能改变了金枪鱼的垂直分布范围,使它们聚集在较浅的水层。

表 1 金枪鱼 FAD 随附群与自由鱼群垂直移动深度的对比

Table 1 The comparison of vertical movement depth of tunas between FAD-associated and unassociated schools

文献 Reference	研究方法 Research method	海域 Sea area	自由鱼群 Free swimming schools	FAD 随附群 FAD-associated schools
[10]	超声波遥测	夏威夷岛附近水域	昼间 85 m	昼间 59 m
[32]	档案标记	夏威夷岛	300—500 m	0—100 m
[33]	档案标记	太平洋东部	昼间平均 183 m, 夜间平均 34 m	昼间 33—37 m, 夜间 21—25 m
[22]	超声波标记	科摩罗群岛水域	—	昼间 70—110 m, 夜间 40—70 m
[27]	超声波遥测	太平洋东部赤道水域	—	昼间 0—50 m, 夜间 100—150 m
[31]	超声波遥测	菲律宾群岛水域	—	昼间平均 20.0 m, 夜间平均 11.2 m

另一方面,金枪鱼下潜的水深又与一天中所处的时段有关:大量的超声波遥测追踪实验表明,金枪

鱼在昼间分布的垂直深度明显深于夜间<sup>[9, 36-37]</sup>,利用档案标记追踪的实验也有相同的结论<sup>[31, 38]</sup>。针

对 FAD 下方大眼金枪鱼垂直移动行为的研究发现<sup>[34, 39]</sup>, 大眼金枪鱼一般在黎明后下潜至 200 m 以深的深散射层, 追踪和捕食饵料生物, 在黄昏后重新聚拢在 FAD 周围<sup>[40]</sup>。这种离开随附物体深潜捕食小型饵料的行为被认为是为了定期补充食物的来源, 大眼金枪鱼在这方面尤为明显<sup>[14]</sup>。但它们并非在所有情况下均会表现出更深的垂直下潜, 这可能还与漂浮物的类型有关。Schaefer 和 Fuller<sup>[27]</sup>对随附于锚泊浮标和漂流船舶的大眼金枪鱼和鲣鱼的垂直移动轨迹进行比较发现, 浮标下方的大眼金枪鱼的垂直分布较鲣鱼更深; 而随附于船舶时, 结果则相反。这种行为表现的差异可能是由于聚集在漂流物体和锚泊物体下的生物种类组成有所不同所致。

### 1.3 随附行为

金枪鱼对 FAD 表现出的随附行为被认为与摄食活动有关联性, 因此一些假说从摄食的角度出发解释金枪鱼向漂流物聚集的动机<sup>[2, 15]</sup>: 譬如“流木指示物”假说认为天然流木常汇集于高生产力的海洋锋面。因此, 流木(或漂流物)本身虽然不能聚集或产生大量的饵料生物, 但它们是高生产力区域的指示物, 鱼类随附于漂浮物的行为是在进化过程中形成的“将这些指示物与富饶水域相联系”的本能; “饵料供应”假说则认为单个或小群的捕食者(如鲯鳅(*Coryphaena hippurus*)、鲨鱼及旗鱼等)向聚集漂流物下的动机就是为了捕食其它的随附鱼类<sup>[41-42]</sup>; 而“休息点”假说是“饵料供应”假说的一种延续, 它认为捕食者每次捕食完随附鱼类, 需要停留在漂流物附近休息, 以便下一次的捕食行动<sup>[43]</sup>。深入了解

金枪鱼随附行为的确切动机极为重要, 因为这能够帮助我们进一步理解 FAD 的大量投放对于金枪鱼摄食模式的潜在影响。

## 2 FAD 下方金枪鱼摄食量变化

金枪鱼在 FAD 附近能够摄食到的食物数量, 是 FAD 影响金枪鱼摄食活动的最为直接的证据, 因此大量的研究选用空胃率作为表征金枪鱼摄食强度的指标, 用于比较两种鱼群之间的差异。如表 2 所示<sup>[16, 25, 44-48]</sup>, 根据海域和金枪鱼种类的不同, 空胃率变化的幅度十分明显: 如在中西太平洋, 漂流 FAD 下鲣鱼的空胃率高达 94.5%, 而在印度洋西部海域, 漂流 FAD 下鲣鱼的空胃率为 52%, 黄鳍金枪鱼为 19.8%, 但毫无例外的是, 它们均要大幅高于同海域自由鱼群中的同类。另一个用于表征摄食强度的指标是胃饱满度, 考虑到金枪鱼自身大小对于摄食能力的影响, 将金枪鱼胃中食物重量占金枪鱼自身体重的百分比作为金枪鱼的摄食量。对于自由鱼群的摄食量, 研究结果表明因水域而异: Ménard 和 Marchal<sup>[49]</sup>发现, 大西洋金枪鱼的摄食量为 7%; Olson 和 Boggs<sup>[50]</sup>估计, 太平洋东部黄鳍金枪鱼的摄食量为 3.9%; 而 Ménard 等<sup>[44]</sup>对比了两类鱼群的摄食量, 自由鱼群中的大眼金枪鱼、鲣鱼和黄鳍金枪鱼的日摄食量分别为 4.82%、5.51% 和 16.03%, 而 FAD 随附群中的同类则分别为 1.27%、1.16% 和 0.89%。由此可见, 虽然摄取的食物相对于个体自身的体重较小, 但自由鱼群的摄食量仍然明显高于随附鱼群。

表 2 随附于和非随附 FAD 的金枪鱼的空胃率

Table 2 The proportion of empty stomach for tuna FAD-associated versus non-FAD-associated

来源 Source	FAD 类型 FAD type	海域 Study area	自由鱼群 free swimming schools	FAD 随附群 FAD-associated schools
[16]	漂流 FAD	大西洋和印度洋水域	鲣鱼 13% 黄鳍金枪鱼 7%	鲣鱼 74% 黄鳍金枪鱼 49%
[44]	漂流 FAD	大西洋赤道水域	25%	85%
[45]	漂流 FAD	印度洋西部水域	鲣鱼 0% 黄鳍金枪鱼 0%	鲣鱼 52% 黄鳍金枪鱼 19.8%
[46]	漂流 FAD	印度洋西部赤道水域	鲣鱼 15%	鲣鱼 70%
[47]	漂流 FAD	中西太平洋水域	鲣鱼 33.2%	鲣鱼 94.5%
[25]	锚泊 FAD	美属萨摩亚水域	1.5%	1%
[48]	锚泊 FAD	夏威夷周围水域	5.4%	33.7%

然而, 一些学者反对简单地以空胃率或胃饱满

度指数作为 FAD 降低金枪鱼摄食强度的证据, 理由

有两点:一是捕捞时间的不同<sup>[16]</sup>,漂流 FAD 集群大多为黎明前捕获,而自由群基本在白天捕获。这样来自于 FAD 集群的样本可能缺乏足够的摄食时间,从而导致摄食不足,而且 FAD 集群遭到捕捞时已经距离午夜的摄食高峰期有数小时之久,考虑到金枪鱼能够非常快速的消化食物,在捕获时已经将胃中的饵料消化殆尽,自然会出现高空胃率结果。针对这个观点,Ménard 等<sup>[44]</sup>比较分析了昼间 FAD 下不同时段金枪鱼的胃饱满度,结果显示金枪鱼的空胃率总是维持在较高的水平,并没有因时间段不同而出现明显的变化。但 Schaefer 和 Fuller<sup>[33]</sup>仍坚持,若不收集夜间不同时段的样本,就很难全面地比较 FAD 集群和自由鱼群的摄食状况。

另一个观点是体长的不同,因为 FAD 集群中往往拥有更多的小型个体<sup>[16, 44]</sup>,而小型个体的摄食能力通常较弱,这也直接导致集群的摄食状况较差。但是一些研究中所用的胃饱满度作为一个相对性指数,事实上已经将发育阶段对于摄食能力的影响加以考虑,因此这一观点似乎并不充分。

在另一个方面,相对于漂流 FAD 集群,锚泊 FAD 集群的空胃率与自由鱼群的差异并不特别明显<sup>[25, 43]</sup>,甚至在一些水域还要低于自由鱼群中的同类,如 Brock<sup>[48]</sup>和 Buckley 等<sup>[51]</sup>发现在法属波里尼西亚、夏威夷群岛和菲律宾群岛等地随附于锚泊 FAD 的黄鳍金枪鱼就比自由状态下的同类的胃中含有更多的食物。出现这种现象的原因可能是因为锚泊 FAD 一般设置在较浅的沿岸海域,本身的饵料水平就高于漂流 FAD 所处的大洋海域。

### 3 FAD 下金枪鱼饵料组成变化

通过对于金枪鱼胃含物中饵料组成比例的分析,可以了解金枪鱼类食性的变化,运用这种方法,还能进一步地探究 FAD 的出现对于金枪鱼摄食策略的影响。在自由鱼群方面,一些研究认为它们主要摄食中上层的小型集群生物<sup>[47]</sup>,譬如布氏侧带小公鱼 (*Stolephorus buccaneeri*)、智利串光鱼 (*Vinciguerria nimbaria*)、沙丁鱼 (*Sardina pilchardus*) 和磷虾类 (Euphausiids) 等。这种现象符合食物链能量流动的观点,因为金枪鱼自由鱼群本身就是具有一定生物量规模的集群,在某一地点能够一次性地捕食到一定生物量的饵料集群,将最大限度地保障鱼群的摄食需求,因此对于这一类小型饵料生物集群的偏好正是自由鱼群的最佳摄食策略。另一方面,金枪鱼作为一种机会主义的捕食者<sup>[52]</sup>,在单一饵料资源不充足的情况下,也会摄食其它的饵料生物,如 Buckley 和 Miller<sup>[25]</sup>发现,美属萨摩亚水域自由鱼群的黄鳍金枪鱼胃中,胃含物重量的四分之三为鱼类,其余部分由软体动物和甲壳类构成;Brock<sup>[48]</sup>对于夏威夷海域的黄鳍金枪鱼胃含物分析则显示,饵料种类按照频次出现的顺序为鱼类(48%)、甲壳纲(42%)和头足纲(10%)。相比之下,FAD 随附群中金枪鱼偏向采取随机性的捕食策略,它们的胃含物通常呈现出多样性,大致包含鱼类、甲壳类和头足类三个大类,类似于自由鱼群应对饵料不足的情况(表 3<sup>[25, 44, 46-48, 53-54]</sup>)。

表 3 随附于 FAD 与自由鱼群的金枪鱼的主要饵料及比例

Table 3 The main prey and ration of tuna FAD-associated versus unassociated schools

来源 Source	区域 Study area	金枪鱼种类 Tuna species	自由鱼群 Free swimming school	FAD 随附群 FAD-associated schools
[47]	中西太平洋	鲣鱼	布氏侧带小公鱼	—
[53]	大西洋东部水域	鲣鱼、大眼金枪鱼和黄鳍金枪鱼	智利串光鱼	—
[54]	太平洋东部赤道水域	鲣鱼、大眼金枪鱼和黄鳍金枪鱼	布氏侧带小公鱼	—
[25]	美属萨摩亚水域	黄鳍金枪鱼	鱼类 75.8%、软体动物 17.4%、甲壳类 4.7%	鱼类 90%、软体动物 3.1%、甲壳纲 5.5%
[44]	大西洋赤道水域	鲣鱼、大眼金枪鱼和黄鳍金枪鱼	串光鱼(63%)和甲壳类	串光鱼(49%)和头足类
[46]	印度洋西部赤道水域	鲣鱼、大眼金枪鱼和黄鳍金枪鱼	鲣鱼;甲壳类(95%)	鲣鱼;甲壳类; 黄鳍金枪鱼; 鱼; 头足类(93%)
[48]	夏威夷岛附近水域	黄鳍金枪鱼	鱼类 66%、甲壳类 28%、头足类 6%	鱼类 15%、甲壳类 85%、头足类 0.2%

FAD 集群倾向于捕食多样化的饵料,可能是因为渔民投放 FAD 时依潮流的走势,而非栖息地的饵料水平<sup>[16]</sup>,因此随附的个体会被 FAD 被动地分配到一些不良的栖息环境,从而被迫采取随机性的捕食策略以停留在 FAD 周围。这一观点也可从饵料分布的水层得到佐证,一些研究发现随附群的金枪鱼的主要食物是海洋中上层生物<sup>[55-56]</sup>。这一现象说明相对于自由鱼群通过扩展水平空间方向搜寻饵料的策略,FAD 群中的个体是通过向垂直方向拓展觅食空间以维持随附于 FAD 的行为。

#### 4 FAD 下金枪鱼生态位宽度变化

生态位宽度衡量了一个物种所能利用的各种资源的总和,当资源的可利用性减少时,一般会使生态位宽度增加,例如在食物供应不足的环境中,消费者将被迫摄食次等摄食对象,而在食物供应充足的环境中,捕食者仅摄食最习惯摄食的少数被捕食者<sup>[57]</sup>。因此,营养生态位宽度为评估 FAD 对于金枪鱼摄食模式的影响提供了一个崭新的视角。对于自由鱼群和 FAD 随附群而言,虽然它们的主要饵料均大致分为鱼类、甲壳类和头足类三种,但自由鱼群通常偏好单一物种形成的规模生物量,譬如索马里水域<sup>[58]</sup>和印度洋西部<sup>[59]</sup>表层的黄鳍金枪鱼均以一种口足类生物 *Natostylla investigatoris* 为食;中西太平洋的鲣鱼偏好中上层的小型鳀科鱼类集群<sup>[45]</sup>;印度洋西部赤道水域的鲣鱼以摄食虾蛄为主<sup>[46]</sup>。相比之下,FAD 周围的个体则会尽可能地利用水域中可得的饵料资源<sup>[59-60]</sup>:在 Potier 等<sup>[46]</sup>的观察中,FAD 下的鲣鱼除了摄食虾蛄,还摄食鱼类等多种生物;Ménard 等<sup>[44]</sup>发现 FAD 下的金枪鱼胃中较少有相同种类的饵料,这些研究均说明 FAD 鱼群较自由鱼群有明显的摄食多样性。

另一个特点是随附鱼群中会发生同类相食的现象<sup>[61]</sup>,如黄鳍金枪鱼在捕食其它随附于漂流 FAD 的鱼类时也会吞食同类的幼鱼<sup>[44]</sup>;Buckley 和 Miller<sup>[25]</sup>也发现在菲律宾水域随附于 FAD 的大个体黄鳍金枪鱼比远离 FAD 的个体具有更高的同类相食概率<sup>[62]</sup>。这一现象可能也源于 FAD 无法为金枪鱼提供充足的食物来源,从而需要金枪鱼捕食平时并不摄食的食物以满足能量的需求,并最终导致生态位宽度扩大。

#### 5 展望

针对 FAD 是否改变了金枪鱼的摄食模式这个问题,虽然有大量的研究可供分析,但部分研究结论仍存在冲突,今后还需从深度(改进研究方法)和广度(扩展研究内容)两个层面继续研究:

(1)对于 FAD 周围金枪鱼摄食行为的研究,大多通过在金枪鱼中植入档案式标记牌(Archival tag)<sup>[38]</sup>以及利用超声波遥感(Ultrasonic remote sensing)技术<sup>[22, 63]</sup>得以实现,但植入过程有可能对鱼体造成伤害,致使试验个体产生异常行为,因此水下摄像机等设备的直接观察在未来具有一定的应用空间,而这点在实现上也相对较为简单直接。

(2)对于金枪鱼摄食量的量化,传统方法是对金枪鱼的胃含物进行肉眼观察,然后进行体重称量和体长测算。但在不同的捕获时刻或对于不同的饵料生物而言,饵料的消化程度也有不同,所以肉眼观测的饵料重量不能代表金枪鱼类真正的摄食量。因此,在计算金枪鱼的摄食量时,应考虑到金枪鱼的胃消化率,进而重建金枪鱼的初始摄食量。利用饵料的消化等级(一般分为四级)重建初始饵料的重量及体积<sup>[46, 64]</sup>,能在一定程度上克服摄食量的计算误差。因此,这种方法应在今后的研究中加以采用。

(3)对于金枪鱼营养生态位的判定,目前使用最多的方法是通过胃含物的种类及各种类的数量进行估算,进而推测金枪鱼在生态系统中的营养级。但 FAD 随附群中的许多个体在捕获时已将胃中的食物消化完毕,导致摄食状况无法获知,而一些生化手段如稳定同位素分析技术则可以弥补传统方法的不足。一般而言,碳(C)的稳定同位素比例( $\delta^{13}\text{C}$ )是食性来源的指标<sup>[65]</sup>,而氮(N)的稳定同位素比例( $\delta^{15}\text{N}$ )被视为消费者营养级的合适指标<sup>[66-68]</sup>,根据不同的组织代谢周期率,就可以获知鱼类在数周甚至数月内的相关营养信息<sup>[69]</sup>,进而弥补胃含物分析中食物被消耗而无法计算的缺陷。目前利用稳定同位素分析自由状态下金枪鱼的营养级的研究较多,但除了 Graham 等<sup>[56]</sup>利用碳、氮同位素研究夏威夷水域 FAD 下的黄鳍金枪鱼随个体发育的食性变化外,该技术在 FAD 对金枪鱼的摄食模式影响的研究中仍非常罕见。中西太平洋渔业委员会(Western and Central Pacific Fisheries Commission, WCPFC)科学委

员会在 2012 年举行的第八届常规会议上, 将“FAD 对于金枪鱼营养级变动的影响”作为优先性最高的项目之一加以支持<sup>[70]</sup>, 可见同位素技术在这一领域的应用潜力。

**致谢:** 美国缅因大学陈勇教授对本文写作给予帮助, 特此致谢。

### References:

- [ 1 ] Pitcher T J. The impact of pelagic fish behaviour on fisheries. *Scientia Marina*, 1995, 59(3/4) : 295-306.
- [ 2 ] Fréon P, Dagorn L. Review of fish associative behaviour: toward a generalisation of the meeting point hypothesis. *Reviews in Fish Biology and Fisheries*, 2000, 10(2) : 183-207.
- [ 3 ] Castro J J, Santiago J A, Santana-Ortega A T. A general theory on fish aggregation to floating objects: an alternative to the meeting point hypothesis. *Reviews in Fish Biology and Fisheries*, 2001, 11(3) : 255-277.
- [ 4 ] Itano D G. A summary of operational, technical and fishery information on WCPFC purse seine fisheries operating on floating objects // Scientific Committee Third Regular Session of Western and Central Pacific Fisheries Commission (WCPFC). Honolulu, United States of America, 2007.
- [ 5 ] Leroy B, Phillips J S, Nicol S, Pilling G M, Harley S, Bromhead D, Hoyle S, Cailliet S, Allain V, Hampton J. A critique of the ecosystem impacts of drifting and anchored FADs use by purse-seine tuna fisheries in the Western and Central Pacific Ocean. *Aquatic Living Resources*, 2013, 26(1) : 49-61.
- [ 6 ] Dagorn L, Bez N, Fauvel T, Walker E. How much do fish aggregating devices (FADs) modify the floating object environment in the ocean? *Fisheries Oceanography*, 2013, 22(3) : 147-153.
- [ 7 ] Fonteneau A. Sea mounts and tuna in the Tropical Eastern Atlantic. *Aquatic Living Resources*, 1991, 4(1) : 13-25.
- [ 8 ] Fonteneau A, Ariz J, Gaertner D, Nordstrom V, Pallares P. Observed changes in the species composition of tuna schools in the Gulf of Guinea between 1981 and 1999, in relation with the Fish Aggregating Devices fishery. *Aquatic Living Resources*, 2000, 13(4) : 253-257.
- [ 9 ] Josse E, Bach P, Dagorn L. Simultaneous observations of tuna movements and their prey by sonic tracking and acoustic surveys. *Hydrobiologia*, 1998, 371-372: 61-69.
- [ 10 ] Holland K N, Brill R W, Chang R K C. Horizontal and vertical movements of yellowfin and bigeye tuna associated with fish aggregating devices. *Fishery Bulletin*, 1990, 88(3) : 493-508.
- [ 11 ] Roger C. Relationships among yellowfin and skipjack tuna, their prey-fish and plankton in the tropical western Indian Ocean. *Fisheries Oceanography*, 1994, 3(2) : 133-141.
- [ 12 ] Marsac F, Fonteneau A, Ménard F. Drifting FADs used in tuna fisheries: an ecological trap? // Le Gall J Y, Cayré P, Taquet M. Pêche thonière et dispositifs de concentration de poissons. Actes Colloques - IFREMER, 2000, 28: 537-552.
- [ 13 ] Polovina J J. Decadal variation in the trans-Pacific migration of northern bluefin tuna (*Thunnus thynnus*) coherent with climate-induced change in prey abundance. *Fisheries Oceanography*, 1996, 5(2) : 114-119.
- [ 14 ] Dagorn L, Holland K N, Itano D G. Behavior of yellowfin (*Thunnus albacares*) and bigeye (*T. obesus*) tuna in a network of fish aggregating devices (FADs). *Marine Biology*, 2007, 151(2) : 595-606.
- [ 15 ] Bromhead D, Foster J, Attard R, Findlay J, Kalish J. A review of the impact of fish aggregating devices (FADs) on tuna fisheries. Final Report to Fisheries Resources Research Fund. Canberra, Australia: Australian Bureau of Rural Sciences, 2003.
- [ 16 ] Hallier J P, Gaertner D. Drifting fish aggregation devices could act as an ecological trap for tropical tuna species. *Marine Ecology Progress Series*, 2008, 353: 255-264.
- [ 17 ] Ohta I, Kakuma S. Periodic behavior and residence time of yellowfin and bigeye tuna associated with fish aggregating devices around Okinawa Islands, as identified with automated listening stations. *Marine Biology*, 2005, 146(3) : 581-594.
- [ 18 ] Dagorn L, Bach P, Josse E. Movement patterns of large bigeye tuna (*Thunnus obesus*) in the open ocean, determined using ultrasonic telemetry. *Marine Biology*, 2000, 136(2) : 361-371.
- [ 19 ] Maldeniya R. Food consumption of yellowfin tuna, *Thunnus albacares*, in Sri Lankan waters. *Environmental Biology of Fishes*, 1996, 47(1) : 101-107.
- [ 20 ] Ortega-García S, Galván-Magaña F, Arvizu-Martínez J. Activity of the Mexican purse seine fleet and the feeding habits of yellowfin tuna. *Ciencias Marinas*, 1992, 18(1) : 139-149.
- [ 21 ] Young J W, Lansdell M J, Campbell R A, Cooper S P, Juanes F, Guest M A. Feeding ecology and niche segregation in oceanic top predators off eastern Australia. *Marine Biology*, 2010, 157(11) : 2347-2368.
- [ 22 ] Cayré P. Behaviour of yellowfin tuna (*Thunnus albacares*) and skipjack tuna (*Katsuwonus pelamis*) around fish aggregating devices (FADs) in the Comoros Islands as determined by ultrasonic tagging. *Aquatic Living Resources*, 1991, 4(1) : 1-12.
- [ 23 ] Cayré P, Et Chabanne J. Marquage acoustique et comportement de thons tropicaux (albacore: *Thunnus albacares* et listao: *Katsuwonus pelamis*) au voisinage d'un dispositif concentrateur de poissons. *Oceanography Tropical*, 1986, 21(2) : 167-183.
- [ 24 ] Yonemori T. Study of tuna behavior, particularly their swimming depths, by the use of sonic tags. *Far Seas Fisheries Research Laboratory Newsletter*. Shimizu, 1982, 44: 1-5.
- [ 25 ] Buckley T W, Miller B S. Feeding habits of yellowfin tuna associated with fish aggregation devices in American Samoa.

- Bulletin of Marine Science, 1994, 55(2/3) : 445-459.
- [26] Marsac F, Cayré P. Telemetry applied to behaviour analysis of yellowfin tuna (*Thunnus albacares*, Bonnaterre, 1788) movements in a network of fish aggregating devices. *Hydrobiologia*, 1998, 371-372: 155-171.
- [27] Schaefer K M, Fuller D W. Behavior of bigeye (*Thunnus obesus*) and skipjack (*Katsuwonus pelamis*) tunas within aggregations associated with floating objects in the equatorial eastern Pacific. *Marine Biology*, 2005, 146(4) : 781-792.
- [28] Borodulina O D. Food composition of yellowfin tuna *Thunnus albacores*. *Journal of Ichthyology*, 1982, 21(6) : 38-40.
- [29] Dragovich A. The food of skipjack and yellowfin tunas in the Atlantic Ocean. *Fishery Bulletin*, 1970, 68(3) : 445-460.
- [30] Dragovich A, Potthoff T. Comparative study of food of skipjack and yellowfin tunas off the coast of West Africa. *Fishery Bulletin*, 1972, 70(4) : 1087-1110.
- [31] Mitsunaga Y, Endo C, Babaran R P. Schooling behavior of juvenile yellowfin tuna *Thunnus albacares* around a fish aggregating device (FAD) in the Philippines. *Aquatic Living Resources*, 2013, 26(1) : 79-84.
- [34] Boggs C H. Depth, capture time, and hooked longevity of longline-caught pelagic fish: timing bites of fish with chips. *Fishery Bulletin*, 1992, 90(4) : 642-658.
- [35] Hanamoto E. Effect of oceanographic environment on bigeye tuna distribution. *Bulletin of the Japanese Society of Fishery Oceanography*, 1987, 51(3) : 203-216.
- [32] Musyl M K, Brill R W, Boggs C H, Curran D S, Kazama T K, Seki M P. Vertical movements of bigeye tuna (*Thunnus obesus*) associated with islands, buoys, and seamounts near the main Hawaiian Islands from archival tagging data. *Fisheries Oceanography*, 2003, 12(3) : 152-169.
- [33] Schaefer K M, Fuller D W. Vertical movements, behavior, and habitat of bigeye tuna (*Thunnus obesus*) in the equatorial eastern Pacific Ocean, ascertained from archival tag data. *Marine Biology*, 2010, 157(12) : 2625-2642.
- [36] Block B A, Keen J E, Castillo B, Dewar H, Freund E V, Marcinek D J, Brill R W, Farwell C. Environmental preferences of yellowfin tuna (*Thunnus albacares*) at the northern extent of its range. *Marine Biology*, 1997, 130(1) : 119-132.
- [37] Brill R W, Block B A, Boggs C H, Bigelow K A, Freund E V, Marcinek D J. Horizontal movements and depth distribution of large adult yellowfin tuna (*Thunnus albacares*) near the Hawaiian Islands, recorded using ultrasonic telemetry: implications for the physiological ecology of pelagic fishes. *Marine Biology*, 1999, 133(3) : 395-408.
- [38] Schaefer K M, Fuller D W. Movements, behavior, and habitat selection of bigeye tuna (*Thunnus obesus*) in the eastern equatorial Pacific, ascertained through archival tags. *Fishery Bulletin*, 2002, 100(4) : 765-788.
- [39] Evans K, Langley A, Clear N P, Williams P, Patterson T, Sibert J, Hampton J, Gunn J S. Behaviour and habitat preferences of bigeye tuna (*Thunnus obesus*) and their influence on longline fishery catches in the western Coral Sea. *Canadian Journal of Fisheries and Aquatic Sciences*, 2008, 65(11) : 2427-2443.
- [40] Bertrand A, Bard F X, Josse E. Tuna food habits related to the micronekton distribution in French Polynesia. *Marine Biology*, 2002, 140(5) : 1023-1037.
- [41] Bard F X, Stretta J M, Slepoukh M. Les Epaves artificielles comme auxiliaires de la pêche thônière en océan atlantique: quel avenir? *La Pêche Maritime*, 1985, 1291: 655-659.
- [42] Kojima S. Fishing for dolphins in the western part of the Japan Sea — II Why do the fish take shelter under floating materials?. *Bulletin of the Japanese Society of Scientific Fisheries*, 1956, 21(10) : 1049-1052.
- [43] Batalyants K Y. On the hypothesis of comfortability stipulation of tuna association with natural and artificial floating objects. *ICCAT Collective Volume of Scientific Papers*, 1992, 40(2) : 447-453.
- [49] Ménard F, Marchal E. Foraging behaviour of tuna feeding on small schooling *Vinciguerria nimbaria* in the surface layer of the equatorial Atlantic Ocean. *Aquatic Living Resources*, 2003, 16(3) : 231-238.
- [50] Olson R J, Boggs C H. Apex predation by yellowfin tuna (*Thunnus albacares*): independent estimates from gastric evacuation and stomach contents, bioenergetics, and Cesium concentrations. *Canadian Journal of Fisheries and Aquatic Sciences*, 1986, 43(9) : 1760-1775.
- [44] Ménard F, Stéquert B, Rubin A, Herrera M, Marchal E. Food consumption of tuna in the Equatorial Atlantic ocean: FAD-associated versus unassociated schools. *Aquatic Living Resources*, 2000, 13(4) : 233-240.
- [45] Jaquemet S, Potier M, Ménard F. Do drifting and anchored fish aggregating devices (FADs) similarly influence tuna feeding habits? A case study from the western Indian Ocean. *Fisheries Research*, 2011, 107(1/3) : 283-290.
- [46] Potier M, Sabatié R, Menard F, Marsac F. Preliminary results of tuna diet studies in the West Equatorial Indian Ocean. *Proceedings of the 3rd session of the IOTC working party on tropical tunas*. Seychelles, 2001, 4: 273-278.
- [47] Wang X F. Evaluation of Ecological Impacts of Drifting Fish Aggregation Devices (FADs) on Skipjack *Katsuwonus pelamis* in the Western and Central Pacific Ocean [D]. Shanghai: Shanghai Ocean University, 2013.
- [48] Brock R E. Preliminary study of the feeding habits of pelagic fish around Hawaiian fish aggregation devices or can fish aggregation devices enhance local fisheries productivity?. *Bulletin of Marine Science*, 1985, 37(1) : 40-49.
- [51] Buckley R M, Itano D G, Buckley T W. Fish aggregation device (FAD) enhancement of offshore fisheries in American Samoa.

- Bulletin of Marine Science, 1989, 44(2): 942-949.
- [52] Sudarsan D, John M E, Nair K N V. Some biological considerations of yellowfin tuna, *Thunnus albacares* (Bonnaterre) taken by longline gear in the Indian EEZ. In workshop on Stock Assessment of Yellowfin Tuna in the Indian Ocean. Colombo, Sri Lanka, 1991.
- [53] Lebourges-Dhaussy A, Marchal E, Menkes C, Champalbert G, Biessy B. *Vinciguerria nimbaria* (micronekton) environment and tuna: their relationships in the Eastern Tropical Atlantic. *Oceanologica Acta*, 2000, 23(4): 515-528.
- [54] Hida T S. Food of tunas and dolphin (Pisces: Scombridae and Coryphaenidae) with emphasis on the distribution and biology of their prey *Stolephorus buccaneeri* (Engraulidae). *Fishery Bulletin*, 1973, 71(1): 135-143.
- [55] Allain V. Trophic structure of the pelagic ecosystems of the western and central Pacific Ocean. Nuku'alofa, Tonga: Western and Central Pacific Fisheries Commission, 2010.
- [56] Graham B S, Grubbs D, Holland K, Popp B N. A rapid ontogenetic shift in the diet of juvenile yellowfin tuna from Hawaii. *Marine Biology*, 2007, 150(4): 647-658.
- [57] Holt R D. Optimal foraging and the form of predator isocline. *American Naturalist*, 1983, 122(4): 521-541.
- [58] Potier M, Marsac F, Lucas V, Sabatié R, Hallier J P, Ménard F. Feeding partitioning among tuna taken in surface and mid-water layers: The case of the yellowfin (*Thunnus albacares*) and bigeye (*T. obesus*) in the western tropical Indian Ocean. *Marine Science*, 2004, 3(1): 51-62.
- [59] Ménard F, Labrune C, Shin Y J, Asine A S, Bard F X. Opportunistic predation in tuna: a size-based approach. *Marine Ecology Progress Series*, 2006, 323: 223-231.
- [60] Sund P N, Blackburn M, Williams F. Tunas and their environment in the Pacific Ocean: a review. *Oceanography Marine Biology Annual Review*, 1981, 19: 443-512.
- [61] Yesaki M. Observations on the biology of yellowfin (*Thunnus albacares*) and skipjack (*Katsuwonus pelamis*) tunas in Philippine waters. Colombo, Sri Lanka: FAO, Indo-Pacific Tuna Development and Management Programme, 1983.
- [62] Barut N C. Food and feeding habits of yellowfin tuna *Thunnus albacares* (Bonnaterre, 1788), caught by handline around payao in the Moro Gulf. Colombo, Sri Lanka: FAO, Indo-Pacific Tuna Development and Management Programme, 1988.
- [63] Yuen H S H. Behavior of skipjack tuna, *Katsuwonus pelamis*, as determined by tracking with ultrasonic devices. *Journal of the Fisheries Research Board of Canada*, 1970, 27(11): 2071-2079.
- [64] Bard F X. Apparent effect of stomach repletion on catchability of large tunas to longline gear. Comparison with other fishing gears. *ICCAT Collective Volume of Scientific Papers*, 2001, 52(2): 452-465.
- [65] Pinnegar J K, Polunin N V C. Contributions of stable-isotope data to elucidating food webs of Mediterranean rocky littoral fishes. *Oecologia*, 2000, 122(3): 399-409.
- [66] Jennings S, Maxwell T A D, Schratzberger M, Milligan S P. Body-size dependent temporal variations in nitrogen stable isotope ratios in food webs. *Marine Ecology Progress Series*, 2008, 370: 199-206.
- [67] McCutchan J H, Lewis W M, Kendall C, McGrath C C. Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. *Oikos*, 2003, 102(2): 378-390.
- [68] Minagawa M, Wada E. Stepwise enrichment of  $\delta^{15}\text{N}$  along food chains: further evidence and the relation between  $\delta^{15}\text{N}$  and animal age. *Geochimica et Cosmochimica Acta*, 1984, 48 (5): 1135-1140.
- [69] Gannes L Z, Del Rio C M, Koch P. Natural abundance variations in stable isotopes and their potential uses in animal physiological ecology. *Comparative Biochemistry and Physiology*, 1998, 119 (3): 725-737.
- [70] Western and Central Pacific Fisheries Commission. List of work programme of the scientific committee. Busan, Republic of Korea, 2012.

#### 参考文献:

- [47] 王学昉. 漂流人工集鱼装置对中西太平洋鲣鱼生态影响的评估 [D]. 上海: 上海海洋大学, 2013.