

Article

Comparative Feeding Performance of *Magallana gigas* and *Argopecten irradians*: Implications for Sustainable Spatial Management in Intensively Cultured Coastal Waters

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Abstract

Sustainable management of intensive aquaculture areas requires a profound understanding of the feeding interactions between cultured species and their environment. This study compared the seasonal feeding performance of the Pacific oyster *Magallana gigas* and the bay scallop *Argopecten irradians* on the southern coast of Korea using the biodeposition method. Our results demonstrated significant interspecific differences: *M. gigas* adopted a ‘high-throughput’ strategy with superior filtration rates, whereas *A. irradians* exhibited a ‘pre-ingestive selective’ strategy characterized by higher pseudofeces production and particle rejection. Based on these findings, we propose three core spatial management strategies: (1) horizontal re-arrangement to optimize food utilization by positioning high-efficiency filter feeders upstream; (2) a dynamic vertical positioning strategy to mitigate metabolic stress during environmental shifts; and (3) an environmental management model incorporating species-specific biodeposition loads. These strategies provide a scientific foundation for maximizing growth efficiency while ensuring the ecological sustainability of intensive aquaculture systems.

Keywords: *Argopecten irradians*; biodeposition; feeding performance; *Magallana gigas*; sustainable aquaculture

Key Contribution: This study proposes optimized spatial arrangement strategies for *M. gigas* and *A. irradians* to ensure sustainable aquaculture by mitigating environmental impacts and maximizing resource utilization efficiency.



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1. Introduction

Humanity relies heavily on marine products for protein supply, with the global system shifting from capture fisheries to aquaculture. Recently, global aquaculture production has surpassed wild capture, establishing itself as the cornerstone of the fisheries industry [1]. In South Korea, total aquaculture production reached approximately 2.29 million tons in 2024, significantly outstripping wild fishery production; notably, Korea maintains a leading global position in shellfish production [2].

Shellfish culture, a representative unfed aquaculture practice, is recognized for its role in enhancing water quality through the filtration of suspended organic matter [3,4].

Despite these benefits, the expansion of intensive farming has raised concerns regarding environmental sustainability. When stocking densities exceed the local carrying capacity, the resulting accumulation of biodeposits often leads to benthic degradation and hypoxia, necessitating strategic farm management [4,5]. In the aquaculture activities of Jinhae Bay and Tongyeong, prolonged intensive culture has been identified as a primary driver of accelerated environmental degradation [6–8]. Specifically, the accumulation of biodeposits from dense bivalve cultures promotes benthic organic enrichment, leading to localized hypoxia and elevated nutrient loading that can trigger phytoplankton blooms [9,10]. Conversely, excessive farming density can result in the localized or layer-specific depletion of available phytoplankton due to the high filtration capacity of the cultured species [11,12]. In areas where species sharing feeding resources, such as Pacific oyster *Magallana gigas* and bay scallop *Argopecten irradians*, are co-cultured, interspecific competition may diminish feeding efficiency and cause economic losses.

M. gigas is a globally significant aquaculture species, currently cultivated in approximately 66 countries [13], with South Korea ranking second worldwide in production [1]. Ecologically, it inhabits intertidal or shallow subtidal areas on both hard and soft substrates [14]. Utilizing these ecological characteristics, oyster farming in Asian countries, such as Korea, China, and Japan, is predominantly conducted using the suspended longline culture system, where oyster spats are attached to cultches and subsequently suspended from vertical ropes in the water column. This intensive culture system allows for the efficient utilization of three-dimensional marine space and maximizes food availability through continuous exposure to ambient currents.

The southern coast of Korea, with its rias topography and high primary productivity, has established a high-efficiency environment for *M. gigas*. Concurrently, rising seawater temperatures driven by climate change have challenged traditional scallop aquaculture throughout major Yesso scallop farming areas, as high-temperature events are increasingly associated with mass mortality and pronounced physiological stress responses in bivalves [15–17]. Consequently, the heat-tolerant bay scallop (*A. irradians*) has emerged as a strategic alternative to mitigate these climate risks. Tongyeong, the largest producer of *M. gigas* in Korea, is experiencing a surge in *A. irradians* production due to recent species diversification strategies [2].

A. irradians is a mobile bivalve primarily inhabiting sandy and gravel-bottomed substrates, as well as highly productive seagrass environments [18]. This species is characterized by a short lifespan of 1–2 years, a hermaphroditic reproductive strategy, rapid growth, high metabolic activity, and a high vulnerability to environmental stressors. To sustain its elevated metabolic rates, *A. irradians* exhibits highly active filter-feeding behavior. Originally native to North America, *A. irradians* was introduced to coastal areas of East Asia, including China, Taiwan, Korea, and Japan [18,19]. Due to its rapid growth rate, which allows for commercial harvesting within a single year, it has become a highly valuable aquaculture species in the region [20]. In Asia, *A. irradians* aquaculture is predominantly conducted using suspended cage-culture systems. In particular, because its introduction to Korea via transplantation from China in 1996 [21] was relatively recent, comprehensive physiological and ecological data required to establish optimized strategic management practices for sustainable production remain limited.

As previously described, the native habitats of the *M. gigas* and the *A. irradians* are distinctly different. In South Korea, however, shellfish aquaculture licenses are categorized by the culture method rather than the target species. Because both species are cultivated using suspended culture systems, longline rope culture for *M. gigas* and suspended lantern net culture for *A. irradians*, their cultivation areas frequently overlap without clear boundaries. However, these two species differ fundamentally in gill morphology and their

corresponding feeding strategies. While *M. gigas* possesses a highly developed ciliary system (e.g., laterofrontal cirri) that allows for broad particle retention and efficient pre-ingestive selection, *A. irradians* exhibits more size-dependent retention efficiencies due to structural differences in gill anatomy [22,23]. These physiological distinctions are expected to influence their respective feeding performance and responses under varying environmental conditions.

Under high-density shellfish aquaculture conditions, the co-existence of these two species can intensify interspecific competition for limited food resources, potentially leading to reduced aquaculture productivity and localized coastal environmental degradation. Therefore, strategic spatial allocation based on primary productivity and species-specific feeding characteristics is essential for sustainable fisheries management.

Generally, physiological indicators such as filtration, clearance, and excretion rates have been utilized as core criteria to evaluate both individual growth performance [24,25] and ecosystem-scale carrying capacity [26–28]. However, many previous studies have relied on controlled laboratory environments to elucidate bivalve feeding mechanisms in response to specific stimuli or environmental conditions [29,30]. This approach limits the ability to fully reflect the complex dynamics of real marine ecosystems, where organic and inorganic matter coexists with a diverse size-spectrum of plankton.

To overcome these limitations, the biodeposition method designed by Galimany et al. [31] was introduced. By continuously supplying ambient seawater, this system maintains natural feeding activities, thereby enabling the distortion-free measurement of physiological responses within the actual ecosystem. Crucially, this apparatus provides a distinct academic advantage by allowing the separate collection of excreted feces and pseudofeces, which facilitates the quantitative determination of the cultured organisms' practical food selectivity, digestion/assimilation rates, and metabolic excretion rates.

Accordingly, the objective of this study is to compare and analyze the feeding performance of *M. gigas* and *A. irradians*, key aquaculture species along the southern coast of Korea, using the field-based biodeposition method. Through this comprehensive assessment, we aim to clarify the underlying physiological mechanisms of both species and, ultimately, propose effective spatial allocation and advanced, sustainable aquaculture management strategies for diversified shellfish farming areas.

2. Materials and Methods

2.1. Study Site and Period

The experiment was conducted at a farm located in Sanyang-eup, Tongyeong, Gyeongsangnam-do, South Korea (34°45'12.7" N, 128°23'46.6" E). At this integrated multi-trophic aquaculture (IMTA) site, rockfish *Sebastes schlegelii* and sea cucumbers *Apostichopus japonicus* were co-cultured alongside the target bivalves. Among these, the target species *M. gigas* and *A. irradians* were cultivated using suspended vertical longline ropes and suspended lantern nets, respectively. The culture depth for both species was maintained at 2–4 m in strict accordance with the national aquaculture management manual [32,33]; however, stocking conditions differed, with *M. gigas* kept at 20–30 individuals per cultch (20 cm cultch spacing, 40 cm hanging line spacing) and *A. irradians* stocked at 20 individuals per tier in a lantern net (40 cm diameter, 2 cm mesh size).

To represent the distinct environmental characteristics of each season, sampling was performed once per season in May, August, and October 2016, and January 2017, representing spring, summer, autumn, and winter, respectively (hereafter referred to by their respective seasons). To minimize the confounding effects of short-term weather anomalies (e.g., recent rainfall), all sampling campaigns were carefully scheduled and conducted

during periods with zero precipitation on both the sampling and preceding day, based on official data from the Korea Meteorological Administration.

2.2. Experimental Species

This study utilized commercial-sized individuals of *M. gigas* (shell height: 59.41–104.29 mm) and *A. irradians* (shell length: 57.63–71.83 mm). To eliminate any confounding effects of vertical environmental gradients within the water column, individuals of average commercial size were randomly sampled across the entire depth range of the suspended cultivation structures for the experiment.

To ensure that the experimental specimens were statistically representative of the broader cultured ecosystem, a larger background population ($n = 30$ per species for each seasonal event) was initially sampled directly from the culture longlines to characterize the true size distribution of the farm. From these median cohorts, eight experimental individuals per species ($n = 8$) were precisely sub-sampled that strictly fell within these mean biometric boundaries to ensure representativeness and minimize demographic variance. Prior to the experiments, all epibiota were carefully removed from the shells. The physiological robustness and quality of the collected data are further supported by the high vitality of the specimens; 100% of the selected individuals exhibited active, continuous filtration and shell opening throughout the trials, with zero mortality or signs of physiological depression.

2.3. Environmental Monitoring and Analytical Procedures

To characterize the environmental conditions at the study site, surface seawater temperature (SST), salinity, pH, and dissolved oxygen (DO) were measured in situ using a YSI 6000 microprobe system (SI Inc., Yellow Springs, OH, USA). For the analysis of chlorophyll-a (Chl-a), dissolved inorganic nutrients (DIN and DIP), and particulate matters, discrete 500 mL surface seawater was collected in plastic bottles. This comprehensive sampling regimen was conducted at 15-min intervals over a 2-h period across 9 distinct time points (including the initial baseline measurement at $t = 0$), performing all samplings in duplicate (yielding a total of 18 samples per physiological trial). To ensure these high-resolution data reflected typical seasonal patterns rather than daily anomalies, the environmental trends were validated against 5-year historical regional data from the National Institute of Fisheries Science (NIFS; Figure S1).

The concentrations of chlorophyll a (Chl-a), dissolved inorganic nitrogen (DIN), dissolved inorganic phosphorus (DIP), total particulate matter (TPM), particulate organic matter (POM), and particulate inorganic matter (PIM) were determined following the standard protocols of the Korean Marine Environmental Measurement Methods [34]. Briefly, Chl-a was extracted from the filters with 90% acetone and quantified spectrophotometrically [35]. The DIN and DIP in the filtrate were determined spectrophotometrically using automated continuous flow analysis (CFA). Specifically, ammonium was analyzed via the indophenol method, nitrite via the sulfanilamide method, nitrate via the cadmium–copper reduction column method, and phosphate (DIP) via the ascorbic acid reduction method. For particulate matter analysis, the 500 mL seawater samples were filtered immediately through the pre-weighed 0.45 μm GF/F glass fiber filters, which were subsequently rinsed with isotonic ammonium formate to eliminate residual salts. The resulting filters were then immediately stored on ice until laboratory analysis. In the laboratory, TPM was determined gravimetrically by drying the filters to a constant weight at 110 °C for 1 h. PIM was determined after subsequent combustion of the filters at 450 °C for 10 min, and POM was calculated as the difference between TPM and PIM ($\text{POM} = \text{TPM} - \text{PIM}$) [34].

2.4. Experimental Design and Gut Transit Time (GTT)

The experimental setup for measuring in situ feeding rates followed the methodology described by Galimany et al. [31]. To simulate natural ambient conditions, seawater was continuously supplied to a header tank via a submersible pump from the upper surface layer (within 1 m depth), corresponding to the daytime productive zone where phytoplankton aggregates due to photosynthetic irradiance. The flow rate to each feeding chamber was strictly monitored and maintained at a fixed rate of 12 L h^{-1} [36,37].

For the feeding trials, the selected specimens ($n = 8$ per species) were placed in separate chambers, while four chambers containing empty shells (two for each species) served as controls. The specimens were oriented with their ligaments facing the inflow to facilitate natural active pumping and selective particle ingestion [38]. Before beginning biodeposition collection, the GTT was determined to establish the appropriate sampling start time. GTT was measured in triplicate for each species by recording the interval between the provision of the microalgae *Tetraselmis suecica* and the initial discharge of true feces [31,39]. To ensure that only experimental biodeposits were collected, the organisms were acclimated under flow-through conditions for a period exceeding the measured GTT to void any pre-existing digestive contents.

2.5. Biodeposition and Physiological Rate Analysis

Biodeposits (feces and pseudofeces) were collected from individual chambers over a standardized 2-h period following established ecophysiological protocols [31,36,40]. This concentrated sampling window was strictly maintained to prevent individual statistical artifacts and to freeze environmental variables (e.g., ambient SST and salinity), thereby capturing a stable feeding snapshot free from tidal or diurnal fluctuations. During the trials, the biodeposits were continuously monitored in real time and collected immediately upon ejection to eliminate localized mixing or physical degradation.

The samples were filtered through pre-weighed $0.7 \mu\text{m}$ pore size Whatman 25 mm GF/F filters and dried at 60°C for 48 h to determine the TPM. Subsequently, the filters were combusted at 450°C for 10 min to measure the PIM. POM was calculated as the weight difference between TPM and PIM, and the organic content of the seston (f) was defined as the POM/TPM ratio.

After the experiment, the soft tissues of the oysters and scallops were dissected, dried at 60°C for 48 h, and weighed to obtain the dry tissue weight. Using these values, several physiological rates and efficiencies were calculated following established methodologies [36,37,40]. A detailed summary of the parameters and their respective equations is provided in Table 1.

Table 1. Calculation of physiological indices for shellfish feeding behavior analysis.

Physiological Indices	Calculation [36,40]
Clearance Rate (CR; L h^{-1})	IFR/PIM (mg L^{-1}) in the sea water
Inorganic Filtration Rate (IFR; mg h^{-1})	IER + IRR
Inorganic Egestion Rate (IER; mg h^{-1})	PIM of feces/feces collection time
Inorganic Rejection Rate (IRR; mg h^{-1})	PIM of pseudofeces/pseudofeces collection time
Filtration Rate (FR; mg h^{-1})	$\text{CR} \times \text{TPM} (\text{mg L}^{-1})$ in the sea water
Rejection Rate (RR; mg h^{-1})	IRR + ORR
Organic Rejection Rate (ORR; mg h^{-1})	POM of pseudofeces/pseudofeces collection time
Rejection Proportion (RP; %)	$(\text{RR}/\text{FR}) \times 100$
Selection Efficiency (SE; %)	$[1 - (\text{organic fraction with pseudofeces}/\text{organic fraction in the sea water})] \times 100$
Organic Ingestion Rate (OIR; mg h^{-1})	$(\text{CR} \times \text{POM in the sea water}) - \text{ORR}$
Organic Egestion Rate (OER; mg h^{-1})	POM of feces/feces collection time
Absorption Rate (AR; mg h^{-1})	$\text{OIR} - \text{OER}$
Absorption Efficiency (AE; %)	$(\text{AR}/\text{OIR}) \times 100$
Biodeposition rate (BR; mg h^{-1})	$(\text{total feces egested h}^{-1}) + (\text{mg total pseudofeces h}^{-1})$

To eliminate size-related variations among the calculated parameters, all physiological rates (clearance and filtration rates) were robustly standardized to a 1 g dry tissue weight unit by employing the allometric scaling equation:

$$Y_s = Y_e \times (1/W_e)^b,$$

where Y_s and Y_e represent, respectively, the standardized and experimentally observed physiological rates, and W_e denotes the dry tissue weight of each individual. The weight-specific exponents b applied were 0.73 for *M. gigas* and 0.70 for *A. irradians* [22,41].

2.6. Statistical Analysis

Statistical analyses were performed using IBM SPSS Statistics 20.0 (SPSS Inc., Chicago, IL, USA). A one-way analysis of variance (ANOVA) followed by Tukey’s honestly significant difference (HSD) post-hoc test was used to evaluate seasonal variations within each species. Additionally, independent-samples *t*-tests were employed to compare significant differences between the two species within each season. Statistical significance was defined as $p < 0.05$, and higher levels of significance were indicated as $p < 0.01$ and $p < 0.001$ where applicable.

3. Results

3.1. Environmental Variables at the Experimental Site

SST ranged from 10.92 °C to 26.10 °C, while salinity remained stable between 31.19 and 33.04 psu (Table 2). The temperature trends during the study period closely mirrored the 5-year historical regional dataset from the National Institute of Fisheries Science (NIFS; Figure S1) [42], confirming that these environmental conditions reflect typical seasonal patterns rather than interannual anomalies. Regarding dissolved oxygen (DO), the optimal levels recorded in this study (6.80–8.50 mg L^{−1}) reflected the typical characteristics of the well-oxygenated surface photic zone where the suspended culture longlines are positioned, remaining unaffected by the localized bottom-water hypoxia often concerned in this estuary.

Table 2. Seasonal variations in physico-chemical environmental parameters at the culture site during the study period.

Date	SST (°C)	Salinity (psu)	DO (mg L ^{−1})	Chl-a (µg L ^{−1})	DIN (mg L ^{−1})	DIP (mg L ^{−1})
Spring	15.40 ± 0.12	33.04 ± 0.02	8.50 ± 0.15	0.70 ± 0.04	0.1456 ± 0.008	0.0140 ± 0.001
Summer	26.10 ± 0.25	31.19 ± 0.06	6.80 ± 0.21	1.00 ± 0.09	0.2466 ± 0.012	0.0241 ± 0.002
Autumn	21.16 ± 0.18	32.73 ± 0.06	6.80 ± 0.11	3.15 ± 0.22	0.2792 ± 0.015	0.0338 ± 0.002
Winter	10.92 ± 0.09	32.13 ± 0.04	7.32 ± 0.14	0.71 ± 0.01	0.1935 ± 0.010	0.0340 ± 0.001

Note: SST, Surface seawater temperature; DO, Dissolved oxygen; Chl-a, chlorophyll a; DIN, dissolved inorganic nitrogen; DIP, dissolved inorganic phosphorus; psu, practical salinity unit.

Regarding nutrient and food availability, the concentrations of Chl-a, DIN, and DIP ranged from 0.70 to 3.15 µg L^{−1}, 0.1456 to 0.2792 mg L^{−1}, and 0.0140 to 0.0340 mg L^{−1}, respectively.

The Chl-a concentration was lowest in spring (0.70 µg L^{−1}) and gradually increased with rising SST, peaking in autumn (3.15 µg L^{−1}). Similarly, DIN concentration reached its minimum in spring (0.1456 mg L^{−1}) and maximum in autumn (0.2792 mg L^{−1}).

Values represent the Mean ± SD derived from a high-frequency continuous monitoring protocol consisting of 9 consecutive sampling events ($n = 9$) within each seasonal 2-h experimental window.

The concentration of TPM exhibited distinct seasonal variations during the study period (Figure 1). Specifically, the TPM concentration reached its annual peak of 20.0 mg L^{-1} in winter. In contrast, the minimum TPM level (approximately $6\text{--}7 \text{ mg L}^{-1}$) was recorded in summer. The organic fraction (f ; POM/TPM) peaked in summer, coinciding with the lowest TPM concentration. Conversely, the f value showed a progressive decline from autumn through winter.

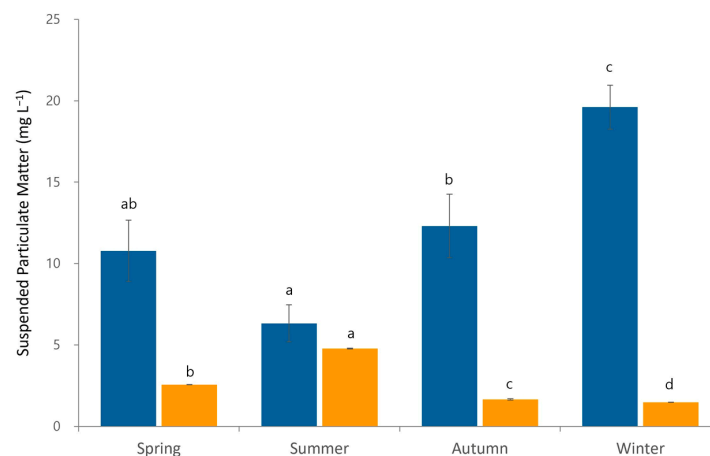


Figure 1. Temporal variations in suspended particulate matter. Blue bars and orange bars represent total particulate matter (TPM) and organic matter fraction (f = particulate organic matter, POM/TPM), respectively. Error bars represent the standard error of the mean ($n = 18$). Different lowercase letters indicate statistically significant differences ($p < 0.05$) among seasons within each parameter by Tukey's HSD test.

3.2. Feeding Characteristics

3.2.1. Gut Transit Time (GTT)

The GTT of *M. gigas* was shortest in summer (46 min) and reached its maximum in winter (138 min). Similarly, *A. irradians* exhibited seasonal variations, with GTTs ranging from 40 min in summer to 85 min in winter. A comparison between the two species revealed that *A. irradians* maintained a relatively shorter GTT than *M. gigas*. Both species showed a distinct negative correlation between GTT and SST (Figure 2).

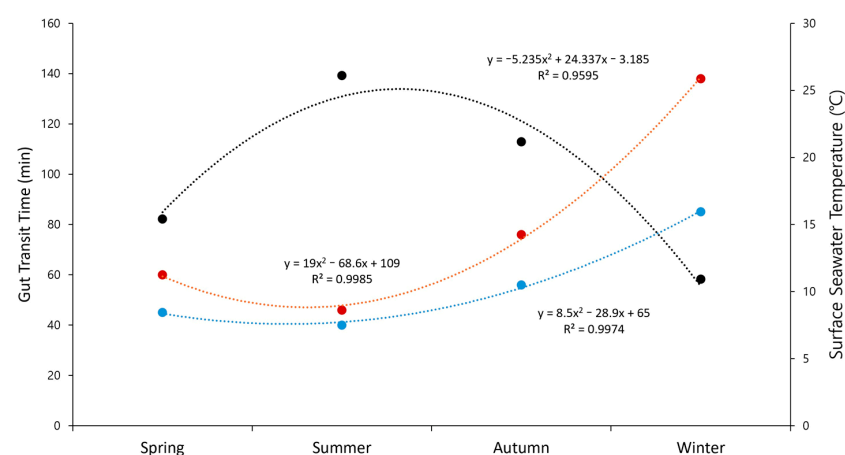


Figure 2. Seasonal variations in gut transit time (GTT) of *M. gigas* and *A. irradians* in relation to surface seawater temperature (SST). Red circles (●) represent *M. gigas* GTT; blue circles (●) represent *A. irradians* GTT; and black circles (●) indicate SST. The dotted lines denote second-order polynomial trendlines. The displayed equations and R^2 values represent the regression analysis and the strength of the seasonal correlation between temperature and GTT for each species.

However, since this regression analysis is based on a limited number of seasonal data points resulting in low degrees of freedom, this curve cannot be utilized as a generalized predictive model. Nevertheless, the observed trends are highly consistent with the general physiological patterns reported in other bivalves, and these findings served as a reliable preliminary reference to determine the appropriate animal stabilization and initial sampling times for the subsequent biodeposition experiments.

3.2.2. Pre-Ingestive Analysis

- Clearance rate (CR)

The CR of both species exhibited distinct seasonal variations throughout the study period, reaching an annual maximum in summer (One-way ANOVA, $p < 0.001$). Post-hoc analysis revealed that the peak in summer was significantly higher than in all other seasons, with no statistically significant differences detected among spring, autumn, and winter. Despite the apparent variations in their mean values during these three seasons, the lack of statistical significance may be attributed to the high individual variability inherent in natural field samples.

In interspecific comparisons, the CR of *M. gigas* was significantly higher than that of *A. irradians* in spring ($p < 0.01$) and autumn ($p < 0.05$). Conversely, no significant differences were found between the two species in summer and winter ($p > 0.05$) (Figure 3a, Table S1).

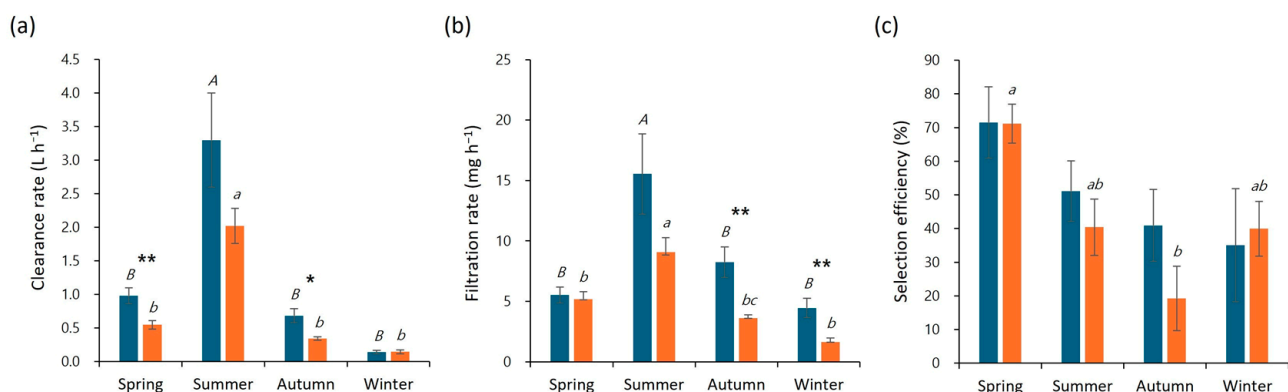


Figure 3. Seasonal variations in (a) clearance rate (CR, L h⁻¹), (b) filtration rate (FR, mg h⁻¹), and (c) selection efficiency (SE, %) of *M. gigas* (blue bars) and *A. irradians* (orange bars). Bars represent the mean values, and error bars indicate the standard error. Different letters above the bars denote significant differences within each species among seasons ($p < 0.05$). Asterisks above the error bars indicate significant differences between the two species within the same season (* $p < 0.05$, ** $p < 0.01$).

- Filtration rate (FR)

Similar to CR, the FR of both species varied significantly by season, peaking in summer (One-way ANOVA, $p < 0.001$). Post-hoc analysis showed that for *M. gigas*, the summer peak was significantly higher than the rates in all other seasons. For *A. irradians*, the FR started at a moderate level in spring and surged to its annual maximum in summer, followed by a sharp decline in autumn that maintained a statistical overlap with the annual minimum in winter.

In interspecific comparisons, the FR of *M. gigas* was significantly higher than that of *A. irradians* in both autumn and winter ($p < 0.01$) (Figure 3b, Table S1).

- Selection efficiency (SE)

In contrast to CR and FR, the SE of *M. gigas* showed no statistically significant seasonal variations throughout the study period (One-way ANOVA, $p > 0.05$), despite the apparent decrease in mean values. This lack of statistical significance may be attributed to the high

individual variability inherent in natural field samples. Conversely, the SE of *A. irradians* exhibited distinct seasonal fluctuations ($p < 0.001$), peaking in spring and reaching its minimum in autumn. Post-hoc analysis for *A. irradians* indicated that the maximum in spring was significantly higher than the minimum in autumn, while the rates in summer and winter maintained a high statistical overlap with both periods.

In interspecific comparisons, no statistically significant differences in SE were detected between the two species within any specific season ($p > 0.05$) (Figure 3c, Table S1).

3.2.3. Post-Ingestive Analysis

- Absorption rate (AR)

The AR of both species varied significantly by season, peaking in summer (One-way ANOVA, $p < 0.001$). Post-hoc analysis showed that for *M. gigas*, the summer peak was significantly higher than the winter lows in autumn and winter ($p < 0.05$), while spring exhibited an intermediate rate. For *A. irradians*, the AR started at a moderate level in spring, surged to its annual maximum in summer, and then progressively declined to its lowest level in winter ($p < 0.05$).

In interspecific comparisons, the AR of *M. gigas* was significantly higher than that of *A. irradians* in spring ($p < 0.05$) and autumn ($p < 0.01$), whereas no statistically significant differences were observed in summer and winter ($p > 0.05$) (Figure 4a, Table S2).

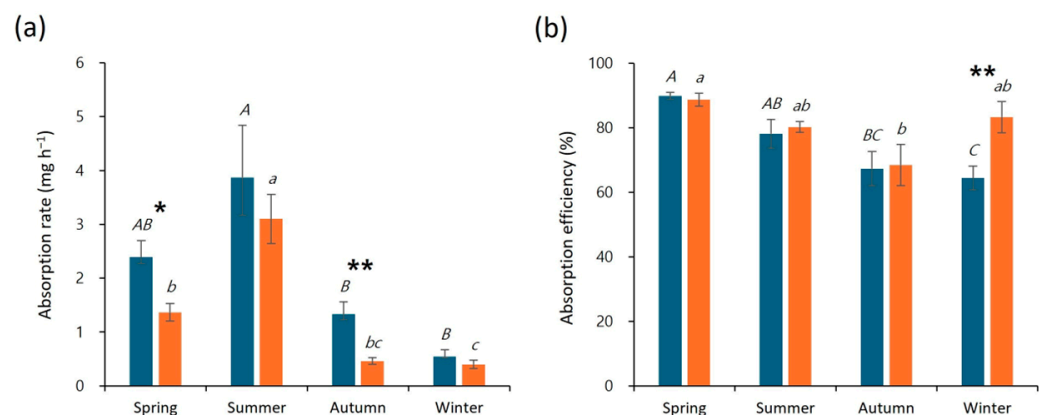


Figure 4. Seasonal variations in (a) absorption rate (AR, mg h⁻¹) and (b) absorption efficiency (AE, %) of *M. gigas* (blue bars) and *A. irradians* (orange bars). Bars represent the mean values, and error bars indicate the standard error. Different letters above the bars denote significant differences within each species among seasons ($p < 0.05$). Asterisks above the error bars indicate significant differences between the two species within the same season (* $p < 0.05$, ** $p < 0.01$).

- Absorption efficiency (AE)

The seasonal pattern of AE differed between the two species; *M. gigas* exhibited a highly significant and progressive decline from spring to winter (One-way ANOVA, $p < 0.001$), whereas *A. irradians* maintained relatively stable and high efficiencies throughout the study period, despite a minor seasonal dip in autumn ($p < 0.05$). Post-hoc analysis revealed that for *M. gigas*, the AE in spring was significantly higher than in autumn and winter. In contrast, for *A. irradians*, a significant difference was exclusively detected between spring and autumn, while summer and winter maintained a high statistical overlap with both the spring maximum and autumn minimum.

Regarding interspecific differences, the AE of *A. irradians* was significantly higher than that of *M. gigas* in winter ($p < 0.01$), while no significant variations were found between the two species in the remaining seasons ($p > 0.05$) (Figure 4b, Table S2).

3.2.4. Waste Production

- Rejection proportion (RP)

The RP of *A. irradians* was significantly higher than that of *M. gigas* in spring ($p < 0.001$) and autumn ($p < 0.01$). In *M. gigas*, the RP showed a gradual increase from spring (13.62%) to winter (34.36%; $p = 0.019$), whereas the RP of *A. irradians* remained at elevated levels (above 47%) in most seasons except for summer, when it dropped to its minimum (19.02%; $p < 0.001$) (Figure 5a, Table S3).

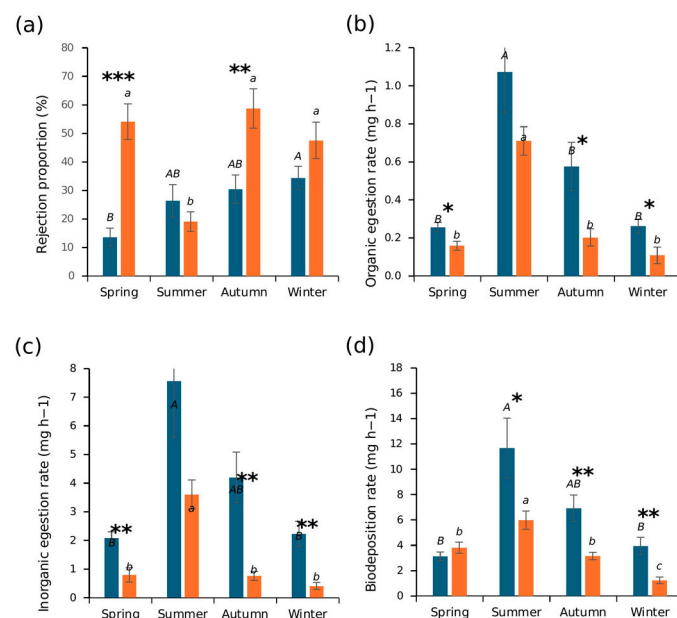


Figure 5. Seasonal variations in (a) rejection proportion (RP, %), (b) organic egestion rate (OER, mg h⁻¹), (c) inorganic egestion rate (IER, mg h⁻¹) and (d) biodeposition (BR, mg h⁻¹) of *M. gigas* (blue bars) and *A. irradians* (orange bars). Bars represent the mean values, and error bars indicate the standard error. Different letters above the bars denote significant differences within each species among seasons ($p < 0.05$). Asterisks above the error bars indicate significant differences between the two species within the same season (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

- Egestion rate (OER and IER)

Both OER and IER exhibited significant seasonal variations, peaking in summer for both species ($p < 0.001$). During this peak period, *M. gigas* recorded the highest OER (1.07 ± 0.21 mg h⁻¹) and IER (7.56 ± 1.97 mg h⁻¹), while *A. irradians* reached 0.71 ± 0.07 mg h⁻¹ and 3.60 ± 0.51 mg h⁻¹, respectively.

In interspecific comparisons, *M. gigas* generally showed higher egestion rates than *A. irradians*. Specifically, the OER of *M. gigas* was significantly higher than that of *A. irradians* in spring, autumn, and winter ($p < 0.05$). Similarly, the IER of *M. gigas* was markedly higher than that of *A. irradians* during the same seasons ($p < 0.01$) (Figure 5b,c, Table S3).

- Biodeposition rate (BR)

Despite the higher rejection proportion of *A. irradians* compared to *M. gigas* in spring and autumn, the BR followed a similar seasonal pattern to the egestion rates, with the maximum values recorded in summer for both *M. gigas* (11.67 mg h⁻¹) and *A. irradians* (5.98 mg h⁻¹; $p < 0.001$). During summer, the BR of *M. gigas* was significantly higher than that of *A. irradians* ($p < 0.05$). Furthermore, *M. gigas* maintained significantly higher BR levels compared to *A. irradians* in autumn and winter ($p < 0.01$) (Figure 5d, Table S3).

4. Discussion

The ecological value of bivalve aquaculture extends beyond biomass production; it functions as a critical nutrient sink and contributes to carbon sequestration through shell biomineralization [3,43–49]. However, intensive cultivation can accelerate organic enrichment in the sediment through the deposition of biodeposits. This accumulation increases sediment oxygen demand (SOD) and elevates sulfide levels, which are primary drivers of benthic environment deterioration [4–8,22,32,33,41].

In our study period, although a slight depression in surface DO (6.80 mg L^{-1}) was observed during summer and autumn compared to May (8.50 mg L^{-1}) and winter (7.32 mg L^{-1}), the oxygen levels remained well above the critical hypoxic threshold (3.0 mg L^{-1}), indicating a highly well-oxygenated condition that posed no physiological stress to the cultured bivalves. Nevertheless, even within such a safe environmental range, the distinct seasonal shifts in temperature and food quality inevitably trigger different physiological coping mechanisms between co-cultured species. Therefore, optimizing the spatial arrangement of farms is crucial to balance such ecological production with environmental health. Since physiological responses vary by species and environmental context [38,39,41], optimizing species positioning according to food availability and species-specific physiological traits is crucial for both environmental sustainability and productivity.

In this study, we compared the seasonal feeding performance of *M. gigas* and *A. irradians* in Tongyeong, the primary bivalve production hub in South Korea. We acknowledge that sampling was conducted on a single day for each season without multi-day temporal replication, which serves as a limitation in generalizing the responses across full seasonal variations. However, this study adopted optimized methods tailored for measuring bivalve physiological characteristics through in situ experiments. To minimize potential temporal bias, the experiments were specifically carried out on days that were highly stable and representative of the typical seasonal characteristics and environmental parameters of the study area. By elucidating the distinct physiological mechanisms of these two species, we aim to provide a scientific basis for strategic spatial arrangement plans in intensive aquaculture regions of the southern coast.

Indeed, Tables 2 and S1 illustrate the SST spanning a five-year period, including the specific timeframe of this study. While the acceleration of climate change—particularly the recently emerging phenomenon of ‘thermal polarization’ [50–52]—can induce complex metabolic suppression and physiological stress in cultured organisms [53,54], the present findings may not fully encompass the entire spectrum of these extreme environmental shifts. Nevertheless, the identified temperature-dependent correlations provide fundamental guidelines for establishing species-specific targeting and optimal spatial arrangement strategies tailored to distinct biological traits.

The marine environmental characteristics of the southern coast of Korea exhibited distinctly contrasting patterns between summer and winter (Table 2, Figure 1). This seasonal pattern appears to be driven by thermal stratification in summer and convective vertical mixing combined with Siberian High-driven winter monsoonal winds in winter. Specifically, the concurrent increase in Chl-a ($1.00 \mu\text{g L}^{-1}$) and DIN (0.2466 mg L^{-1}) during summer suggests an influx of terrestrial nutrients driven by increased summer rainfall, which exceeded the consumption rate of proliferating phytoplankton. This aligns with previous reports suggesting that seasonal nutrient cycling in the southern coastal waters of Korea is more predominantly influenced by freshwater discharge and nutrient fluctuations than by physical factors such as ocean currents [55,56]. In contrast, during winter, a distinct pattern of low Chl-a ($0.71 \mu\text{g L}^{-1}$) combined with elevated DIN (0.1935 mg L^{-1}) and DIP (0.0340 mg L^{-1}) was observed. Furthermore, TPM concentrations exhibited a distinct

inverse correlation with the f ratio value. This suggests that winter particulate matter dynamics are predominantly governed by physical resuspension driven by a combination of Siberian High-driven winter monsoonal winds and convective vertical mixing; in particular, this is highly consistent with earlier studies reporting that physical resuspension accounts for up to 25% of the marine carbon cycle in this region [54,57].

Consistent with findings from previous studies, the GTT was significantly shortened with increasing SST (Figure 2). As temperature rises, metabolic activity becomes more active, thereby accelerating the overall digestion process. Such physiological changes stimulate intestinal peristalsis, leading to a reduction in the time it takes for food to pass through the digestive tract. This quantitative acceleration of the digestive process aligns with previous reports on various marine bivalve species [37–39], reinforcing that temperature-dependent GTT reduction is, as demonstrated, a generalized physiological response in filter-feeding bivalves.

The pre-ingestive analysis (Figure 3a,b; Table S1) revealed that both *M. gigas* and *A. irradians* exhibited distinct temperature-dependent patterns in their CR and FR. *M. gigas* achieves optimal growth under water temperatures of 20–26 °C [58] and salinities of 24–28 ppt [32], yet it displays broad eurythermal and euryhaline resilience, capable of surviving across a wide thermal spectrum (4–35 °C) and tolerating short-term low-salinity exposure down to 5 ppt [59]. The suitable growth temperature range for *A. irradians* is 18–28 °C with an optimum at 23 °C; although it possesses a wide critical thermal tolerance ranging from 1 °C to 31 °C, its growth effectively ceases when temperatures drop below 5 °C [33]. In our study, the ambient SST during the experimental trials ranged from 10.9 °C to 26.1 °C, with specific seasonal mean values of 15.40 ± 0.12 °C in spring, 26.10 ± 0.25 °C in summer, 21.16 ± 0.18 °C in autumn and 10.92 ± 0.09 °C in winter. Based on these established literature baselines, summer and autumn corresponded to the optimal growth windows for both species, whereas spring and winter fell within their tolerable survival limits. Interestingly, even between the two optimal periods (summer and autumn), both species exhibited prominent seasonal discrepancies in their CR and FR, with significantly higher feeding activities recorded in summer ($p < 0.001$). These observations are consistent with previous findings by Bougrier et al. [60] and Riisgård and Larsen [61], who documented that filtration activity increases with rising temperature within the optimal range.

Reproductive cycles and species-specific thermal limits significantly modulated these seasonal feeding discrepancies. In the South Sea of Korea, *M. gigas* spawns between July and September [32], whereas *A. irradians* spawns from May to June [33]. Based on these established reproductive windows, the maximum CR and FR recorded during summer appear to be closely linked to the distinct physiological demands of each species' adult stage. Although both bivalves reached their seasonal feeding peaks in summer without significant interspecific divergence (Figure 3a,b), the elevated feeding in *M. gigas* likely reflects an active, post-spawning energetic compensation to rebuild somatic reserves after its intensive spawning event. Conversely, for earlier-spawning *A. irradians*, summer represents a critical window for somatic growth and subsequent winter gametogenesis, driven by favorable high temperatures. In autumn, however, *M. gigas* maintained significantly higher FR ($p < 0.01$) and CR ($p < 0.05$) than *A. irradians* under cooling conditions. This divergence underscores contrasting metabolic energy strategies: *M. gigas* sustains elevated feeding to offset post-spawning deficits—a cold-tolerance capacity well-documented in New Zealand [62] and Mexico [63]—whereas *A. irradians* exhibits an abrupt, threshold-like decline in CR below its thermal preference [64].

Furthermore, examining the physiological compensation mechanisms by integrating CR and FR with seston data (Figures 1 and 3a,b) reveals that both species reached their

maximum feeding rates in summer, synchronized with the annual peak of the organic content proportion in seston. This aligns with previous studies indicating that bivalves actively regulate their filtration rates in response to the organic matter concentration of suspended particulate matter [65–67]. In contrast, the lower organic content of seston observed in spring, autumn, and winter corresponded with a general reduction in both CR and FR in both species. Notably, the CR of *A. irradians* reached its lowest value in winter, a pattern consistent with previous studies demonstrating that reduced seston quality leads to a decline in CR and FR in bivalve suspension-feeders [68–70]. In addition, these results are consistent with previous studies demonstrating that scallops adopt a strategy of reducing FR and increasing pseudofeces production in response to a decline in seston quality [23,69,71].

Meanwhile, the SE of *M. gigas* remained statistically constant throughout the study period, likely due to its well-developed laterofrontal cirri and labial palp sorting that ensure consistent pre-ingestive selection regardless of seston shifts (Figure 3c, Table S1) [37,70]. Conversely, *A. irradians* lacks laterofrontal cirri, demonstrating a markedly size-dependent retention efficiency alongside qualitative selection mediated through organic content assessment at the gill and palp level [22,23,69,71]. This structural difference explains the seasonal fluctuations observed in *A. irradians*, which peaked in spring and reached their minimum in autumn (Figure 3c, Table S1).

The highest SE in *A. irradians* during spring is attributable to the combined effect of moderate TPM load and relatively low SST (15.4 °C); this suppresses quantitative feeding (CR and FR) while extending gut transit time to approximately 45 min (Figures 2 and 3), thereby providing a physiological time window for more precise particle selection and high-selectivity pre-ingestive sorting [23,71]. Although particle size distribution was not explicitly measured, the elevated rejection proportion suggests that scallops actively sorted a considerable fraction as pseudofeces to retain only the most nutritious fraction. In contrast, the markedly reduced SE in autumn is more parsimoniously explained by the decline in the organic fraction of seston (*f*-ratio) relative to total particulate matter (Figure 1), rather than particle size alone. Despite the highest chl-*a* concentration recorded (3.15 µg L^{−1}), the concurrent increase in total particulate load diluted the nutritional value of available seston, forcing *A. irradians* to increase pseudofeces rejection in response to reduced seston quality without achieving efficient organic enrichment (Figures 1 and 3) [23,69,71].

Regarding post-ingestive processing (Figure 4, Table S2), the seasonal absorption rate (AR) followed a trend similar to CR and FR. In contrast, absorption efficiency (AE)—a qualitative index of digestive efficiency—peaked in spring for both species, but was significantly higher in *A. irradians* than in *M. gigas* during the winter. This winter feeding superiority of the scallop under low-quality food conditions—characterized by low chl-*a* (0.71 ± 0.01 µg L^{−1}) and high TPM (19.6 ± 1.35 mg L^{−1})—is primarily driven by its enhanced pre-ingestive rejection of inorganic particles (higher SE and RP) and an optimized gut transit time (85 min vs. >140 min for *M. gigas*), which lowered egestion rates.

These findings suggest that *A. irradians* employs a more energy-efficient post-ingestive strategy under nutritionally dilute seston conditions, aligning with previous reports that suspension-feeders with highly selective pre-ingestive sorting mechanisms maintain superior digestive and absorption efficiencies [23,69,71]. This confirms that the morphological diversity of particle separation structures is a primary determinant of interspecific differences in energetic efficiency across varying environments [72]. Collectively, these results clarify the divergent energy acquisition strategies: *M. gigas* adopts a “high-quantity” strategy, maximizing absorption through elevated feeding throughput (CR and FR), whereas *A. irradians* employs an “optimization” strategy, maintaining high AE to compensate for lower quantitative feeding activity (AR).

The waste production analysis (Figure 5a–d and Table S3) revealed that the pseudofeces rejection rate (RP) was significantly higher in *A. irradians* than in *M. gigas* in spring ($p < 0.001$) and autumn ($p < 0.01$). Pseudofeces production represents an active pre-ingestive sorting mechanism involving mucus secretion, which itself carries an energetic cost [23]. Nevertheless, by selectively excluding low-quality inorganic particles prior to ingestion, this process yields a net gain in digestive efficiency that outweighs its metabolic cost [66,69,71]. The significantly elevated RP in *A. irradians* relative to *M. gigas* in spring and autumn thus represents a net-beneficial compensatory strategy, enabling this species to maintain relatively high AE despite characteristically lower CR and FR.

In contrast, the BR was consistently higher in *M. gigas* than in *A. irradians* across most of the study period, with no significant interspecific difference observed in spring (Figure 5d). The elevated BR in *M. gigas* reflects its high filtration capacity, through which large volumes of particulate matter are processed and deposited as biodeposits, contributing to benthic–pelagic coupling at the local scale [3]. Collectively, these findings suggest that *M. gigas* and *A. irradians* employ fundamentally distinct energy acquisition strategies. *M. gigas* adopts a ‘high-throughput’ strategy, maximizing organic absorption through elevated CR and FR and generating substantial biodeposition. In contrast, *A. irradians* employs an ‘optimization’ strategy, compensating for lower quantitative feeding activity through enhanced pre-ingestive particle discrimination and elevated pseudofeces rejection, thereby sustaining relatively high digestive efficiency under varying seston conditions.

When applying these findings to field conditions, potential discrepancies between the experimental setup and actual aquaculture environments must be taken into account. In commercial farms, the *M. gigas* is typically cultured on open vertical longlines, whereas the *A. irradians* is reared within multi-tiered lantern nets; this structural dissimilarity can alter localized hydrodynamics and particulate matter distribution [73,74]. In contrast, our in situ biodeposition system isolated individual specimens and supplied ambient seawater directly, thereby excluding any microenvironmental shading effects associated with specific cultivation structures. Furthermore, as this study exclusively utilized adult individuals, different patterns might emerge in the field when culturing from the early juvenile stage through to market size [62,62,75]. Nevertheless, despite these methodological limitations, this approach holds significant academic value as it successfully isolated species-specific physiological responses from the confounding interferences of culture structures. By eliminating the confounding variables introduced by aquaculture gear, this study provides fundamental baseline data comparing the unaltered feeding performance and metabolic efficiencies of the two bivalves in response to seasonal environmental shifts.

Current aquaculture management in South Korea is predominantly focused on physical infrastructure, often overlooking the species-specific environmental loading and physiological requirements [76,77]. Based on the distinct physiological differences between *M. gigas* and *A. irradians* identified in this study, we propose three core strategies for sustainable aquaculture management.

First, horizontal spatial arrangement based on filtration capacity should be considered. *M. gigas*, exhibiting high clearance and filtration rates, is better suited to inshore areas with high terrestrial organic input [3,78]. In contrast, *A. irradians* may be better suited for mid-channel or moderately exposed areas where seston is dominated by larger phytoplankton cells, rather than fine inorganic particles from terrestrial runoff [22,23]. Such spatial separation may reduce interspecific competition and seston depletion, improving overall system productivity. Although this study applied a fixed flow rate (12 L h^{-1}), previous studies also support improved scallop performance under hydrodynamically stable and food-consistent conditions [79].

Second, dynamic vertical management may enhance feeding efficiency, particularly for *A. irradians*. Its high-rejection production indicates substantial energetic costs associated with pre-ingestive selection. Therefore, adjusting culture depth in response to vertical seston gradients could reduce exposure to excessive particulate loading. As seston distribution varies with hydrodynamic conditions, continuous monitoring would allow placement in layers that minimize selection inefficiency [80,81].

Finally, biodeposition-based environmental management should be incorporated into farm design. Given the higher fecal production of *M. gigas*, oyster culture may contribute more significantly to benthic organic enrichment. Since biodeposition patterns are influenced by local currents, increasing spacing between oyster lines may help disperse organic matter and reduce localized accumulation [82]. This approach may also alleviate intraspecific food competition and improve water exchange within culture systems [3,65].

The BR measured in this study provides a useful parameter for optimizing farm spacing within ecological carrying capacity models [82]. Integrating species-specific physiological traits with system design variables, including stocking density, vertical positioning, and hydrodynamic effects [3,83,84], will be essential for balancing productivity and environmental sustainability. Ultimately, applying these species-specific strategies as a conceptual framework could offer a practical foundation to support sustainable aquaculture modeling during future farm re-allocation or license renewals.

5. Conclusions

In conclusion, this study provides a comprehensive comparative analysis of the seasonal feeding performances of *Magallana gigas* and *Argopecten irradians* in the Tongyeong region, revealing distinct, species-specific feeding strategies. *M. gigas* exhibits a “high-quantity” strategy characterized by elevated clearance and filtration rates (CR and FR) and a robust biodeposition rate (BR), driving massive energy and nutrient cycling within the ecosystem. Conversely, *A. irradians* adopts an “optimization” strategy, maintaining a remarkably high absorption efficiency (AE) and high pseudofeces rejection rate (RP) to thrive under low-temperature or high-seston conditions despite its lower quantitative intake.

These divergent physiological mechanisms demonstrate the necessity of transitioning from uniform management to species-specific practices in bivalve aquaculture. Specifically, understanding these species-specific traits and the empirical feeding parameters obtained in this study can provide critical baselines for ecological carrying capacity and optimized spatial modeling, ultimately contributing to sustainable aquaculture management in coastal ecosystems.

While this study establishes a foundational guideline for spatial arrangement based on typical seasonal conditions, it does not fully incorporate the compounding effects of climate change, such as ‘thermal polarization,’ or varying ambient current speeds under field conditions. Future research should integrate these real-time environmental variables into hydro-biogeochemical models to refine carrying capacity estimations. Ultimately, implementing these tailored spatial allocation strategies during farm re-licensing or renewals will provide a robust framework for a sustainable, ecosystem-based aquaculture model that balances environmental health with maximized economic productivity.

Supplementary Materials: The following supporting information can be downloaded at <https://www.mdpi.com/article/10.3390/fishes11070390/s1>: Figure S1. Monthly variations in surface seawater temperature from 2013 to 2017 [42]; Table S1. Seasonal variations in clearance rate, filtration rate, and selection efficiency of *M. gigas* and *A. irradians*; Table S2. Seasonal variations in absorption rate and absorption efficiency of *M. gigas* and *A. irradians*; Table S3. Seasonal variations in rejection

proportion, organic egestion rate, inorganic egestion rate and biodeposition rate of *M. gigas* and *A. irradians*.

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Abbreviations

The following abbreviations are used in this manuscript:

SST	Surface Seawater Temperature
DO	Dissolved Oxygen
Chl-a	Chlorophyll <i>a</i>
DIN	Dissolved Inorganic Nitrogen
DIP	Dissolved Inorganic Phosphorus
TPM	Total Particulate Matter
POM	Particulate Organic Matter
PIM	Particulate Inorganic Matter
GTT	Gut Transit Time
CR	Clearance Rate
IFR	Inorganic Filtration Rate
FR	Filtration Rate
IRR	Inorganic Rejection Rate
ORR	Organic Rejection Rate
RR	Rejection Rate
RP	Rejection Proportion
SE	Selection Efficiency
OIR	Organic Ingestion Rate
IER	Inorganic Egestion Rate
OER	Organic Egestion Rate
AR	Absorption Rate
AE	Absorption Efficiency
BR	Biodeposition Rate
SOD	Sediment Oxygen Demand

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