

功能性氨基酸在水产甲壳类动物中的研究进展和应用前景

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摘要: 传统氨基酸根据其在体内合成能力, 一般分为必需氨基酸和非必需氨基酸。目前最新研究认为, 部分氨基酸除了合成蛋白质以外, 也能够合成一系列功能性物质, 并对动物营养代谢和免疫功能具有十分重要的调节作用, 为此提出功能性氨基酸这一概念。功能性氨基酸在甲壳类促生长、提高免疫和存活率等方面效果显著。近些年来, 甲壳类动物养殖病害严重, 对高效抗病功能性饲料需求较高。功能性氨基酸将在未来甲壳类配合饲料升级中扮演着重要的角色。文章总结功能性氨基酸在甲壳类蜕壳、抗应激、增强饲料诱食性及提高繁殖和幼体培育等方面的具体作用, 为相关功能性饲料技术开发提供参考。

关键词: 氨基酸; 功能性; 健康; 甲壳类

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甲壳类是重要水产养殖种类, 主要包括十足类虾蟹种类。甲壳动物含有丰富的蛋白质、脂肪盐和矿物盐等多种营养物质, 深受市场欢迎。我国甲壳类水产品资源丰富, 种类繁多, 是世界甲壳类水产品主要供给国。根据2021年中国渔业统计年鉴数据, 2020年我国甲壳类的养殖和捕捞产量分别为603万吨和197万吨。甲壳类水产动物在我国社会经济发展和食品良性供应上发挥着重要的作用。我国主要养殖的甲壳类品种(如南美白对虾 *Litopenaeus vannamei*、斑节对虾 *Penaeus monodon*、中华绒螯蟹 *Eriocheir sinensis* 和三疣梭子蟹 *Portunus trituberculatus* 等)均为杂食性或肉食性动物, 能够摄食鱼、虾、贝、藻, 甚至同类相食, 个别种类喜腐食, 对蛋白质和氨基酸要求较高。大部分养殖品种已能够做到利用人工配合饲料进行养殖, 并且效果显著。个别品种, 如三疣梭子蟹和青蟹, 仍以投喂冰鲜杂鱼为主, 由于冰鲜杂鱼品质不稳定, 极易引起污染环境、浪费严重、饲料系数高、易诱发疾病及破坏资源等问题^[1]。另一方面, 采用配

合饲料养殖甲壳类, 不仅可避免上述缺点, 也能提高养殖动物产品品质与营养价值。

过去几十年里, 我国甲壳类水产养殖产业(尤其对虾产业)得到较好的发展, 相关配套产业(如饲料加工和开发)也比较成熟。但是, 目前主要存在以下几点问题: (1)养殖问题: 个别甲壳类(如对虾)养殖密度高, 且病害严重, 例如南美白对虾的白便问题一直未能得到解决; (2)环境问题: 甲壳类养殖地区水体盐度温度变化大, 养殖密度大, 且养殖池塘底部有害物质沉积严重, 养殖动物长期应对不同养殖胁迫条件, 导致蜕壳和生长受阻; (3)饲料问题: 对虾摄食快慢是决定养殖效果的关键因素之一, 如何在营养方面提高饲料诱食性是关键; (4)产品品质: 我国对个别甲壳类品种(如蟹类)的品质要求较高, 如大众对“红膏蟹”比较青睐。近些年来, 国内外许多研究也报道了甲壳类的基本营养需求, 这在一定程度上为该品种配合饲料的发展提供一定的基础。在三大类营养物质中, 蛋白质(氨基酸)在甲壳类生长、发育和免疫中起到了关键性的

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作用,它不仅提供甲壳类所需的能量,也是其功能性物质的重要成分或前体。因此,最近几年国内外研究者相继提出“功能性氨基酸”这一概念,指除了合成蛋白质外还具有其他特殊功能的氨基酸,其不仅对动物的正常生长及维持是必需的,而且对多种生物活性物质的合成也是必需的^[2]。近些年,相关工作在甲壳类中得到一定开展。因此,本文通过总结相关研究工作,为甲壳类水产养殖动物的饲料开发和技术升级提供理论依据。

1 提供组织能量

相比较于猪和家禽动物,鱼类对饲料蛋白质需求高,其中主要原因之一是鱼类大量利用氨基酸为能量物质,而对脂肪酸和葡萄糖作为能源利用相对较低^[3,4]。与鱼类相似,甲壳类的蛋白质需求量较高,大多在30%—50%,例如南美白对虾幼虾蛋白质需求量在40%左右^[5—8]。此外,甲壳类对饲料非蛋白能利用相对有限,对脂肪和淀粉的需求分别为 $\leq 10\%$ 和 $\leq 20\%$ ^[9,10]。另一方面,甲壳类的饲料氮保留率整体不高,在17%—30%,甚至低于一些肉食性鱼类^[11—13]。这也间接证明大量饲料氨基酸未能成为体蛋白,而是直接作为能源被降解。此外,甲壳类(如南美白对虾和中华绒螯蟹)的耗氧:氮排率普遍小于40,也证明氨基酸是其重要的能量底物^[14—16]。Rosas等^[17]指出,南美白对虾能够较好适应以蛋白质为主要能量来源的饲料,而非基于淀粉基础的饲料。我们同位素示踪实验结果也证明,氨基酸是南美白对虾的主要能量物质,当然在各个器官中所占比重有所不同^[18]。例如,谷氨酰胺和天冬氨酸是肌肉重要能量底物,其氧化效率显著高于其他能量底物(如葡萄糖和棕榈酸)。南美白对虾鳃部对葡萄糖氧化效率最高,其次是谷氨酰胺和天冬氨酸。对虾在应对不同胁迫情况下,往往需要更多能量或功能物质去调节体内生理平衡。例如,研究发现环境低温及高温均会导致ATP含量增加,表明南美白对虾在应对温度胁迫的过程中可能需要更多能量^[19]。早期研究已表明,氨基酸(如丙氨酸)是非常重要的功能和能量物质,在应对环境急性渗透压的变化中起到非常重要的作用^[20]。由此可见,氨基酸作为部分器官或组织的重要能源,能够保障甲壳类适应不同环境,也是发挥氨基酸功能性的重要机制之一。另一方面,关于甲壳类利用氨基酸作为能源的研究相对有限,相关结论仍存在一定争议,未来需要大量工作进一步验证。氨基酸也是糖类、脂类和其他功能物质的前体物,在生理上扮演重要的功能,这里不做详细介绍。

2 促进蜕壳

众所周知,蜕壳是甲壳类养殖非常重要的一个生理环节,其主要作用是:(1)生长需要,蜕去旧壳有利于生长;(2)繁殖需要;(3)除去旧壳上的寄生虫和细菌。蜕壳后期水的摄入非常重要,因为这一过程决定下一生长阶段的身体大小^[21]。蜕壳是一种复杂生理活动,氨基酸在各个阶段中扮演着重要的作用(表1)。例如,蜕壳后期是能量和矿物盐的急需期,需要注意营养物质的充足提供。一般认为,蜕壳后对钙需求大,需要根据各个水环境不同盐度和硬度调整钙的补充。但值得注意的是,虾壳通常含有25%—40%蛋白质、15%—20%几丁质、45%—50%碳酸钙,15—40 mg/kg虾青素,其中蛋白质中含有60%胶原蛋白^[22,23]。因此,氨基酸和蛋白质的补充对蜕壳的成功和新壳的形成起到非常重要的作用。蜕壳和生长并不是完全相关,在某些非正常条件下,如温度和盐度刺激可提高蜕壳频率,但对生长反而无帮助^[29,30]。通过环境因子改变而促进的蜕壳能否带来总体养殖效率的提高还不得而知。已有部分证据表明,这种方式会引起蜕壳成功率下降,导致不必要的损失^[31—33]。与此相反,通过功能性氨基酸添加,强化饲料营养而提高蜕壳成功率和生长是比较可取之道。氨基酸在甲壳类蜕壳中扮演的作用已得到一定的研究,虾体内游离氨基酸的组成也从侧面反映出虾对饲料氨基酸的需求。例如,游离脯氨酸和甘氨酸被证明是蜕壳期间的重要能量物质,也是在蜕壳前期合成新壳的重要底物^[29,30]。研究结果表明,中华绒螯蟹的血清蜕壳激素和蜕皮甾酮随着饲料添加1%—2%精氨酸而增加,并且可提高蜕壳频率^[31]。在表1中,我们总结氨基酸在不同蜕壳期间的作用,相关研究相对有限,需要进一步验证。

3 抵抗环境胁迫

由于养殖环境复杂多变,甲壳类动物往往面临环境盐度、温度和氨氮变化等的胁迫。其中,渗透压调节能力是甲壳类养殖成功的重要因素^[32]。相比较于脊椎动物,甲壳类动物体内含有较高的游离氨基酸,主要为甘氨酸、谷氨酸、丙氨酸、精氨酸和牛磺酸^[33,34]。研究证实,血淋巴游离氨基酸水平会随着外界应激条件刺激而产生变动^[31]。值得注意的是,游离谷氨酸、脯氨酸、甘氨酸、丙氨酸、牛磺酸和精氨酸已被证明是海洋无脊椎动物渗透压调节的重要物质^[35—39]。例如,对三疣梭子蟹研究表明,体内游离氨基酸(主要包括丙氨酸、甘氨

表 1 氨基酸在甲壳类不同蜕壳时期的作用

Tab. 1 Main functions of amino acids at different stages of the molt cycle in shrimp

蜕壳时期 Molt cycle	阶段 Stage	时间 Duration	壳状态 Exoskeleton	摄食 Feeding	氨基酸作用 Main functions of amino acids
后期 Postmolt	A	1—2h	软壳	无	调节渗透压, 参与蛋白合成
	B	2—5h	微硬	微量	
间期 Intermolt	C	8—10d	外壳完全硬	正常	能量来源和 蛋白合成
前期 Premolt	D0	1—2d	外壳开始分解	正常	胶原蛋白合成, 渗透压调节, 荷尔蒙释放
	D1	1—2d	新内壳未成形	下降	
	D2	2d	新壳形成	下降	
	D3	1d	旧壳新壳之间形成裂缝	下降	
	D4	1d	大量吸水、旧壳裂开	无	
蜕壳 Molt	E	15min	蜕壳	无	提供能量、 渗透压调节

注: 蜕壳各个时期分类参考自Rao 等^[50]
Note: The stages of molt cycle adapted from Rao *et al.*^[50]

酸、天冬氨酸和谷氨酸)在适应环境盐度骤变中发挥着重要的作用^[40]。有研究表明,适当提高饲料蛋白水平是应对盐度应激的有效办法^[41]。南美白对虾幼虾投喂含有额外添加的2.26%—2.70%甘氨酸能够有效提高急性盐度刺激下的存活率^[42]。在应激条件下,动物往往需要更多能量去适应新的生活环境。作为甲壳类动物重要的能量物质,氨基酸在抵抗其他应激中也扮演着比较重要的作用。过去研究表明,氨基酸在提升甲壳类抵抗其他各类胁迫(如低温、饥饿和高氨氮)过程中扮演着重要的角色^[36, 43—45]。例如,高温与氨氮复合胁迫对南美白对虾游离氨基酸含量影响显著,从而造成南美白对虾渗透压生理调节功能紊乱^[38]。此外,肝胰腺中脯氨酸和丙氨酸的积累是甲壳类适应低温胁迫的主要手段之一^[46—48]。对南美白对虾的研究表明,低鱼粉基础饲料通过添加额外脯氨酸提升饲料脯氨酸从2.02%—2.6%能够显著性增加幼虾抵御高氨氮环境^[49]。由此可见,氨基酸作为能量和渗透压调节物质在抵御各种胁迫中发挥重要的作用。

4 诱食剂

游离氨基酸已被证明是鱼虾的重要诱食剂。例如,真龙虾(*Panulirus argus*)的嗅觉和味觉对牛磺酸及其衍生物非常敏感^[51]。对罗氏沼虾的研究表明,复合氨基酸(甘氨酸+丙氨酸)的诱食效果好于单一氨基酸和中草药,且氨基酸类诱食剂比中草药更有助于提高罗氏沼虾肝胰腺消化酶的活性^[52]。对中华绒螯蟹的研究表明,各个单体氨基酸(苯丙氨

酸除外)都具有一定的诱食效果^[53]。值得注意的是,同一氨基酸在不同种类中的刺激性有一定差别,甚至起到相反的作用。因此,相关氨基酸的诱食性在不同甲壳类养殖品种中应该谨慎对待。此外,酵母粉、乌贼膏、鱼溶浆和磷虾粉等也被认为具有较好的诱食效果^[54],可以和氨基酸配合使用。另一方面,虽然很多原料或氨基酸对幼虾有较好的摄食刺激性,但考虑到加工加热等因素,可能导致有效游离氨基酸减少,作用减弱。相关研究表明,乌贼粉和乌贼膏对南美白对虾摄食无显著性提高^[55],这可能与饲料加工方式有关。国外研究者基于氨基酸诱食性原理,利用金枪鱼副产品水解物加黏合剂与已完成制粒的饲料搅拌均匀,然后投喂南美白对虾,诱食效果明显^[56]。氨基酸的诱食作用也可能与养殖动物消化能力的提升有关。例如,微胶囊和晶体蛋氨酸有助于提高南美白对虾肝胰腺蛋白酶的活性^[57]。

5 提高免疫力和抗氧化性

环境胁迫可造成甲壳类的免疫力降低和机体自由基代谢紊乱。氨基酸作为细胞和组织的主要营养成分,在维护动物的免疫力和抗氧化中发挥着重要的作用^[58, 59]。甲壳类没有特异性免疫系统,而主要依赖非特异性免疫系统抵抗病菌的侵入^[60]。研究表明,南美白对虾受弧菌感染后,各个组织的氨基酸代谢得到一定改变以应对感染后能量需求的增加。例如,酪氨酸在鳃和肝胰腺中的代谢均表现出显著变化^[61]。目前关于各个氨基酸在甲壳类动物中的作用尚未全面展开,但个别报道已证实相关氨基酸具有一定增加免疫的作用。例如,精氨酸代谢可产生NO、多胺和磷酸精氨酸,能够提高机体免疫力^[28]。对南美白对虾的研究表明,NO介导的信号传导可能在应对高温胁迫中起着重要作用^[19]。对中华绒螯蟹的研究表明,饲料添加1%—2%精氨酸能够提高生长、存活率及抗病力^[31]。另一个研究也表明,饲料添加0.47%或者0.73%的色氨酸能够提高抗病力和存活率^[62]。对斑节对虾的研究表明,复合植物蛋白源并添加包膜赖氨酸和蛋氨酸可降低饲料中20%的鱼粉用量,并增强对虾非特异性免疫力^[63]。如表 2 所示,近些年已有研究表明,相关传统必需氨基酸(如甘氨酸、脯氨酸和谷氨酸)及其代谢产物具有相关功能作用,尤其可提高免疫力和抗应激能力,从而促进生长。考虑到近些年对虾养殖病害频发,养殖成功率较低,在原有配方基础之上,适当添加相关功能性氨基酸意义重大。相关研究工作亟待开展。

活性氧自由基(ROS)具有很强的化学反应活性,使蛋白质失活,造成生物膜系统和生物结构的损坏,也可引起细胞DNA和RNA在结构和功能上的损伤,并进一步造成器官的损害^[64]。内源性抗氧化化是控制自由基和组织氧化损伤的重要防御体系,主要包括超氧化物歧化酶、谷胱甘肽、谷胱甘肽过氧化物酶、谷胱甘肽还原酶、过氧化氢酶(一种含血红素的酶)和抗氧化性营养素。氨基酸及其衍生物是甲壳类重要的抗氧化剂。例如,谷胱甘肽由谷氨酸、胱氨酸和甘氨酸合成,是一种具有较强抗氧化性的营养物质。饲料添加0.2 g/kg谷胱甘肽能够有效提高南美白对虾免疫力和抗氧化能力^[65]。另一个实验研究表明,饲料甘氨酸水平高于2.44%能够有效提高对虾在高盐度刺激下的抗氧化和抗病力^[42]。

6 提高繁殖和幼体培育

已有证据表明氨基酸在性腺发育中扮演重要角色,进而影响甲壳类的繁殖。此外,养殖蟹类的卵巢是重要的可食用部位,其发育好坏也决定了商品的价值。卵黄原蛋白生成是其卵巢发育的重要步骤,该蛋白主要合成于胰腺和卵巢,受一系列激素调控,并在卵巢积累(图1)。温为庚等^[66]通过分析野生斑节对虾卵巢发育过程中不同组织的氨基酸组成发现,随着卵巢发育,野生斑节对虾卵巢的氨基酸总量逐渐上升,但到临产时下降,而必需氨基酸总量整体逐渐上升。早期卵巢氨基酸积累

主要受大量卵黄蛋白积累影响,而总氨基酸后期下降可能原因之一是大量非必需氨基酸作为能源被消耗。通过同位素示踪技术,我们在蓝蟹(*Callinectes sapidus*)中的研究(相关数据暂未发表)表明,谷氨酸和天冬氨酸在卵巢中的氧化效率分别为5.62和2.09 [nmol CO₂/(mg 组织·2h)],远高于葡萄糖和棕榈酸的氧化效率,分别为0.08和0.74 [nmol CO₂/(mg 组织·2h)]。由此可见,卵巢可能主要以氨基酸(谷氨酸和天冬氨酸)作为能量底物,而非葡萄糖和脂肪酸。此外,处于卵巢中期发育阶段的野生斑节对虾中,卵巢的天冬氨酸、谷氨酸、脯氨酸、酪氨酸和赖氨酸质量分数达到极大值,总和占总氨基酸的42.5%^[66]。这点印证了在实际生产中,养殖户往往为了促使对虾卵巢发育,会投喂沙蚕、乌贼和牡蛎等作为饵料,其中以沙蚕的效果最好。这可能与饵料中富含相关氨基酸有关。此外,部分实验已证明,氨基酸可对甲壳类动物的激素分泌产生调控作用。例如,中华绒螯蟹血清的生长激素和胰腺腺的IGF2激素会随着饲料精氨酸的添加而增加^[31]。氨基酸可能通过调控激素分泌而控制卵巢发育,相关研究相对有限,大量研究亟待展开。

蛋白质和氨基酸也是甲壳类卵和幼体的主要组成成分,在其发育和生长中扮演着十分重要的角色^[67, 68]。繁殖亲本的营养状态往往影响卵的营养组成并影响其质量。例如,相比较于35%蛋白组,投喂45%蛋白饲料的白滨对虾(*Litopenaeus setiferus*)拥有更好的精子质量^[69]。此外,甲壳类幼体的

表2 不同氨基酸及其代谢产物在水产甲壳类动物中的作用

Tab. 2 Nutritional and physiological functions of amino acids and their metabolites in crustaceans

氨基酸Amino acid	代谢物Metabolite	主要作用Main fuction	品种Species	参考文献Reference
精氨酸Arg	NO和多胺	提高抗氧化和免疫力	中国对虾; 日本囊对虾; 南美白对虾	[76]
精氨酸Arg	磷酸精氨酸	能量储存物质, 参与渗透压调节	蓝蟹和岸蟹	[77, 78]
精氨酸、鸟氨酸和蛋氨酸Arg, Orn and Met	NO、多胺、牛磺酸和磷酸精氨酸	参与渗透压和离子调节	蓝蟹	[79]
谷氨酰胺、甘氨酸和天冬氨酸Gln, Gly and Asp	核苷酸和ATP	抗氧化和提高生长	斑节对虾	[80, 81]
赖氨酸和蛋氨酸Lys and Met	肉碱、牛磺酸和多胺	提高免疫力、抗氧化和能量代谢	南美白对虾和窄爪小龙虾	[82, 83]
谷氨酰胺Gln	氨基葡萄糖、谷氨酸、ATP	作为性识别糖蛋白合成底物; 提高伤口愈合速度和维持正常健康养殖	鞭藻虾	[84, 85]
甘氨酸Gly	谷胱甘肽	提高生长、抗氧化和免疫力	南美白对虾	[86]
脯氨酸Pro	1-吡咯啉-5-羧酸	提高生长、抗氧化力和免疫力	南美白对虾	[49]
谷氨酸Glu	GABA和ATP	提高生长、抗氧化系统和抗应激能量	南美白对虾	[85]
色氨酸Try	血清素、褪黑素	调节生长、繁殖和残杀行为	斑节对虾和青蟹	[87, 88]
牛磺酸Tau	牛磺胆酸和羟乙基磺酸	提高免疫力、生长和脂肪利用	日本沼虾和南美白对虾	[89—91]

注: GABA, γ -氨基丁酸

Note: GABA, γ -aminobutyric acid

游离氨基酸不但提供能量,还能刺激蛋白合成,从而促进生长和发育^[70]。例如,南白对虾幼体投喂牛磺酸强化轮虫能提高其存活率和发育^[71]。类似的,通过强化卤虫的赖氨酸含量投喂南美白对虾幼体,可提高幼体的存活率、生长和抗逆性^[70]。因此,在早期甲壳类动物生长和发育中,足量的氨基酸补充发挥十分关键的作用。例如,通过优化藻类培养方式,可以提升氨基酸含量和质量,从而达到甲壳类幼体开口饵料营养的强化^[72]。

7 研究现状和前景

综上所述,氨基酸在甲壳类发育、生长和繁殖过程中扮演着十分重要的作用(表2)。因此,合适的饲料氨基酸添加对养殖甲壳类的生长、健康和产品品质具有重要的影响。当前,商业饲料的氨基酸使用主要集中在传统必需氨基酸(如赖氨酸和蛋氨酸)的添加,主要评价指标仍然以生长和饲料利用率为主。近些年来,养殖环境越发恶劣,养殖动物健康问题频发,通过传统生长实验得出的氨基酸适宜添加量满足不了功能性的额外需求。因此,通过额外补充一定形式的氨基酸来调控甲壳类健康养殖是未来发展途径之一。近些年来,富含功能性氨基酸小肽类原料也越来越受行业关注,但相关应

用效果在不同条件和品种中有一定差异。通过了解相关功能性氨基酸作用及需求量,也有助于我们进一步精细化使用这些功能性原料。

目前,关于甲壳类相关功能性氨基酸代谢和作用的研究仍然十分薄弱,大量工作亟待开展。主要问题集中于以下几个方面:(1)氨基酸在不同养殖甲壳类动物中的代谢特征尚未阐明,导致研究基础相对薄弱,大量理论参考于鱼类甚至是哺乳类动物;(2)甲壳类动物特殊的摄食行为方式可能导致游离氨基酸出现一定的溶失,影响应用效果,相关数据薄弱;(3)不同地区或种类的甲壳类养殖环境差异较大,如何发挥特定条件下的功能性氨基酸的应用技术是未来重点工作之一。

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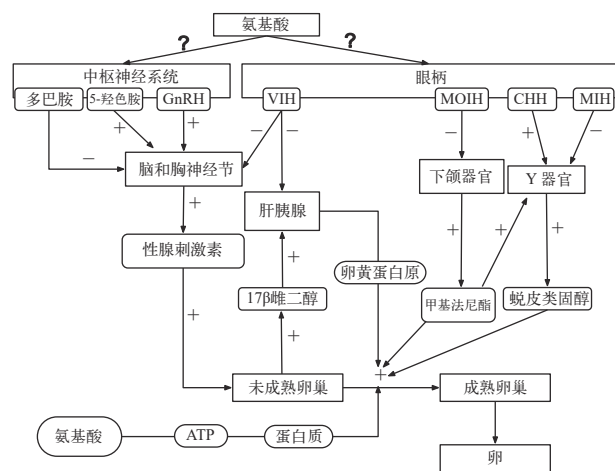


图1 甲壳类雌性卵巢发育调控机制以及氨基酸可能存在的作用
Fig. 1 Roles of internal and external factors in the regulation of reproduction in female crustaceans

CHH. 甲壳类高血糖激素; GnRH. 促性腺激素释放激素; MOIH. 下颌器官抑制激素; MIH. 蜕皮抑制激素; VIH. 抑制卵黄生成素; ‘+’ 和 ‘-’ 分别代表激活和抑制; 参考自 Pamuru^[73] 和 Subramoniam^[74, 75]

CHH. Crustacean hyperglycemic hormone, GnRH. Gonadotropin-releasing hormone, MOIH. Mandibular organ-inhibiting hormone, MIH. Molt-inhibiting hormone, VIH. Vitellogenesis-inhibiting hormone, ‘+’ and ‘-’ denotes activation and inhibition, respectively (Adapted from Pamuru^[73] and Subramoniam^[74, 75])

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THE ROLE OF FUNCTIONAL AMINO ACIDS IN AQUATIC CRUSTACEANS

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Abstract: Traditionally, amino acids are classified as essential amino acids and non-essential amino acids based on their ability of syntheses from metabolic intermediates. Currently, many scientists gave a new concept of functional amino acids, which are defined as those amino acids that participate in and regulate key metabolic pathways and immune systems. These amino acids not only provide blocks for protein synthesis, but also as substrates for many functional compounds. It has been reported that these amino acids can improve health, survival, growth, development, and reproduction of organisms. Crustaceans (e.g., shrimp and crabs) are the second largest aquaculture species worldwide, their feed development play a vital role in industry development. Functional amino acids hold great promise in prevention and treatment of metabolic diseases, intrauterine growth restriction, and infectious diseases (including viral infections). However, there are still some technical difficulties and challenges in the use of crystalline amino acids for research and practical production. At present, the knowledge about amino acid metabolism and functions in crustaceans is still limited, and much of them are based on studies of mammals and fish species. This article highlights current knowledge about the functions of amino acids on molt, adaptation of stress, immune, and antioxidant responses, spawning and larval development of crustaceans. It will help to advance the field of protein nutrition and guide the development of future crustacean feeds.

Key words: Amino acids; Functional; Health; Crustaceans