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·综述·

海洋鱼类的转换效率及其影响因子

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A review of the conversion efficiency and its influencers in marine fishes

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Abstract: A review of conversion efficiency and its influencers in marine fishes is presented in this paper. The conversion efficiency is the efficiency of food utilization for growth, usually expressed as energy conversion efficiency, i.e. growth efficiency, when measured in energy, or food conversion efficiency when measured in biomass. So, estimation of conversion efficiency is basically a work on determinations of food consumption and weight growth of fish. Influence factor of conversion efficiency are mostly those influencing food consumption and weight growth, containing abiotic, biotic, and physiological factors, and limitations of controlled conditions in experiments, in many cases, which leads to results not reflecting the natural states. The abiotic influencers include water temperature, salinity, pH, dissolved oxygen, ammonia nitrogen, current surrounding, and photoperiod, of which water temperature and photoperiod are the most important. In experiments without food limitation, the growth rate of fish increases generally with rising of water temperature, and reaches a maximum at an optimum temperature. But that the optimum temperature for growth goes down at low ration levels indicates that the temperature influence on growth depends upon food availability for fishes. The photoperiod can speed up or keep down the fish growth with its alternation during a year. The biotic influencers contain food availability, competition, and predation. The food availability is considered as a key factor, as important as water temperature, manipulating food consumption and growth of fish. It is density dependent and is diversified temporally and spatially due to climate change, physical and chemical oceanography processes in the ecosystem. The availability of food that contains high calorie is a primary reason why food type shifts evidently the food conversion efficiency in a species of fish. Comparatively, the energy conversion efficiency is much more steady with the change of food type. The competition influence on feeding and growth of fish is actually associated with food availability. For physiological influencers, it has been proved that the inheritance is not a decisive factor

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affecting feeding and growth of fish, but the genetic variance and the establishment of genetic predominance are related closely to food environments. Hormone is another physiological factor. Apparent variations in consumption, growth, and conversion efficiency between stages of life history are observed commonly in fish. It is much like the results of the changes of incretion and pertinent metabolic function. A literature review of previous publications reveals obvious variation in conversion efficiency among species of marine fishes.

Key words: marine fishes; food conversion efficiency; influencers; revie..

转换效率(conversion efficiency)是指单位时间内生物的生产量占食物消耗量的比例，一般从能量的角度来考量，称之为生长效率(growth efficiency)[1,2]，或者能量转换效率；当从生物量的角度来考量时，多称之为食物转换效率。中国学者也将食物转换效率称为生态生长效率[3,4]，并将能量转换效率和食物转换效率统称为生态转换效率[5]。Paloheimo和Dickie[1,6,7]通过对鱼类摄食与生长的研究，发现鱼类的总生长效率(K_1)与摄食量(C)之间存在对数线性关系，即

$$\ln K_1 = -a - bC,$$

并定义总生长效率(K_1)和净生长效率(K_2)分别为

$K_1 = \frac{\triangle W}{C\triangle t}$ 和 $K_1 = \frac{\triangle W}{AC\triangle t}$，式中，$\triangle W/\triangle t$ 表示鱼类在单位时间内的生长，AC 是食物同化量。于是

$$\frac{\triangle W}{\triangle t} = Ce^{-a-bC}$$

这便是以摄食量表示的鱼类的生长。

1 鱼类转换效率的研究方法

对鱼类转换效率的计算通常是基于对摄食和生长这两个变量的评估。其中，对鱼类摄食量的评估相当复杂。它通常包括两种含义，一是个体水平上的摄食量评估，如一定大小的某种鱼类对某种特定类型的食物的摄食量，二是种群水平上的摄食量评估，如具有一定年龄结构和生物量(B)的种群的摄食量(Q)，通常表示为一定时间范围(一般为1年)内单位生物量的摄食量(Q/B)[8]。对鱼类个体日摄食量的研究有许多方法，常用的方法可以归纳为五类，即直接测定法、生物能量学方法、根据耗氧量间接计算法、基于消化道内含物的方法、化学污染物质量平衡法。对鱼类种群摄食量的估算主要有两类方法，一是基于基础生物能量学模型的评估方法，二是多元回归模型。有关鱼类摄食量的研究方法与进展，郭学武等[9]已有综合报道。

对鱼类生长量的确定，相对于摄食量的评估要容易得多。一般地，在人为控制的实验中，根据实验开始时和结束时鱼的个体平均生物量即可获得其生长量。对自然种群的生长估算，通常有两种方法，一是根据鱼的耳石、脊椎、鳍条、鳞片或身体的其它硬的部位所记录的生长进行推算，这种方法又叫回算法(back calculation)；二是通过长度频率分析(length frequency analysis)，这种方法基于von Bertalanffy生长方程，已多年来被用于评估海洋鱼类的生长率、年龄结构和死亡[10-13]，并有多种相关软件问世，如：ELEFAN、SLCA、Projection Matrix 和 MULTIFAN，以MULTIFAN的应用最为广泛。

2 鱼类转换效率的影响因子

由于转换效率决定于鱼类的摄食量与生长量，因此，大凡影响鱼类摄食与生长的因子，皆可能影响鱼类的转换效率。

2.1 人为控制条件的限制性

摄食与生长的数据来源，总的来说不外乎人为控制下的实验(包括室内实验和野外观察)和在自然水域的现场取样两种途径。随着研究方法的不断完善和认识水平的不断提高，人们越来越多地倾向于使用现场资料研究鱼类的摄食、生长和转换效率，以尽量避免研究结果与实际情形可能存在的差异，因为在许多情况下，对禁闭在有限空间的鱼类的研究结果往往不能反映自由生活在天然环境下的鱼类的真实情形[14]。有证据表明，在室内被强制摄食的鱼类[15,16]或者捕获后即放入现场网箱中的鱼类[17]，其排空率都会下降。在人为控制的实验条件下，人为提供的饵料与鱼类在自然环境下所摄食的饵料往往在种类、成分与大小方面存在差异，而鱼类的排空率却恰恰会受到饵料种类、成分与大小的影响[18,19]。在自然环境中，大多数鱼类是在大范围内自由觅食的，而在人为控制的实验条件下，却是给饵则摄食，不给饵则不得不禁食。研究表明，在养殖环境中，鱼类的摄食频率(每日投喂次数)虽然对于食物的转换效率可能影响不大，但对于摄食与生长皆有显著影响[20,21]。鱼类在较长时间的禁食后，若重新摄食，往往有一个补偿生长阶段。补偿生长期的长短和在这一时期的摄食、生长与转换效率都可能随着禁食时间的长短而有所不同[22]。尽管如此，在很多情况下室内研究是不可缺的。研究发现，对活动能力较弱的鱼类，如岩礁鱼类和底上鱼类，室内研究能够获得比较准确的结果，而对于活动能力强的鱼类，如大多数具有长距离洄游习性的鱼类，现场研究则具有明显的优越性[5]。

2.2 非生物因子

影响鱼类摄食、生长与转换效率的非生物因子包括温度、盐度、pH、溶解氧、氨氮、流场、光周期等。对于海洋中自由生活的鱼类来说，温度和光周期是两个主要的影响

因子。

由于鱼类是变温动物，因此水温是影响其生理过程（包括摄食与生长）的关键环境因素[23, 24]。在食物没有限制的实验室研究中，鱼类的生长率随着温度的升高而增加，并在某一最适温度下达到最大值[24]。当食物供给量减少时，生长的最适温度也会下降[25, 26]。因此，温度对鱼类生长的影响依赖于食物的可获得性：在适温范围内，若鱼类能获得最大量的食物，其生长将随着温度的升高而加快，若不能获得最大量食物时，生长可能会随着温度的升高而下降，因为温度的升高增大了鱼类的代谢需求[27]。温度影响生长的一个著名的例子是北美的一种淡水杜父鱼（*Cottus extensus*），其幼鱼白天在水温很低（5℃）的底层摄食，夜间则迁移至温度较高（13～16℃）的表层，在这里其食物的消化速率（排空率）和生长速率皆显著增加[28]。

光周期也是影响鱼类生理过程（如越冬、产卵、索饵以及与之相关的洄游）的重要因素，尤其对于生活在温带水域的种类。光周期在周年内不同时期的变动，对鱼类的生长可起到加速或者抑制作用。其影响机理是光周期作用于鱼类的松果体和视网膜这两个能在夜间分泌降黑素的器官，而降黑素的水平高低指示夜间的长短[29]。虽然降黑素与鱼类生理反映之间的联系还不是很清楚，但一般认为，降黑素通过中枢神经系统调整下丘脑的释放激素的分泌，释放激素继而控制垂体的激素分泌[30]。溯河产卵的鲑的生长受光周期的影响非常显著[31, 32]。对于海洋鱼类和淡水鱼类来说，虽然受光周期的影响比鲑弱，但依然是极其重要的[33, 34]。与鱼类生长密切相关的摄食与转换效率同样受到光周期的影响，但这方面的研究报导还比较少[35]。

2.3 生物因子

影响鱼类生长的生物因子包括食物的可获得性、竞争与捕食等[36]，其中食物的可获得性是和温度同等重要的影响鱼类生长的关键因子[37, 38]，它是指有益于鱼类生长与生理活动的高营养、高能量、大小合适并且鱼类喜食的食物的可获得性。食物的可获得性又叫密度依赖因子，因为它既取决于饵料的密度，同时又取决于鱼类的密度。所以用鱼类个体所能分配的食物的可获得性来描述更为恰当，而且不难理解鱼类的密度依赖性生长往往就是食物的可获得性影响下的生长[39]。在食物的可获得性较低时期，鱼类的生长率会下降。Magnussen[40]研究发现，法罗海底平原的鳕平均体重从1989到1995年间增加了62%，期间年均水温有下降趋势，他认为，体重的增加很可能就是由于食物的可获得性增加的缘故。

评估食物的可获得性对鱼类生长的影响，可以基于鱼类饵料的丰度进行直接研究，但在许多情况下，饵料的丰度指标往往是缺乏的，部分原因是由于鱼类食谱的非单纯性。这种情况下可以替代的惯用方法，便是基于对鱼类胃含物的分析。Yaragina和Marshall[41]研究了东北大西洋鳕的肝条件指数（liver condition index, LCI）与饵料鱼—毛鳞鱼（*Mallotus villosus*）和大西洋鲱（*Clupea harengus*）的丰度及可获得性，发现所有体长组的年均LCI皆与毛鳞鱼的现存生物量非线性相关，当毛鳞鱼的现存量低于10 $\times 10^6$t时，LCI迅速下降。毛鳞鱼和大西洋鲱的丰度及其在鳕鱼胃含物中的出现频率皆与鳕鱼的LCI正向相关。

食物的可获得性不仅存在季节和年间变化，而且不同海区乃至同一海区的不同水域间皆存在差异。这些差异的存在，与气候变化、生态系统的物理海洋学过程和化学海洋学过程密切相关[42]。如上升流或下降流产生的辐散或辐聚作用可使水域的物理、化学特征发生重大变化，从而导致食物的可获得性产生变化，进而影响鱼类的分布与生长[43, 44]。

对高热含量食物的可获得性是食物种类影响鱼类转换效率的重要原因。由于食物的热含量会因不同食物种类所含的蛋白质、脂肪量的不同而不同（通过测定化学组分计算鱼类及其食物的热含量时，通常忽略碳水化合物[45]，因为其含量一般小于0.06%[46]，但也有例外情形[47]），而且鱼类本身的热含量也会因为蛋白质与脂肪含量的季节变化而不稳定，因此，鱼类的食物转换效率受食物种类的影响很大。但是，能量转换效率则要稳定得多[48]。能量转换效率反映的是鱼类摄入的能量有多少转化为生产力，由于摄入的能量再分配的原因，能量转换效率在数值上永远小于1。而食物转换效率反映了食物的饵料效果，在海洋自然生态系统里，它在数值上永远小于1，而在人工养殖或实验生态系统里有时可能大于1，因为有时所投喂的食物，其含水量远远低于摄食者自体的含水量[33, 49]。食物转换效率与鱼类养殖中通常使用的食物转化比（food conversion ratio = 摄入的食物重/鱼体增重）在概念上正好相反。竞争对摄食与生长的影响是和食物的可获得性相联系的。通常情况下，如果食物的可获得性没有限制，当两条或者更多的鱼处于近距离时，会刺激每条鱼摄食更多的食物[50]。然而对于有限的食物可获得性的竞争则会导致生长的减缓[51]。因为处于竞争中的鱼类，为获得更多的饵料必须付出更多的活动，而这将会降低其特定生长率[52]。从有利于发展的角度来看，鱼类种群之间应是尽可能避免竞争的。渤海的小型中上层鱼类优势种群之间似乎就存在一种互益性摄食格局，如赤鼻稜鳀（*Thrissa kammalensis*）具有较低的日摄食量和较高的转换效率，表现出对浮游动物的高效利用，这样可以缓和与其他小型中上层鱼类（如鳀 *Engraulis japonicus*）的食物竞争，而斑鰶（*Clupanodon punctatus*）则以摄食沉积碎屑为主，几乎不参与对浮游动物的食物竞争[53]。

2.4 生理因子

Thorpe和Morgan[54]根据对大西洋鲑（*Salmo salar*）不同种群的研究，证明遗传并不是鱼类摄食的决定因素。

不同种群的大西洋鳕的摄食响应都发生在同样的食物粒径/鱼体长比率上，生长响应也是如此。Purchase 和 Brown[55]对大西洋鳕（*Gadus morhua*）的研究得到类似结论。他们对西北大西洋的 4 个鳕种群的摄食、生长与食物转换效率的研究显示，虽然这四个种群间存在较大的遗传变异，但其生长的快慢与其遗传特性并没有必然联系。然而，鱼类的遗传变异及其遗传优势的建立则与食物环境密不可分。Sherwood 等[56]对河鲈（*Perca flavescens*）和湖红点鲑（*Salvelinus namaycush*）乳酸脱氢酶（LDH）的研究揭示，鱼类个体发育过程中的食物环境会强烈影响种群的 LDH 酶标属性。

鱼类的摄食、生长与转换效率在其生活史的不同阶段往往具有显著差别。这种事实的存在，是以生活史某一阶段（或体长范围狭窄）的个体的摄食、生长与转换效率推断包括生活史多个阶段（或体长范围宽广）的种群的情形时往往出现偏差或者不准确的原因所在[57]。一般地，日摄食量占体重百分比、生长速率以及转换效率都是幼鱼大于成鱼，低龄鱼大于高龄鱼。如 15℃ 下大马哈鱼（*Oncorhynchus nerka*）的日摄食量占体重的百分比由体重 4g 时的 16.9% 下降到体重 216g 时的 4.5%[58]；1～6 龄大西洋鳕的食物转换效率为 98%～9%[59]。另一普遍现象是，在繁殖季节，性腺成熟的鱼类摄食量会明显下降，甚至停止，如大西洋鲱（*Dorosoma cepedianum*）在 5、6 月份生殖季节日摄食量分别下降 25% 和 35%[60]。

激素也是影响鱼类摄食、生长与转换效率的因素之一。鱼类生活史不同阶段摄食与生长的改变可能与其内分泌和代谢功能的改变有关。有证据表明，甲状腺素、类固醇激素、胰岛素等都会影响鱼类的摄食与生长[61,62]。

2　海洋鱼类的转换效率

由于鱼类的转换效率受多种因素的影响，因此种间与种内差异都相当显著。表 1 给出了所能收集到的海洋鱼类的转换效率，看上去似乎难以给出一个恰当的变动范围。但 Stewart 和 Binkowski[63]曾报道鱼类的食物转换效率一般为 10%～30% 或者更高，Brett 和 Groves[45]曾以 29% 表示一般肉食性鱼类的能量转换效率。

表 1　已检索到的海洋鱼类的食物转换效率（FCE）和能量转换效率（ECE）

Tab.1　List of food conversion efficiency (FCE) and energy conversion efficiency (ECE) in marine fishes in available previous publications

种类 species	学名 scientific name	FCE（%）	ECE（%）	饵料 diets	备注 notes	来源 resources
玉筋鱼	*Ammodytes personatus*	10.4	32.2	卤虫 *Artemia salina*	14.0～18.0℃	[64]
星康吉鳗	*Astroconger myriaster*	9.2		玉筋鱼段 sand lance flitch	17.1～22.0℃	[4]
		3.8		枪乌贼 squid	21.7～26.3℃	[4]
线鳚	*Cebidichthys violaceus*	15～45	6.3～18	搭配海藻 modified seaweed	植食性 herbivorous fish	[65]
		26	12.2	天然海藻 natural seaweed		[65]
矛尾鰕虎鱼	*Chaeturichthy stigmatias*	30.0±5.6	37.4±7.0	玉筋鱼 sand lance	17.6±2.3℃	[5]
斑鰶	*Clupanodon punctatus*	16.5	31.7	天然饵料 natural diets	25.2±3.0℃	[66]
石斑鱼	*Epinephelus salmoides*	21.2～31.4		小杂鱼 trash fish		[67]
大西洋鳕	*Gadus morhua*		12	合成颗粒 pellets	5℃	[68]
			11	合成颗粒 pellets	8℃	[68]
			24	欧鲽鱼片 plaice fillets	15℃	[69]
		9～98			年龄组 1～6 age groups 1～6	[59]
			43.9～11.5		体重 250～2000g body weight 250～2000g	[70]
			50	浮游动物 zooplankton	稚鱼 juveniles	[71]
红鳍东方鲀	*Hexagrammos otakii*	25.1±8.0	23.2±7.4	玉筋鱼 sand lance	19.2±0.9℃	[5]
庸鲽	*Hippoglossus hippoglossus*	83～140		合成颗粒 pellets	8～18℃	[33]
小鳞鱵	*Hyporhamphus sajori*	13.96	16.12	天然饵料 natural diets	28.0～29.6	[72]
花鲈	*Lateolabrax japonicus*		23.8～28.1	合成颗粒 pellets	30℃，幼鱼 young fish	[73]
尖吻鲈	*Lates calcarifer*	20～35		碎鱼 minced fish	含 2% 动物饲料添加剂 with 2% animal feed supplement	[74]

(续表 1)

种类 species	学名 scientific name	FCE (%)	ECE (%)	饵料 diets	备注 notes	来源 resources
柠檬鲨	*Negaprion brevirostris*	10 ~ 25		冻鲹 frozen blue runner	幼鱼 young fish	[75]
南极鱼	*Notothenia neglecta*		6			[76]
真鲷	*Pagrosomus major*	9.22	19.4	小黄鱼鱼糜 ground small yellow croaker	17 ~ 20.4℃	[77]
		23.6 ± 2.8	26.0 ± 3.3	玉筋鱼 sand lance	19.4 ± 0.5℃	[5]
石鲽	*Platichthys biocoloratus*	18.4		枪乌贼 squid	4.2 ~ 6.9℃	[3]
		8		鹰爪虾 *Trachypenaeus curvirostris*	6.3 ~ 8.9℃	[3]
		16.5		鲳鱼 pomfret	6.7 ~ 11.7℃	[3]
		19.9 ~ 24.5		玉筋鱼 sand lance	11.2 ~ 19.9℃	[3]
鲬	*Platycephalus indicus*	7		带鱼段 hairtail flitch	8.5 ~ 12.0℃	[4]
		24.7		玉筋鱼 sand lance	11.6 ~ 16.8℃	[4]
眼斑雀鲷	*Plectroglyphidodon lacrymatus*	0.1		天然饵料 natural diets	珊瑚礁鱼类 coral-reef fish	[78]
鲐	*Pneumatophorus japonicus*	15.4 ± 3.1	21.6 ± 4.3	玉筋鱼 sand lance	23.1 ± 0.5℃	[5]
大菱鲆	*Scophthalmus maximus*		25 ~ 38	合成颗粒 pellets		[79, 80]
		32 ~ 147		合成颗粒 pellets	10 ~ 22℃	[49]
黑鲈鲉	*Sebastes pachycephalus*	14.6		玉筋鱼 sand lance	17.0 ~ 21.0℃	[4]
黑鲪	*Sebastes schlegeli*	12.5	14.1	玉筋鱼 sand lance	17.0 ~ 21.0℃	[64]
		6.5 ~ 34.7		乌贼、鱼、虾 squid, fish, shrimp	年水温 4.0 ~ 27.3℃ annual temperature 4.0 ~ 27.3℃	[81]
		39.0 ± 4.7	46.1 ± 5.0	玉筋鱼 sand lance	14.7 ± 0.5℃	[5]
乌颊鲷	*Sparus aurata*	< 18.7		竹筴鱼片 jack mackerel fillets		[82]
黑鲷	*Sparus macrocephalus*	18.9		斑鰶段 gizzard shad flitch	16.9 ~ 22.0℃	[4]
		6.5 ~ 14.2		沙蚕 clamworm	21.6 ~ 27.4℃	[4]
		8.4		枪乌贼 squid	21.9 ~ 26.3℃	[4]
		12.9 ± 2.8	14.8 ± 3.3	玉筋鱼 sand lance	19.8 ± 0.5℃	[5]
黄线狭鳕	*Theragra chalcogramma*		26	鲱鱼片 herring fillets	5℃	[83]
赤鼻棱鳀	*Thrissa kammalensis*	35.1	39.3	天然饵料 natural diets	22.4 ± 0.6℃	[53]
皱唇鲨	*Triakis scyllium*	14.2 ~ 33.6		玉筋鱼 sand lance	13.5 ~ 27.3℃	[4]
		23.7		枪乌贼 squid	21.7 ~ 26.5℃	[3]
		19.7		沙蚕 clamworm	24.4 ~ 27.4℃	[3]

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