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夏季高温期三倍体和二倍体长牡蛎生理能量学及碳收支的比较研究*

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摘要 为解析夏季高温期三倍体与二倍体长牡蛎(*Crassostrea gigas*)摄食和代谢生理以及能量/碳分配策略的差异, 于 2022 年 8 月, 以三倍体和二倍体长牡蛎为研究对象, 在山东荣成桑沟湾采用现场流水法测定滤水率、吸收效率、耗氧率、排氨率等摄食和代谢相关生理参数, 并基于能量收支方程估算能量分配与碳分配情况。结果显示, 三倍体长牡蛎的滤水率、同化效率均高于二倍体长牡蛎, 但无显著差异(P>0.05); 三倍体与二倍体长牡蛎的耗氧率、排氨率存在显著差异(P<0.05), 三倍体长牡蛎的耗氧率显著低于二倍体长牡蛎(P<0.05), 但排氨率显著高于二倍体长牡蛎(P<0.01)。能量收支与碳收支的结果显示, 三倍体长牡蛎的摄食能/碳、同化能/碳均高于二倍体长牡蛎, 但无显著差异(P>0.05); 三倍体与二倍体长牡蛎的呼吸能/碳、排泄能/碳、生长余力存在显著差异(P<0.05), 三倍体长牡蛎的呼吸能/碳显著低于二倍体长牡蛎(P<0.05), 但排泄能/碳、生长余力显著高于二倍体长牡蛎(P<0.05)。三倍体和二倍体长牡蛎的氧氮比波动范围分别为 7.91~14.11 和 59.81~94.19, 因此, 三倍体长牡蛎的主要供能物质为蛋白质, 二倍体长牡蛎的主要供能物质为糖类和脂肪。研究结果为揭示夏季高温期长牡蛎倍性效应关联的能量分配方式差异提供了数据支撑。

关键词 长牡蛎; 三倍体; 二倍体; 夏季高温; 生理能量学

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长牡蛎(*Crassostrea gigas*)又称太平洋牡蛎, 是世界上养殖范围最广、产量最高的经济贝类, 也是我国最重要的海水养殖贝类种类。然而, 近几十年来, 在国内外沿海区域均出现了夏季长牡蛎大量死亡的现

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象。例如，1995 年大连沿海养殖的长牡蛎死亡率达到 40%~50%，有的甚至达到 70%以上，仅存的个体也表现出生长缓慢、出肉率低的情况(隋锡林等, 2002)；2008 年法国养殖的长牡蛎死亡率达到 40%~100% (Li *et al*, 2009)；2009 年桑沟湾崖头长牡蛎养殖区死亡率高达 51% (廉伟等, 2010)；2019 年乳山养殖区死亡率达 50%~90% (魏钰恒等, 2020)。死亡高峰期多发生在 8 月中下旬。诸多研究表明，造成长牡蛎大规模死亡是温度、溶氧、盐度、疾病、饵料和繁殖等因素共同作用的结果(Soletchnik *et al*, 2007; 林思恒, 2016)。其中，高温是一个最重要的非生物胁迫因素(Gagnaire *et al*, 2006)，夏季高温使长牡蛎酶代谢水平发生紊乱，导致长牡蛎生长缓慢或停止生长(王如才等, 2008)；另外，性成熟个体的繁殖活动造成了糖原的大量消耗，体质虚弱叠加高温胁迫易诱发长牡蛎大量死亡(毛玉泽等, 2005; Royer *et al*, 2007)。

长牡蛎三倍体因其高度不育性，具有生长速度快、抗逆能力强、经济性状优等特点(Amiard *et al*, 2004; Nell *et al*, 2005; Guo *et al*, 2008)，近些年来，在我国尤其是北方沿海地区形成了一定的养殖规模。有关长牡蛎三倍体与二倍体之间的生物学和生理学等差异在国内外已有较多的研究，多集中在长牡蛎三倍体与二倍体生长特性(王昭萍等, 2002)、软组织成分(Laing *et al*, 1994; 曾志南等, 1999; 孔令锋等, 2001; Lin *et al*, 2002)、性腺发育(Normand *et al*, 2009)、抗病力(Gagnaire *et al*, 2006; Azema *et al*, 2016; Haure *et al*, 2021)、免疫性能(Duchemin *et al*, 2007)和鳃结构等差异方面(孔令锋等, 2003)。但关于长牡蛎三倍体与二倍体摄食、代谢生理与能量收支以及碳收支比较的研究尚未见报道。本研究聚焦夏季高温期这一特殊时段，采用现场流水法，研究长牡蛎三倍体与二倍体的摄食和代谢生理特征，对比分析三倍体与二倍体应对高温环境的能量分配策略。研究结果可揭示长牡蛎倍性效应而引发的生理差异，进而服务于养殖容量评估提供数据支撑。

1 材料与方法

1.1 实验材料

实验于 2022 年 8 月 15—30 日在山东省荣成市楮岛码头实验室进行。实验用三倍体及二倍体长牡蛎均取自山东荣成桑沟湾近海养殖区，这 2 种牡蛎均为 2022 年 5 月放苗的个体，初始壳高均为 10 mm 左右，实验用三倍体长牡蛎壳高为(63.07±6.21) mm (n=30)，二倍体长牡蛎壳高为(52.95±4.12) mm (n=30)。挑选健康、形态和大小一致的个体各 30 只，清洗壳表面的污物和附着生物后，将其暂养于 6.6×10^3 L 养殖池内；养殖池海水由桑沟湾近海持续泵入，自然海水保持流水状态，暂养 3 d 后，选取 9 只牡蛎开始进行相关实验。

1.2 实验方法

1.2.1 *实验系统搭建与设计* 实验采用现场流水法测定 2 种长牡蛎的滤水率、同化效率、耗氧率和排氨率。实验系统搭建于桑沟湾楮岛码头实验室，搭建方法参考王晓芹等(2017)，如图 1 所示。

实验期间，于每日 08:00、12:00 和 18:00 测定实验海水的温度(T)、盐度(S)、溶解氧(DO)、pH、叶绿素 a (Chl-a)。T、S、DO 和 pH 采用便捷式水质参数分析仪(YSI WTW, 美国)测定，Chl-a 采用叶绿素浊度仪(ACLW-USB, 日本)测定。实验期间水温为(24.84±0.56) ℃，盐度为 30.12±0.17，pH 为 8.17±0.16，DO 为(7.68±0.78) mg/L，Chl-a 为(2.36±0.11) μg/L，颗粒有机物(POM)为(6.20±1.11) mg/L，颗粒有机碳(POC)为(0.49±0.09) mg/L。

1.2.2 *实验方法* 滤水率及同化效率测定：实验共布设

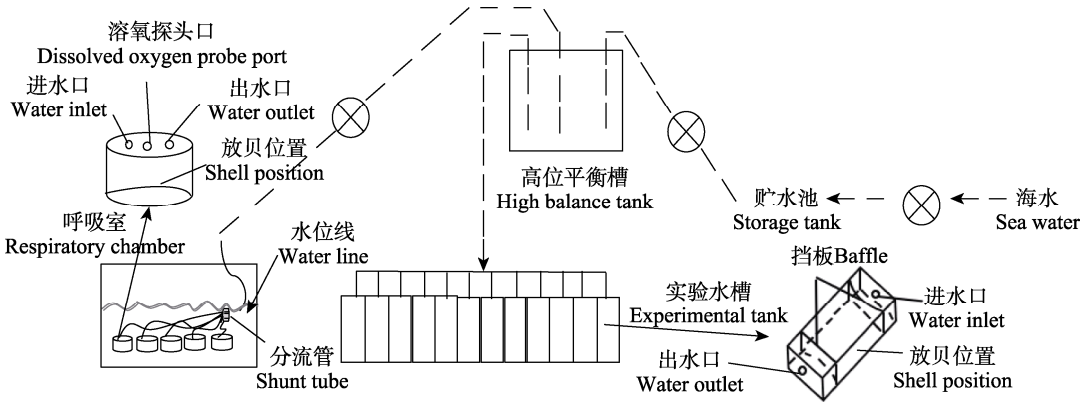

图 1 现场流水系统示意图

Fig.1 Diagram of experimental flow-through system

12 个流水槽, 实验前, 先将流速调节到 180~200 mL/min, 流速稳定之后, 将已标记号码的长牡蛎逐一放入流水槽中, 每个流水槽放置 1 个长牡蛎, 形成 9 个实验组(放置牡蛎)、3 个对照组(不放牡蛎), 每隔 3 个实验组放置 1 个对照组, 保证实验用水的均匀性。观察流水槽内牡蛎的状态, 在牡蛎开口的那一刻开始计时, 在牡蛎适应好的第 1、2、3 小时从流水槽出水口接水样 100 mL, 利用便携式颗粒计数器 PAMAS (测定粒径范围为 2~200 μm, S4031GO, 德国)测定水样瓶中的水体颗粒物数量, 并在程序中设定每个水样测定 3 次, 即每个水样可得到 3 组数据。同时, 在入水口取水样 1 000 mL, 每个时间点取 2 个平行样, 用预先 450 ℃灼烧 6 h 并称重(W_0)的 Whatman GF/F 玻璃纤维滤膜(孔径为 0.7 μm, 直径为 47 mm)抽滤, 抽滤时用 0.5 mol/L 的甲酸铵冲洗, 将带有样品的滤膜在 60 ℃烘干 48 h 称重(W_{60}), 再经 450 ℃灼烧 6 h 后称重(W_{450})(精确至 0.000 1 g), 测定水体中悬浮颗粒物(TPM)和 POM 的浓度; 另取, 1 000 mL 的入水口海水, 抽滤至预先 450 ℃灼烧 6 h 的 Whatman GF/F 滤膜(孔径为 0.7 μm, 直径为 25 mm)上, 将带有样品的滤膜经雾化的盐酸酸化, 60 ℃烘干至恒重后, 采用 Elementar EL 型元素分析仪(Elementar 公司, 美国)测定水体中 POC 的浓度。

粪便的收集: 滤水实验结束后, 用吸管虹吸粪便至预先 450 ℃灼烧 6 h 并称重的 Whatman GF/F 玻璃纤维滤膜(孔径为 0.7 μm, 直径为 47 mm)上, 抽滤时用 0.5 mol/L 的甲酸铵冲洗, 将带有样品的滤膜在 60 ℃烘干 48 h 称重(W_{60}), 再经 450 ℃灼烧 6 h 后称重(W_{450})。以此测定粪便中 TPM 和 POM 的浓度。

耗氧率及排氨率测定: 实验共布设 12 个呼吸室, 将已标记号码的长牡蛎逐一放入呼吸室中, 每个呼吸室放置 1 只长牡蛎, 形成 9 个实验组(放置牡蛎)、3 个对照组(不放牡蛎)。开始实验前, 将牡蛎在呼吸室中流水驯化至开口。随后, 关闭呼吸室进出水口, 开始正式实验, 采用十通道实时溶氧测定仪(PreSens Precision Sensing, 德国)连续监测各个呼吸室的溶解氧动态变化情况, 以“呼吸室内溶氧含量变化率大于初始溶氧的 10%, 但溶氧含量不能低于 5 mg/L”作为实验结束判断标准, 既保证呼吸室内溶氧的差异性, 又避免实验动物受溶氧胁迫现象的发生。耗氧实验结束后, 用聚乙烯塑料瓶取 100 mL 海水, 用玻璃纤维滤膜(孔径为 0.45 μm, 直径为 47 mm)过滤掉浮游生物, 加入 2~3 滴三氯甲烷以隔绝空气, 用于氨氮的测定, 氨氮的测定依据《海洋调查规范》(GB/T12763-2007)中次溴酸钠氧化法。

实验结束后, 用游标卡尺测量长牡蛎的壳长、壳高和壳宽; 用电子天平称量长牡蛎的壳湿重, 解剖软组织、称量其湿重, 之后将其放入烘箱中 60 ℃烘干 72 h, 称其壳干重和软组织干重(精确至 0.01 g)。

1.3 实验指标的计算

1.3.1 生理率指标

滤水率(CR, L/h)= FR×(C_0–C_t)/C_0　　(1)

式中, FR 为流水槽的流速(L/h), C_0 和 C_t 分别为对照组和实验组实验水槽中的颗粒物数量。

同化效率(AE, %)=

(F–E)/[(1–E)×F]×100% (Conover, 1966)　　(2)

式中, $E = W_1/W_2$, $W_1 = W_{60} – W_{450}$, $W_2 = W_{60} – W_0$, F 和 E 计算方法相同, F 为饵料中有机物干重的比例, E 为粪便中有机物干重的比例。

耗氧率(OR, mgO_2/h) = (DO_0 – DO_t) × V/t　　(3)

式中, DO_0 和 DO_t 分别为实验结束时对照组和实验组水中溶解氧浓度(mg/L), V 为呼吸室体积(L), t 为耗氧用时(h)。

排氨率(RE, mgN/h) = (N_t – N_0) × V/t　　(4)

式中, N_0 和 N_t 分别为实验结束时对照组和实验组水中的氨氮浓度(mg/L), V 为呼吸室体积(L), t 为实验持续时间(h)。

组织干重标准化 $Y_s = (W_s/W_e)^b \times Y_e$　　(5)

式中, Y_s 是生物软组织干重标准化后的生理参数, W_s 是标准重量(1 g), W_e 为测得的动物软组织干重(g), Y_e 是未标准化的生理参数, b 为 0.67 (Wang *et al*, 2015)。

氧氮比=(OR/16)/(RE/14)(Widdows *et al*, 1988)　　(6)

1.3.2 收支方程

贝类能量收支方程: $C = P + R + U + F$　　(7)

式中, C 为摄食能, P 为生长能(生长余力), R 为呼吸能, U 为排泄能, F 为排粪能。

生长余力(SFG) [P, J/(h·g)] = A – (R + U)　　(8)

式中, 同化能(A)=C × AE, C = CR [L/(h·g)] × POM(mg/L) × 23 (J/mg POM), 本研究在计算能量收支时, 采用如下能量转换因子: 1 mg POM=23 J, 1 mg O_2=14.25 J, 1 mg NH_4^+-N= 24.93 J (Slobodkin *et al*, 1961; Widdows *et al*, 1979; Gnaiger, 1983)。

由能量收支方程转换为碳收支方程:

$C_c = P_c + R_c + U_c + F_c$　　(9)

式中, C_c 为摄食碳, P_c 为生长碳(生长余力), R_c 为呼吸碳, U_c 为排泄碳, F_c 为粪便碳。

生长余力[P_c, mg POC/(h·g)]=A_c–(R_c +U_c)　　(10)

式中, 同化碳(A_c)=C_c ×AE, C_c =CR[L/(h·g)]×POC(mg/L), F_c = C_c × (1–AE), R_c = 0.85 × (12/32) × OR, U_c = (12/28) ×RE (Bayne *et al*, 1983)。

1.4 数据统计与分析

实验数据用 Excel 2010 软件整理，实验结果以平均值±标准差(Mean±SD)表示；采用 SPSS 26 统计软件进行单因子方差分析(one-way ANOVA)的基础上，采用 Duncan´s 多重比较检验组间差异，P<0.05 为差异显著，P<0.01 为差异极显著；采用 Graphpad prism 7.0 软件作图。

2 结果与分析

2.1 三倍体和二倍体长牡蛎的摄食生理比较

三倍体和二倍体长牡蛎的滤水率和同化效率见图 2。三倍体长牡蛎的单位软组织干重滤水率和同化效率分别为(5.66±1.90) L/(h·g)和 52.98%，二倍体长牡蛎的单位软组织干重滤水率和同化效率分别为(4.76±1.70) L/(h·g)和 47.02%；三倍体长牡蛎的滤水率和同化效率高于二倍体长牡蛎，但均无显著差异(P>0.05)。

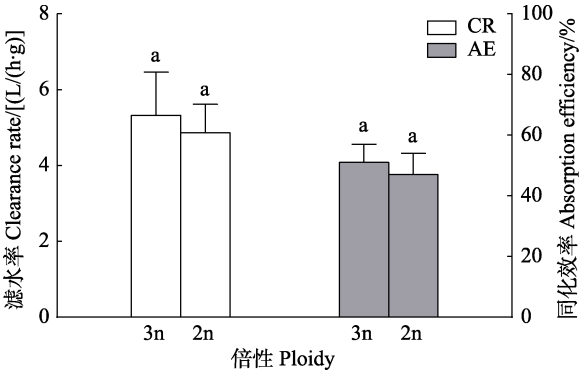

图 2 三倍体和二倍体长牡蛎的滤水率和同化效率
Fig.2 Clearance rate and absorption efficiency of triploid and diploid *C. gigas*

同种生理率不同倍性长牡蛎之间标有的不同字母的数据之间差异显著(P<0.05)。下同。
There are significant differences between the data labeled with different letters for the same physiological rate and different ploidy of *C. gigas* (P<0.05). The same below.

2.2 三倍体与二倍体长牡蛎的代谢生理比较

三倍体和二倍体长牡蛎的耗氧率和排氨率见图 3。三倍体长牡蛎的单位软组织干重耗氧率和排氨率分别为(1.15±0.15) mg/(h·g)和(0.091±0.011) mg/(h·g)，二倍体长牡蛎的单位软组织干重耗氧率和排氨率分别为(1.76±0.19) mg/(h·g)和(0.020±0.002) mg/(h·g)；三倍体长牡蛎的耗氧率显著低于二倍体长牡蛎(P<0.05)，排氨率显著高于二倍体长牡蛎(P<0.01)。

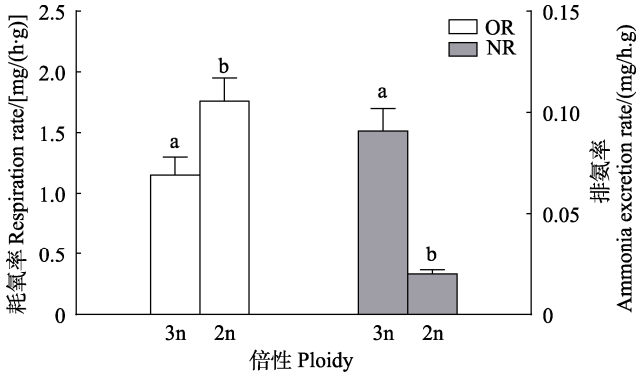

图 3 三倍体与二倍体长牡蛎的耗氧率和排氨率
Fig.3 Respiration rate and ammonia excretion rate of triploid and diploid *C. gigas*

三倍体和二倍体长牡蛎的氧氮比见图 4。三倍体和二倍体长牡蛎的 O/N 值分别为(11.36±3.15)%和(77.00±17.19)%，二倍体长牡蛎的 O/N 值显著高于三倍体长牡蛎(P<0.01)。

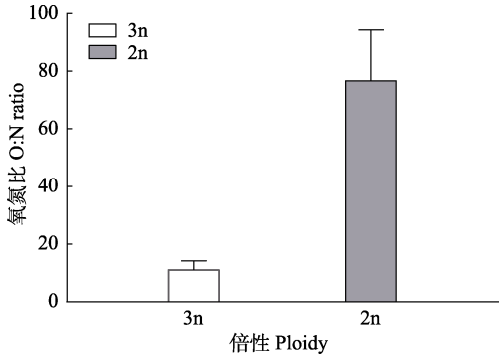

图 4 三倍体与二倍体长牡蛎的氧氮比
Fig.4 Oxygen to nitrogen ratio of triploid to diploid *C. gigas*

2.3 三倍体与二倍体长牡蛎的能量收支与碳收支比较

三倍体和二倍体长牡蛎的能量收支见表 1。从表 1 可以看出，三倍体长牡蛎的摄食能、同化能均高于二倍体长牡蛎，但无显著差异(P>0.05)；三倍体与二倍体的呼吸能、排泄能、生长余力存在显著差异性，三倍体长牡蛎的耗氧能显著低于二倍体长牡蛎(P<0.05)，但排氨能、生长余力显著高于二倍体长牡蛎(P<0.05)。

三倍体和二倍体长牡蛎的碳收支结果见表 2。可以看出，三倍体长牡蛎从食物中摄取并同化的碳主要用于自身生长，代谢碳占比较少；而二倍体长牡蛎的同化碳主要用于呼吸消耗，其次用于生长，排泄碳最少。三倍体长牡蛎的摄食碳和同化碳均高于二倍体长牡蛎，但无显著差异(P>0.05)；三倍体与二倍体长牡蛎的代谢碳和生长余力存在显著差异(P<0.05)，三倍体长牡蛎的呼吸碳显著低于二倍体长牡蛎(P<0.05)，但排泄碳、生长余力显著高于二倍体长牡蛎(P<0.01)。

表 1　三倍体与二倍体长牡蛎的能量收支(以软组织干重计)

Tab.1　Energy budget of triploid and diploid *C. gigas* (based on dry weight of soft tissue)

倍性 Ploidy	摄食能 *C*/[J/(h·g)]	同化能 *A*/[J/(h·g)]	呼吸能 *R*/[J/(h·g)]	排泄能 *U*/[J/(h·g)]	生长余力 *P*/[J/(h·g)]
3n	781.23±145.40[a]	413.90±77.03[a]	16.39±3.50[a]	2.270±0.286[a]	395.24±73.24[a]
2n	569.30±131.47[a]	267.69±61.82[a]	25.08±2.45[b]	0.487±0.165[b]	242.12±59.21[b]

注：同一列不同上标字母为差异显著(P<0.05)。下同。

Note: Data with different superscript letters in the same column are significantly different (P<0.05). The same below.

表 2　三倍体与二倍体长牡蛎的碳收支(以软组织干重计)

Tab.2　Carbon budget of triploid and diploid *C. gigas* (based on dry weight of soft tissue)

倍性 Ploidy	摄食碳 C_c/[mgC/(h·g)]	同化碳 A_c/[mgC/(h·g)]	呼吸碳 R_c/[mgC/(h·g)]	排泄碳 U_c/[mgC/(h·g)]	生长余力 P_c/[mgC/(h·g)]
3n	2.85±0.79[a]	1.51±0.45[a]	0.37±0.08[a]	0.039±0.005[a]	1.10±0.37[a]
2n	1.99±0.64[a]	0.94±0.30[a]	0.56±0.12[b]	0.008±0.003[b]	0.37±0.18[b]

3　讨论

3.1　三倍体和二倍体长牡蛎的摄食生理比较

滤水率是反映贝类滤水能力的一项重要的动态指标，受多种因素影响(张媛等, 2015; 王冲等, 2020)。本研究发现，同一区域同一时期投苗的三倍体和二倍体长牡蛎在夏季高温期的滤水率无显著性差异，但三倍体长牡蛎的滤水率高于二倍体长牡蛎。Mizuta 等(2021)研究发现，在美国 Gloucester Point 海域，同种规格的三倍体与二倍体美洲牡蛎(*Crassostra virginica*)的滤水率分别为(5.63±0.98)和(4.69±0.43) L/(h·g)，美洲牡蛎的滤水率与倍性无显著相关性，但三倍体美洲牡蛎均高于二倍体，这与本研究结果一致。已有研究表明，三倍体与二倍体长牡蛎滤水率的差异和鳃面积与干肉重的比值有关，三倍体长牡蛎较高的鳃面积与干肉重比使得鳃丝对海水颗粒物的截留效率高于二倍体长牡蛎(Haure *et al*, 2003)。

同化效率是反映滤食性贝类对食物颗粒消化吸收能力的重要指标。本研究中，三倍体与二倍体长牡蛎的同化效率无显著差异，但三倍体长牡蛎同化效率高于二倍体长牡蛎。Osterheld 等(2023)研究发现，三倍体和二倍体紫贻贝(*Mytilus galloprovincialis*)的同化效率分别为(86.0±2.4)%和(84.8±1.4)%，紫贻贝的同化效率与倍性无显著相关性，这与本研究结果一致。已有研究表明，滤食性贝类的同化效率主要是由纤毛和消化酶活性控制(MacDonald *et al*, 1998)，三倍体长牡蛎较高的消化酶活性，使得机体能够较大限度地对食物消化吸收(Kesarcodi-Watson *et al*, 2001b)。

3.2　三倍体和二倍体长牡蛎的代谢生理比较

耗氧率和排氨率是维持滤食性贝类正常新陈代谢和其他生命活动的重要指标。目前，对长牡蛎代谢生理的研究多集中于二倍体，且发现处于不同发育阶段的长牡蛎生理代谢存在差别，尤其是对于性成熟的个体(毛玉泽等, 2005)。本研究聚焦夏季高温这一重要时段，对比分析了二倍体和三倍体的代谢生理差异。结果表明，在繁殖季节，三倍体和二倍体长牡蛎的耗氧率和排氨率具有显著差异，三倍体长牡蛎耗氧率显著低于二倍体，但排氨率显著高于二倍体。Kesarcodi-Watson 等(2001a)研究发现，三倍体与二倍体悉尼岩牡蛎(*Saccostrea commercialis*)的耗氧率分别为 0.57 mg/(h·g)和 0.70 mg/(h·g)，排氨率分别为 0.042 mg/(h·g)和 0.021 mg/(h·g)，三倍体悉尼岩牡蛎的耗氧率显著低于二倍体，但排氨率显著高于二倍体，这与本研究结果一致。已有研究结果表明，贝类呼吸代谢与杂合度呈负相关关系，杂合度越高的贝类，其呼吸代谢越低(Tremblay *et al*, 2016)；贝类杂合度与基因的剂量状态效应无关，而与等位基因多样性有关，其中与等位基因多样性相关的多态位点酶主要有 6 种，如酯酶-1、酯酶-3、磷酸葡萄糖变位酶-1、6-磷酸葡萄糖酸脱氢酶和磷酸葡萄糖异构酶，多态位点酶浓度越高，杂合度越高(Hawkins *et al*, 1994)。此外，贝类氨氮排泄量较高与体内存在较强的蛋白质代谢和周转有关，主要机理在于体内天冬氨酸转氨酶(Aat)浓度较高，使氨基酸的脱氨基作用加快，促进了蛋白质的代谢和周转(Hawkins *et al*, 1996; 周钱森等, 2022)。

氧氮比(O/N)是生物利用代谢底物的一个重要参数，用于评估生物体对外界环境的适应能力，它反映生物在特定状态下蛋白质、糖类、脂肪代谢之间的比例关系(任黎华等, 2014; 姜娓娓等, 2017)。当外界环境发生变化时，生物体供能的代谢底物会发生相应的变化，当 O/N≈7.0~9.3 时，生物体对能量需求较低，主要以蛋白质代谢为主(霍恩泽等, 2021; 周建聪等, 2022)；当 O/N>24 时，生物体主要以糖类和脂肪代谢

为主(Mayzaud *et al*, 1973)。本研究发现，在夏季高温环境下，三倍体和二倍体长牡蛎的 O/N 值的波动范围分别为 7.91~14.11 和 59.81~94.19，因此，三倍体长牡蛎的主要供能物质为蛋白质，二倍体长牡蛎的主要供能物质为糖类和脂肪，这种代谢底物的差异使得处于该时期的三倍体长牡蛎糖原含量明显高于二倍体。许多研究发现，三倍体双壳类在繁殖期的糖原含量明显高于二倍体(Berthelin *et al*, 2000; Ojea *et al*, 2004; Qin *et al*, 2019)，这与本研究结果一致。已有研究表明，贝类体内蛋白质代谢较高与体内氨氮排泄量增加及对能量需求低有关(Hawkins *et al*, 1996)；贝类体内糖类和脂肪代谢较高与产卵期能量需求高有关(毛玉泽等, 2005)。

3.3 三倍体和二倍体长牡蛎的能量/碳分配比较

生长余力是评估生物整体生理活动状态的一项重要的生理指标(Bayne, 2017)。通过解析倍性效应对长牡蛎摄食能/碳在体内分配的情况，可以反映倍性效应对长牡蛎生长余力的影响。本研究中，倍性对长牡蛎的摄食能/碳、同化能/碳均无显著影响，但三倍体长牡蛎的摄食能/碳、同化能/碳均大于二倍体长牡蛎，倍性对长牡蛎的代谢能/碳有显著影响，三倍体长牡蛎的呼吸能/碳显著低于二倍体长牡蛎，而排泄能/碳显著高于二倍体长牡蛎；经此能量/碳分配，三倍体长牡蛎的生长余力显著高于二倍体长牡蛎。张国范等(2000)对长牡蛎和 Qin 等(2019)对香港牡蛎(*Crassostrea hongkongensis*)的研究发现，三倍体贝类的生长速度快于二倍体，养殖 1 年后，三倍体贝类的体重为二倍体的 1.5 倍左右。Osterheld 等(2023)研究发现，与二倍体相比，三倍体紫贻贝具有更高的生长潜力，三倍体紫贻贝的生长余力约为二倍体的 3.5 倍。这与本研究结果一致。已有研究表明，三倍体双壳类较高的生长余力与机体低代谢水平有关(Shpigel *et al*, 1992; Hawkins *et al*, 2000; Qin *et al*, 2019)；此外，三倍体长牡蛎的性腺发育程度低，其性腺指数为二倍体长牡蛎的 1/5 (周一兵等, 2000)；与二倍体相比，三倍体双壳类的生长优势在于软组织部储备的能量大多用于生长，少数用于配子发育(Ruiz-Verdugo *et al*, 2000; Normand *et al*, 2008)。

本研究从个体水平生理生态学层面研究发现，与二倍体相比，在夏季高温季节，三倍体长牡蛎通过调整摄食和代谢生理行为，在能量分配策略上表现出一定的优势，但三倍体长牡蛎应对不利环境所采取的响应策略内在的分子机制尚不明确，后续尚需结合组学等系统生物学技术从分子层面深入诠释。

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Comparative Study on the Feeding Metabolism and Carbon Budget of the Triploid and Diploid Pacific Oyster (*Crassostrea gigas*)

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Abstract　*Crassostrea gigas*, also known as Pacific oysters, are economic shellfish with the widest range of cultivation, the highest yield in the world, and the most important type of mariculture shellfish in China. However, many *C. gigas* have died during summer in coastal areas worldwide in recent decades. In 2008, the mortality rate of *C. gigas* cultured in France reached 40%–100%. In 2009, the mortality rate of *C. gigas* in some area of Sanggou Bay reached 51%. In 2019, the mortality rate of the Rushan area reached 50%–90%, with the death peak occurring in middle and late August. There were many reasons for the large-scale death of *C. gigas*, such as temperature, dissolved oxygen, salinity, disease, food availability, and reproduction levels, among which high temperature was the most important abiotic stress factor. The high temperature in summer disturbed the enzyme metabolism of *C. gigas*, resulting in slow or impeded growth. Furthermore, the reproduction and spawning of *C. gigas* caused a large amount of protein consumption, and physical weakness combined with high-temperature stress induced many deaths. Therefore, considering the problems faced by *C. gigas* culture during high summer temperatures, the introduction of new varieties will increase the economic benefits to the industry.

Due to its high sterility, triploid *C. gigas* has attributes such as a fast growth rate, resilience excellent economic characteristics, and high energy conversion efficiency. In recent years, a certain farmed scale has formed in China, especially in northern coastal areas. There have been many studies on the biological and physiological differences between triploid and diploid *C. gigas* worldwide, mainly focusing on the differences in growth characteristics, soft tissue components, gonadal development, disease resistance, and gill structure. However, comparisons between triploid and diploid *C. gigas* feeding, metabolic physiology, energy budget, and carbon budget have not been reported. Focusing on the specific period of high temperatures in summer, this study investigated the feeding and metabolic physiological characteristics of triploid and diploid *C. gigas* using the field

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flow method, and compared and analyzed their energy allocation strategies in response to a high-temperature environment. The study provide data support for revealing the physiological differences caused by the ploidy effect of *C. gigas* in order to assist with evaluating the culture capacity.

Triploid and diploid *C. gigas* were selected as research objects in August 2022 to analyze the differences in feeding and metabolic physiology and energy/carbon allocation strategies during high temperatures in summer. Physiological parameters related to intake and metabolism, such as water filtration rate, absorption efficiency, oxygen consumption rate, and ammonia discharge rate, were determined based on the field flow method in Sanggou Bay, Rongcheng, Shandong Province, and energy allocation and carbon allocation were estimated based on the principle of the energy budget. The results revealed that the water filtration rate and assimilation efficiency of triploid *C. gigas* were higher than those of diploid *C. gigas*, but there were no significant differences ($P>0.05$). There were significant differences in the oxygen consumption rate and ammonia discharge rate between triploid and diploid *C. gigas* ($P<0.05$). The oxygen consumption rate of triploid *C. gigas* was significantly lower than that of diploid *C. gigas* ($P<0.05$), but ammonia discharge rate was significantly higher than that of diploid *C. gigas* ($P<0.01$). The results of the energy and carbon budget analyses showed that the feeding energy/carbon and assimilation energy/carbon values of triploid *C. gigas* were higher than those of diploid *C. gigas*, but there was no significant difference ($P>0.05$). There were significant differences in respiratory energy/carbon, excretion energy/carbon, and growth power between triploid and diploid *C. gigas* ($P<0.05$). Respiratory energy/carbon values of triploid *C. gigas* were significantly lower than those of diploid *C. gigas* ($P<0.05$), but excretion energy/carbon and growth power values were significantly higher than those of diploid *C. gigas* ($P<0.05$). The oxygen/nitrogen ratio of triploid and diploid *C. gigas* fluctuated in the range of 7.91–14.11 and 59.81–94.19, respectively. Moreover, the main energy supply substances of triploid *C. gigas* were proteins, while the main energy supply substances of diploid *C. gigas* were carbohydrates and fats. These results revealed the differences in energy allocation patterns associated with the ploidy effect of *C. gigas* during high temperatures in summer.

From the perspective of individual physiology and ecology, this study found that, compared with diploid *C. gigas*, triploid *C. gigas* showed certain advantages in energy allocation strategies by adjusting feeding and metabolic physiological behaviors during the high-temperature summer. However, the internal molecular mechanism of response strategies adopted by triploid *C. gigas* to cope with an adverse environment is still unclear. Further interpretation at the molecular level needs to be combined with omics and other systems biology techniques.

Key words *Crassostrea gigas*; Triploid; Diploid; Summer high temperature; Physiological energetics