

Article

Population Ingestion Rate of *Aurelia coerulea* on Mesozooplankton in Masan Bay, Korea

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Abstract

Aurelia coerulea is a bloom-forming scyphozoan that recurs in Masan Bay, a semi-enclosed embayment on the southern coast of Korea. To quantify its population-level predation impact on mesozooplankton, medusae and zooplankton were sampled monthly at six stations from May to September 2013, except for August. Individual ingestion rates were estimated from gut-content analysis combined with temperature-dependent digestion time, and population ingestion rates were evaluated relative to mesozooplankton biomass and production. Medusa abundance peaked in May (2.11 medusae m⁻³) and declined sharply thereafter, whereas the individual body size and the total population biomass increased. *Oithona similis* was the dominant prey, indicating positive selectivity from June to September despite its low biomass in the ambient zooplankton community. Mesozooplankton abundance, biomass, and production ranged from 4300 to 26,900 ind. m⁻³, 6.9 to 20.6 mg C m⁻³, and 2.26 to 5.82 mg C m⁻³ d⁻¹, respectively. Individual ingestion rates of the jellyfish on the mesozooplankton ranged from 0.31 to 5.31 mg C medusa⁻¹ d⁻¹. Population ingestion rates ranged from 0.06 to 0.66 mg C m⁻³ d⁻¹, equivalent to 0.3–6.6% and 1.1–11.8% of the biomass and production of the mesozooplankton, respectively. Predation impact of *A. coerulea* on mesozooplankton in Masan Bay varied seasonally and depended primarily on medusa abundance, because population ingestion rates decreased after May despite increasing individual ingestion rates associated with medusa growth. A modified calculation of the population ingestion rate, considering jellyfish distribution only in the upper layer under water-stratification conditions in summer, was also discussed.

Keywords: *Aurelia coerulea*; gut contents; predation impact; mesozooplankton; semi-enclosed embayment; Masan Bay

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1. Introduction

Moon jellyfish (*Aurelia* spp.) are widespread scyphozoans in coastal waters worldwide, and recurrent blooms have frequently been reported from enclosed or semi-enclosed embayments [1–3]. Dense populations of *Aurelia* species can exert substantial top-down effects on pelagic food webs by consuming zooplankton, fish eggs, and larvae, thereby reducing zooplankton standing stock, potentially promoting phytoplankton blooms through reduced grazing pressure, and suppressing fish recruitment [4–8].

Evaluation of this role at the population level requires estimates of both individual feeding rates and medusa abundance in relation to prey availability. Among the available approaches, gut-content analysis combined with temperature-dependent digestion time is particularly useful for field populations because it allows identification of ingested prey and estimation of feeding under natural conditions [9–11].

Recent studies have further emphasized that the ecological consequences of gelatinous zooplankton blooms should be evaluated within the broader context of coastal pelagic food-web alteration and ecosystem service provisioning. Jellyfish blooms can redirect carbon and energy flow toward microbial pathways, compete with forage fish for zooplankton prey, restructure plankton dynamics and trophic linkages, alter energy-transfer pathways, and negatively affect fisheries production in coastal ecosystems [8,12–15]. In Korean coastal waters, blooms involving *A. coerulea* and *Nemopilema nomurai* have been linked to reduced anchovy production and challenges to coastal fisheries and ecosystem services [16]. These findings highlight the need to evaluate local *Aurelia* blooms not only in terms of individual feeding rates, but also in terms of population-level predation impact relative to ambient mesozooplankton biomass and production.

Moon jellyfish in Korean coastal waters were long regarded as *Aurelia aurita*, but molecular analyses identified the species as *Aurelia* sp. 1 [17], which was subsequently synonymized with *Aurelia coerulea* von Lendenfeld, 1884 [18]. Recurrent blooms of *A. coerulea* medusae have been reported since the late 1990s in several embayments, including Gyeonggi Bay on the west coast and Masan Bay on the south coast, and large-scale occurrences have continued to be reported nationwide [19]. Despite the repeated occurrence of these bloom events and their potential ecological importance, direct quantitative evaluation of jellyfish predation on zooplankton in Korean waters remains scarce. The only quantitative study on the energetics of *Aurelia* in Korean coastal waters estimated the minimum population food requirements from respiration rates in Sihwa Lake [20]. A field-based, gut-content-derived estimate of the population-level impact of predation on mesozooplankton has not been reported. Masan Bay is a semi-enclosed coastal embayment in which dense polyp colonies of *A. coerulea* have been reported from artificial substrates, such as port walls, and management actions such as polyp removal have been proposed to reduce medusa outbreaks [21]. In addition, Masan Bay undergoes strong seasonal hydrographic changes, including summer stratification and bottom hypoxia [22], which may influence both medusa's vertical habitat and predator–prey overlap [23,24].

The present study aimed to provide the first field-based, gut-content-derived estimate of the population-level predation impact of *A. coerulea* on mesozooplankton in Masan Bay, Korea. We quantified individual and population ingestion rates, examined feeding selectivity in relation to ambient mesozooplankton composition, and evaluated predation impact relative to mesozooplankton biomass and production.

2. Materials and Methods

2.1. Hydrographic Variables

Samples were collected monthly at six stations in Masan Bay from May to September 2013 (8 May, 25 June, 16 July, and 23 September), except in August when the research vessel was unavailable (Figure 1). At each station, temperature, salinity, and dissolved oxygen concentration were measured at 1 m intervals using a YSI Pro-Plus multiparameter sonde (Yellow Springs, OH, USA). Dissolved oxygen data were not obtained in September due to a sensor malfunction. For the upper-layer temperature correction described below (Section 2.4), seawater density (ρ , kg m⁻³) was calculated from the vertical profiles of temperature and salinity using the UNESCO equation of state for seawater (EOS-80) [25].

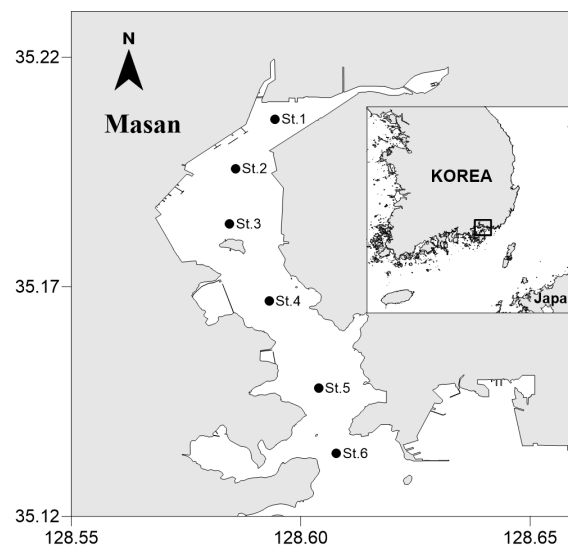


Figure 1. Map of the sampling stations in Masan Bay, located on the southern coast of Korea.

2.2. Mesozooplankton

Mesozooplankton were collected at each station by oblique tows from near-bottom to the surface for 2–3 min using a conical net equipped with a flowmeter (mouth diameter, 60 cm; mesh size, 200 μm ; General Oceanics 2030R, Miami, FL, USA). Samples were fixed onboard with neutralized formalin to a final concentration of 3% and subsequently identified and counted under a dissecting microscope (Olympus SZX, Tokyo, Japan). The carbon biomass of mesozooplankton was estimated from taxon-specific body size measurements using published conversion relationships [26–33]. Prosome length was used for copepods and copepodites, trunk length for larvaceans, total length for chaetognaths, carapace length for decapod larvae, and body length for cladocerans, polychaete larvae, bivalve larvae, and gastropod larvae. For *Noctiluca scintillans*, biomass was estimated using a per-cell carbon conversion constant. The production rate of each taxonomic group (P , $\text{mg C m}^{-3} \text{ d}^{-1}$) was estimated based on its biomass (B , mg C m^{-3}) and experimentally determined specific growth rates (g , d^{-1}) following Uye and Shimazu [34], Sato et al. [29], Lindley [31], and Tada et al. [33].

$$P = B \times g$$

The production rates of all taxonomic groups were summed to obtain the community production rate of mesozooplankton (CP , $\text{mg C m}^{-3} \text{ d}^{-1}$).

$$CP = \sum P$$

2.3. Abundance, Biomass, Growth, Gut Contents, and Population Ingestion Rate of *Aurelia coerulea*

To estimate abundance and biomass of *A. coerulea*, medusae were collected from the bottom to the surface by 5–8 min oblique tows of a conical net equipped with a flowmeter (mouth diameter, 60 cm; mesh size, 500 μm ; General Oceanics 2030R). All medusae were counted onboard, and wet weight was measured using an electronic balance. For bell diameter and individual wet weight measurements, all collected individuals were measured at stations where catch numbers were small (≤ 10 individuals). At stations with larger catches (Stations 2 and 3 in May, where 89 and 142 medusae were collected, respectively), individuals were randomly selected for measurement without regard to body size, yielding 41–45 individuals per station (29–51% of the total catch). The resulting sample sizes ($n = 6$ –94 medusae per sampling date across all stations combined) are likely sufficient for reliable estimation of the mean wet weight, as random samples of this magnitude yield

robust mean estimates under standard statistical principles. These measurements were used to estimate growth rate. The daily growth rate (G , d^{-1}) was calculated as the specific change in mean wet weight between two sampling dates:

$$G = \frac{\ln W_t - \ln W_0}{t - t_0}$$

where W_t and W_0 are the mean wet weights (g) at sampling dates t and t_0 , respectively.

For gut-content analysis, 3–21 medusae per sampling date were collected gently using a scoop net to minimize gut-content expulsion. Individuals for gut-content analysis were not selected by size but reflected the range of body sizes encountered during collection, thereby avoiding size-selective bias. The relatively small number of medusae analyzed for gut contents reflects the physical constraint of gentle scoop-net collection, which is a common procedure in field gut-content studies of *Aurelia* medusae [10,11]. The observed high variability in individual gut carbon content is an inherent characteristic of field populations and does not result from selection bias [35]. Bell diameter and wet weight were measured, after which specimens were fixed in 5% formalin. Feeding selectivity of medusae was evaluated by comparing prey composition in gut contents with that in ambient mesozooplankton using the χ^2 -based selectivity index of Pearre [36]. When taxonomic resolution differed between gut-content and environmental samples, prey items were pooled to the higher taxonomic level. Results are presented mainly for prey taxa that were dominant in the gut contents and ambient community in each month.

$$C = \pm \left(\frac{\chi^2}{n} \right)^{\frac{1}{2}}$$

where n is the total number of given prey taxon both in medusae and in the water.

The population ingestion rate of *A. coerulea* on mesozooplankton (PIR , $\text{mg C m}^{-3} \text{ d}^{-1}$) was calculated as:

$$PIR = \frac{A \times GC}{DT} \times 24$$

where A is medusa abundance (medusae m^{-3}), GC is gut carbon content per medusa (mg C medusa^{-1}), and DT is digestion time (h). Digestion time was estimated using the temperature-dependent equation of FitzGeorge-Balfour et al. [37]:

$$\log_{10} DT = -0.0234T + 0.713.$$

where T is water temperature ($^{\circ}\text{C}$). Unless otherwise stated, the mean temperature of the entire water column averaged across all stations was used in the digestion-time calculation. Because no comparable temperature-dependent digestion-time equation has been established specifically for *A. coerulea* medusae, this equation, derived for *A. aurita* s.l., was used as an approximation for *Aurelia* medusae feeding on mixed natural prey.

2.4. Upper-Layer Temperature Correction

To examine the potential effect of restricted vertical habitat use during stratified periods, population ingestion rate was recalculated using upper-layer mean temperature instead of whole-water-column mean temperature. This scenario-based correction was applied only to the June and July sampling dates, when stratification and bottom hypoxia were evident. The upper-layer boundary was defined as the depth at which a distinct density gradient, calculated from temperature and salinity using the UNESCO equation of state for seawater (EOS-80) [25], coincided with a sharp decrease in dissolved oxygen concentration to $<4 \text{ mg L}^{-1}$. This criterion was based on previous evidence that *Aurelia* medusae can be restricted by sharp pycnoclines and hypoxic water during stratified periods [23,24]. Because medusa vertical distribution was not directly measured, whole-water-

column medusa abundance was retained and only digestion time was recalculated using upper-layer temperature. Therefore, this correction represents a conservative temperature-based scenario rather than a directly measured layer-specific population ingestion rate.

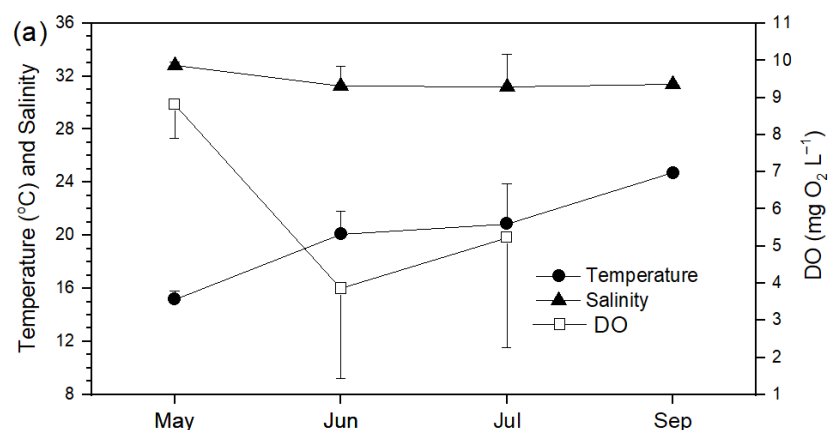
2.5. Statistical Analysis

The relationship between individual ingestion rate (IR) and medusa wet weight (WW) was examined using $\log_{10}$ -transformed ordinary least squares (OLS) linear regression (Model 1: $\log_{10}(\text{IR}) \sim \log_{10}(\text{WW})$), and the relationship between weight-specific ingestion rate (wsIR) and wet weight was examined using a separate log–log regression (Model 2: $\log_{10}(\text{wsIR}) \sim \log_{10}(\text{WW})$), where $\text{wsIR} = \text{IR}/\text{WW}$. To evaluate whether the size–ingestion relationship was independent of seasonal variation, a date-controlled analysis was performed by fitting a linear model with $\log_{10}$ -transformed ingestion rate as the response variable, $\log_{10}$ -transformed wet weight as a continuous covariate, and sampling date as a categorical factor (Model 3: $\log_{10}(\text{IR}) \sim \log_{10}(\text{WW}) + \text{Date}$). Because individual ingestion rate was calculated using temperature-corrected digestion time, water temperature was not included directly as an explanatory variable to avoid circularity. The improvement in fit from Model 1 to Model 3 was assessed by an F-test (analysis of variance; ANOVA). An additional model that included the interaction between wet weight and sampling date was fitted (Model 4: $\log_{10}(\text{IR}) \sim \log_{10}(\text{WW}) \times \text{Date}$) and compared with Model 3 using an F-test to assess whether the size–ingestion slope differed among sampling dates. The significance threshold for all tests was $\alpha = 0.05$. All statistical analyses were performed in R (version 4.4.1).

3. Results

3.1. Temperature, Salinity, Dissolved Oxygen

Mean water temperature increased continuously during the study period, from 15.1 °C in May to 24.7 °C in September, whereas mean salinity remained within a relatively narrow range of 31.2–32.8 (Figure 2a). Vertically, temperature and salinity showed little stratification in May and in September, but a clear contrast between warm, low-salinity surface–mid water and cold, high-salinity mid–bottom water developed in June and July (Figure 2b). In addition, dissolved oxygen concentration decreased to $<4 \text{ mg L}^{-1}$ at 4 m in June and 5 m in July, indicating the development of bottom hypoxia.



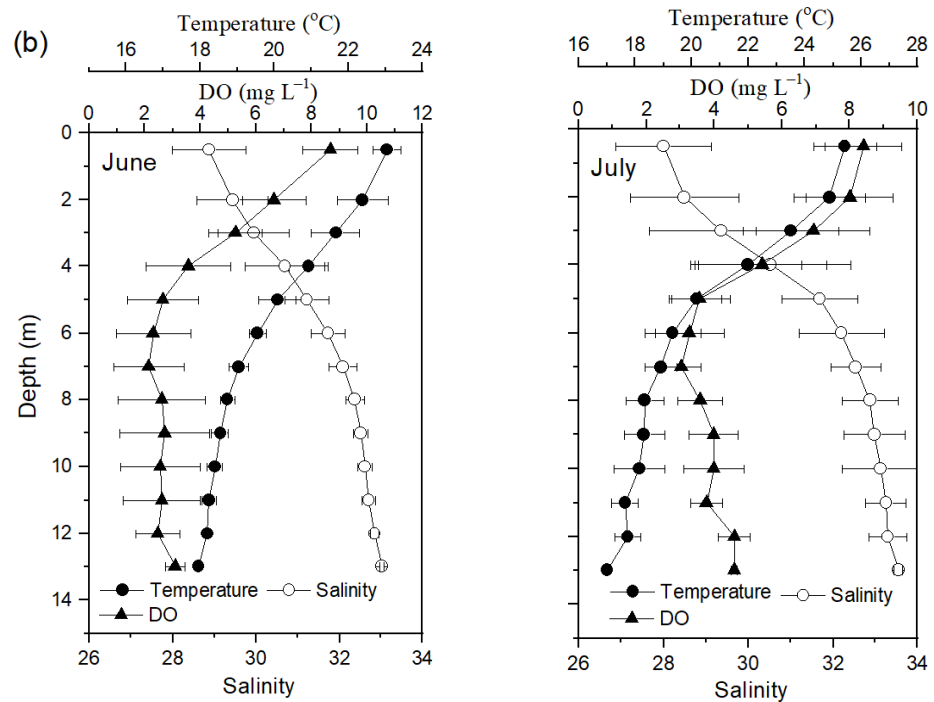


Figure 2. Seasonal variations in (a) mean water temperature, salinity, and dissolved oxygen concentration from May to September, and (b) vertical profiles of water temperature, salinity, and dissolved oxygen concentration in June and July in Masan Bay. Vertical and horizontal lines denote SD.

3.2. Mesozooplankton Abundance, Biomass, and Production Rate

Mesozooplankton abundance showed considerable variation, peaking at 26,857 ind. m^{-3} on 8 May, coinciding with a bloom of *Noctiluca scintillans*, then declining to 8991 ind. m^{-3} by 25 June, reaching a minimum of 4345 ind. m^{-3} on 16 July, and increasing slightly to 6682 ind. m^{-3} by 23 September (Figure 3a).

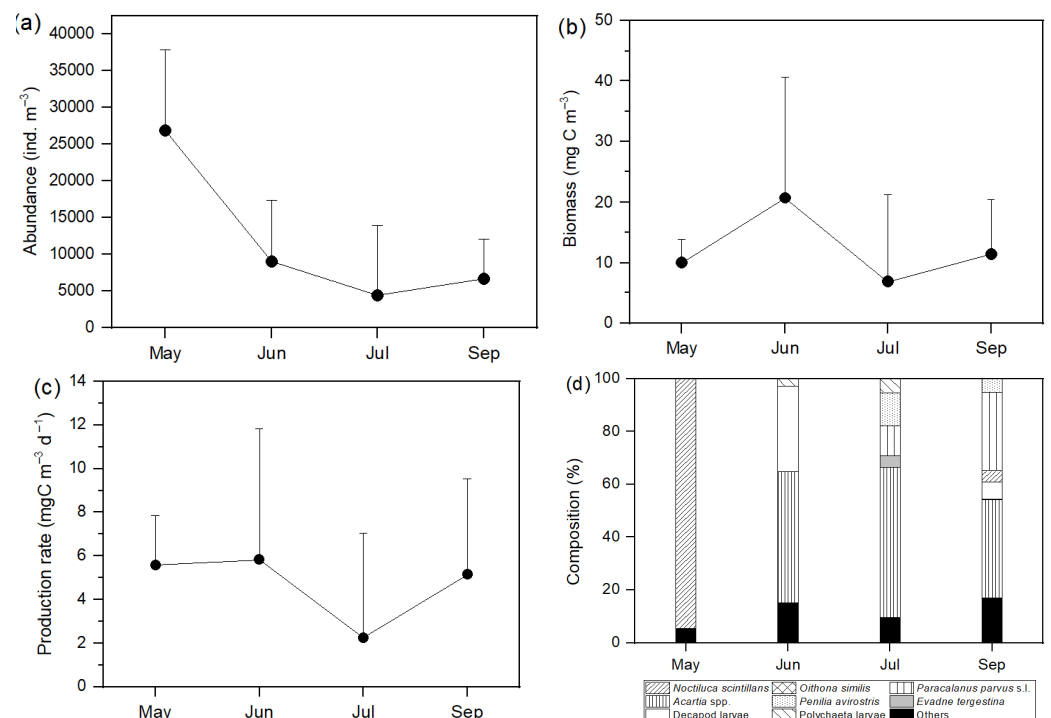


Figure 3. Seasonal variations in (a) abundance, (b) biomass, (c) production rate, and (d) taxonomic composition of mesozooplankton in Masan Bay. Vertical lines denote SD.

Carbon biomass increased from 9.96 mg C m^{-3} in May, peaked at $20.62 \text{ mg C m}^{-3}$ in June, fell to its lowest value of 6.88 mg C m^{-3} in July, and then recovered to $11.37 \text{ mg C m}^{-3}$ in September (Figure 3b).

Production rate followed a pattern similar to that of biomass, ranging from a minimum of $2.26 \text{ mg C m}^{-3} \text{ d}^{-1}$ in July to a maximum of $5.82 \text{ mg C m}^{-3} \text{ d}^{-1}$ in June (Figure 3c).

Except for the overwhelming dominance of *Noctiluca scintillans* in May (94.6%), copepods were the dominant taxonomic group in terms of carbon biomass throughout the study period (Figure 3d). Particularly, *Acartia* spp. accounted for approximately 37–57% of biomass from June to September. Other dominant taxa included decapod larvae in June (32.4%), *Paracalanus parvus* s.l. in July (11.4%) and September (29.6%), and *Penilia avirostris* in July (12.7%). The biomass contribution of *Oithona similis*, the dominant prey taxon in medusa gut contents, was only 0.03–0.29%.

3.3. *Aurelia coerulea* Abundance, Biomass, and Growth Rate

The abundance of medusae peaked at $2.11 \text{ medusae m}^{-3}$ on 8 May, then dropped sharply to $0.03 \text{ medusae m}^{-3}$ on 25 June, remained at a similar level on 16 July, and increased only slightly to $0.06 \text{ medusae m}^{-3}$ by 23 September (Figure 4a). In contrast, biomass increased continuously from 0.17 g m^{-3} in May to 23.65 g m^{-3} in September, reflecting individual growth (Figure 4a,b).

The largest increase in mean body size was observed between May and June. Bell diameter increased from 1.1 to 12.5 cm and wet weight from 0.14 to 80.7 g, yielding a mean daily growth rate of 0.132 d^{-1} (Figure 4b). Thereafter, growth rate decreased to 0.059 d^{-1} between June and July and to 0.004 d^{-1} between July and September, indicating near-stagnation in somatic growth.

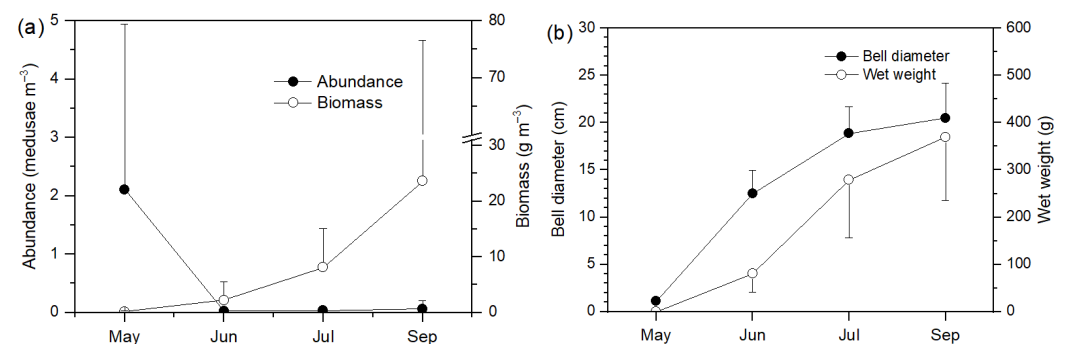


Figure 4. Seasonal variations in (a) abundance and biomass and (b) bell diameter and wet weight of *Aurelia coerulea* medusae in Masan Bay. Vertical lines denote SD.

August sampling was not conducted owing to vessel unavailability and the commitment of field personnel to other urgent survey operations during that period. This gap limits direct evaluation of the medusa abundance, vertical depth, and predation rates during the period when summer stratification and bottom hypoxia may be strongest. However, medusa abundance had already declined sharply by July (to 0.03 ind. m^{-3} , a 98.5% decrease from the May peak), and individual growth was near-stagnant between July and September (daily growth rate of 0.004 d^{-1}). Therefore, the absence of August data is unlikely to have materially affected the interpretation of the main seasonal patterns in abundance, growth, or population ingestion rate.

3.4. *Aurelia coerulea* Ingestion Rate, Gut Contents, and Selectivity

The monthly mean ingestion rate of medusae increased from $0.31 \text{ mg C medusa}^{-1} \text{ d}^{-1}$ in May to a maximum of $5.31 \text{ mg C medusa}^{-1} \text{ d}^{-1}$ in September (Figure 5a).

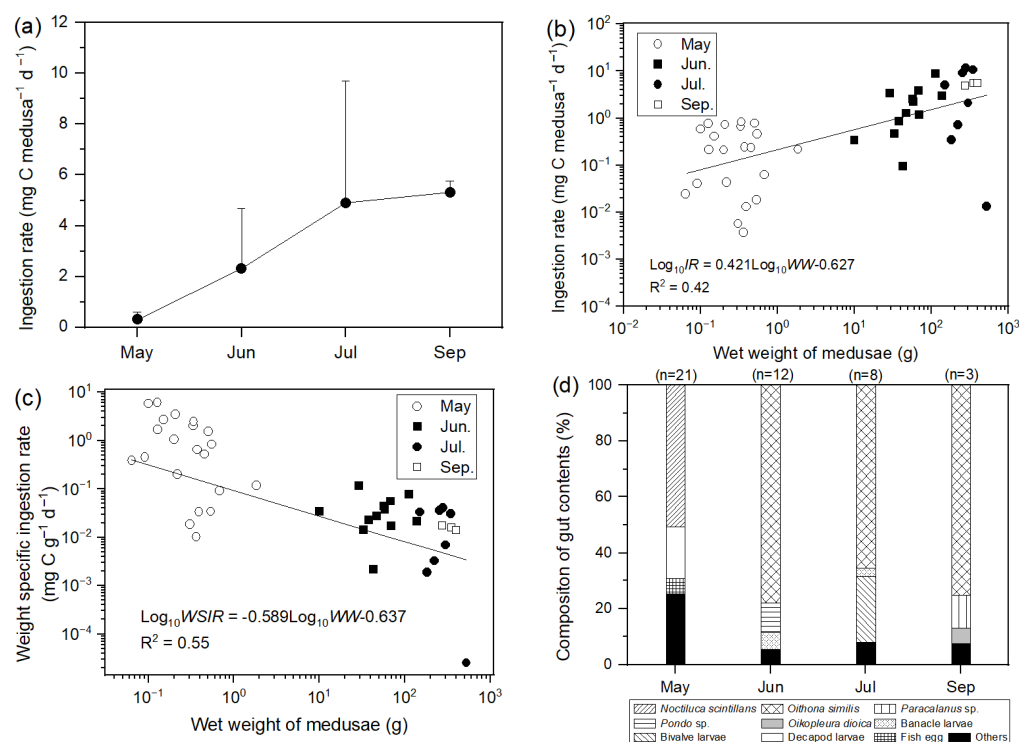


Figure 5. Seasonal variations in (a) ingestion rate, (b) relationship between individual ingestion rate and wet weight, (c) relationship between weight-specific ingestion rate and wet weight on a log–log scale, and (d) gut contents of *Aurelia coerulea* medusae in Masan Bay. Vertical lines denote SD. The numbers in parentheses at the top indicate the number of medusae analyzed.

Log_{10} -transformed individual ingestion rate increased significantly with wet weight in the simple pooled regression ($p < 0.001$; Table 1, Figure 5b). As a descriptive pattern, weight-specific ingestion rate decreased significantly with wet weight on a log–log scale ($p < 0.001$; Table 1, Figure 5c), suggesting that larger medusae consumed more prey in absolute terms but less in proportion to body mass. After accounting for sampling date as a categorical covariate, the effect of wet weight on ingestion rate was no longer significant ($p = 0.816$; Table 1), and the interaction between wet weight and sampling date was also not significant ($p = 0.163$; Table 1). These results indicate that the apparent size–ingestion relationship in the pooled data was substantially associated with seasonal co-variation; however, the limited within-date sample sizes ($n = 3$ – 21) constrain the statistical power of this within-date analysis, and an independent body-size effect cannot be fully excluded.

Table 1. Summary of linear regression models for the relationship between individual ingestion rate and wet weight of *Aurelia coerulea* medusae.

Model	Model Description	Slope	$R^2/F/t$	p -Value
1	$\text{log}_{10}(\text{IR}) \sim \text{log}_{10}(\text{WW})$	0.42	$R^2 = 0.42$	<0.001
2	$\text{log}_{10}(\text{wsIR}) \sim \text{log}_{10}(\text{WW})$	−0.58	$R^2 = 0.57$	<0.001
3	$\text{log}_{10}(\text{IR}) \sim \text{log}_{10}(\text{WW}) + \text{Date}$	0.09	$t = 0.23$	0.816
4	$\text{log}_{10}(\text{IR}) \sim \text{log}_{10}(\text{WW}) \times \text{Date}$	—	$F = 1.808$	0.163

Notes: IR, individual ingestion rate (mgC medusa⁻¹ d⁻¹); wsIR, weight-specific ingestion rate (mgC g⁻¹ d⁻¹); WW, wet weight (g); Date, sampling date as categorical factor (May, Jun, Jul, Sep); $n = 44$ individuals. $\text{wsIR} = \text{IR}/\text{WW}$. Slope in Model 3 represents the partial effect of $\text{log}_{10}(\text{WW})$ after accounting for sampling date. Significance threshold: $\alpha = 0.05$.

In May, the major prey item of small medusae was *Noctiluca scintillans*, which also dominated the mesozooplankton carbon biomass and accounted for 50.6% of total gut contents (Figures 3d and 5d). In contrast, *Oithona similis* was the dominant prey during the warm season (77.9% in June, 65.3% in July, 75.2% in September), despite its low biomass in the mesozooplankton community. Feeding selectivity was evaluated for taxa that were dominant in either the ambient mesozooplankton community or the medusa gut contents, including *O. similis*, which was prominent in the gut contents despite its low biomass contribution to the ambient community. Selectivity was low for most taxa (−0.05–0.18), whereas *O. similis* showed consistently positive selectivity (0.30–0.48) (Figure 6).

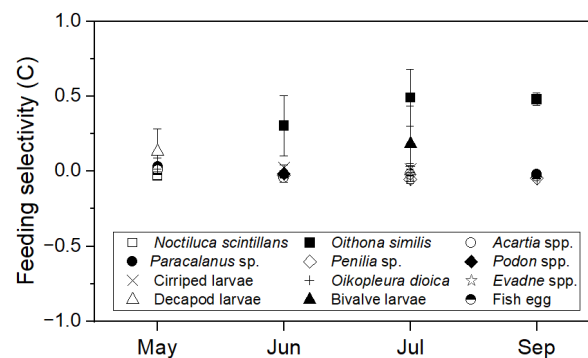
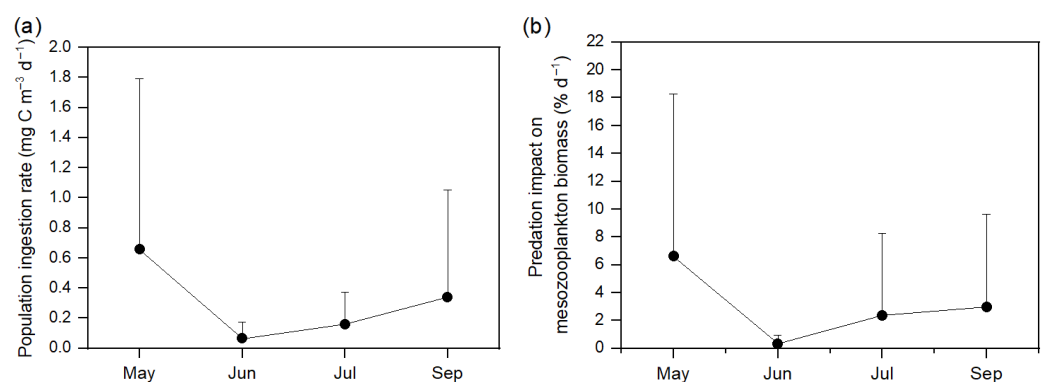


Figure 6. Seasonal variations in feeding selectivity of *Aurelia coerulea* medusae estimated from gut contents and ambient mesozooplankton in Masan Bay. Vertical lines denote SD.

3.5. *Aurelia coerulea* Population Impact on Mesozooplankton

The population ingestion rate of medusae on the mesozooplankton community was the highest in May, reaching $0.66 \text{ mg C m}^{-3} \text{ d}^{-1}$ when medusae were abundant (Figures 4a and 7a). This corresponded to 6.6% of mesozooplankton biomass and 11.8% of mesozooplankton production rate (Figure 7b,c). Following the sharp decline in medusa abundance in June, population ingestion rates remained low, ranging from 0.06 to $0.34 \text{ mg C m}^{-3} \text{ d}^{-1}$, equivalent to 0.3–3.0% of mesozooplankton biomass and 1.1–7.1% of mesozooplankton production rate, respectively.



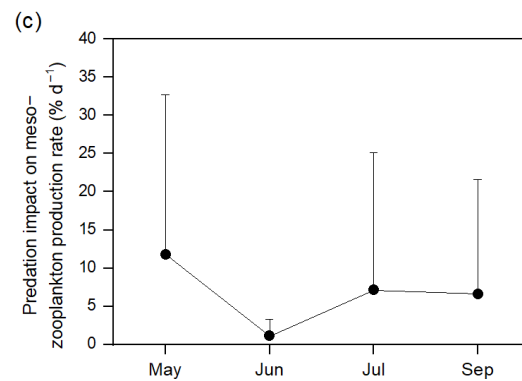


Figure 7. Seasonal variations in (a) population ingestion rate, (b) predation impact on mesozooplankton biomass, and (c) predation impact on mesozooplankton production rate of *Aurelia coerulea* medusae in Masan Bay. Vertical lines denote SD.

4. Discussion

4.1. Seasonal Pattern of Medusa Abundance and Growth

The abundance of *Aurelia coerulea* medusae in Masan Bay decreased sharply from 2.11 medusae m⁻³ on 8 May to 0.03 medusae m⁻³ on 25 June (Figure 4a). *Aurelia* medusae populations are known to fluctuate strongly over short time scales depending on local environmental conditions and the combined effects of recruitment, transport, and mortality [38]. Previous studies indicate that advective loss driven by water exchange can be a major cause of seasonal decline in medusa abundance in semi-enclosed embayments; Goldstein et al. [39] explained that water exchange accounted for 82.6–86.7% of the decrease in *Aurelia* medusae abundance in shallow fjords. Using particle-tracking models, Choi et al. [40] showed that *A. coerulea* medusae were steadily transported out of the inner bay over time. The rapid decrease observed after May, therefore, suggests that physical export may have contributed substantially to the seasonal reduction in population size in Masan Bay.

Somatic growth was the fastest between May and June, when the daily growth rate reached 0.132 d⁻¹, but it subsequently declined from 0.059 d⁻¹ to 0.004 d⁻¹ between June and September (Figure 4b). This seasonal pattern accords with the general life-history pattern of temperate *Aurelia* populations, in which rapid growth occurs in spring and early summer, and growth slows later in the season [38]. The marked reduction in growth rate after June suggests a seasonal shift in energy allocation, with less energy directed to somatic growth during summer. Previous studies have shown that food availability influences both growth and reproductive maturation in *Aurelia* medusae and that energy allocation may shift from body growth toward reproduction as medusae mature [41,42]. It should be noted, however, that the daily growth rate was calculated from changes in mean wet weight between successive sampling dates and should therefore be interpreted with caution. Because medusa abundance declined sharply during the same period, the observed increase in mean body size may reflect not only somatic growth of individual medusae but also changes in population size structure, including selective loss of smaller individuals. Accordingly, the estimated growth rate is better interpreted as a population-level index of seasonal change in medusa body size rather than a strict estimate of individual somatic growth. Nevertheless, the continuously increasing mean bell diameter and wet weight observed from May to September (Figure 4b), together with particle-tracking evidence indicating steady export of medusae from the inner bay rather than recruitment of new cohorts [40], are broadly consistent with the growth of a single cohort throughout the study period. This approach of estimating growth rate from successive mean wet weights has been widely applied in field studies of *Aurelia* medusae in comparable semi-enclosed systems [43–45].

4.2. Ingestion Rate and Prey Selectivity

The ingestion rates estimated in the present study ranged from 0.31 to 5.31 mg C medusa⁻¹ d⁻¹ (Figure 5a), which is within the range reported previously for *Aurelia* medusae, including 2.2–21.8 mg C medusa⁻¹ d⁻¹ in Tokyo Bay [10], 0.06–29.8 mg C medusa⁻¹ d⁻¹ in the Honjo District [11], and 8–15 mg C medusa⁻¹ d⁻¹ in Kiel Bight [46] (Table 2). However, the upper end of the range observed in Masan Bay is still lower than values reported from several other coastal systems with higher mesozooplankton prey abundance or biomass. This difference likely reflects, to a substantial extent, among-system differences in zooplankton prey availability, given that *Aurelia* predation rates generally increase with prey abundance or concentration [45–48].

Feeding selectivity of *A. coerulea* was low for most mesozooplankton taxa during the study period, with mean C values ranging from −0.05 to 0.18, indicating that medusae fed largely in proportion to ambient prey availability, consistent with previous field studies showing broadly opportunistic feeding in *Aurelia* [9,11,49]. The only persistent exception was *Oithona similis*, which showed positive selectivity of 0.30–0.48 from June to September despite its low biomass composition in the ambient community (Figures 3d and 6). This pattern is unlikely to reflect a general preference for weakly motile prey, because other weakly motile or non-motile prey, such as bivalve larvae and fish eggs, did not show similarly high selectivity. Rather, it may be associated with the ambush-feeding behavior of *Oithona*, characterized by near-motionless suspension and short, intermittent jumps, which may alter encounter, capture, and escape dynamics, thereby increasing its relative vulnerability to capture by *Aurelia* medusae [50,51]. In addition to this behavioral vulnerability, the comparatively small body size of *O. similis* relative to the co-occurring *Acartia* spp. and *Paracalanus parvus* may have further contributed to its capture or retention by medusae, in line with previous evidence that prey-size-dependent selectivity and capture efficiency can occur in *Aurelia aurita* [52]. For selectively favored prey such as *Oithona similis*, abundance may decline sharply even when the overall predation impact on total mesozooplankton appears moderate.

Table 2. Summary of ingestion, clearance, and predation-impact estimates for *Aurelia* medusae reported in field or field-linked studies.

No	Species/Location	Season	Jellyfish Abundance or Biomass	Prey/Zooplankton Abundance or Biomass	Ingestion/Clearance/Population Ingestion Rate	Predatory Impact (% of Abundance, Biomass, or Production)	Ref.
1	<i>Aurelia aurita</i> Tokyo Bay, Japan	Jun–Dec	nd	<i>O. davisae</i> : avg. 6.57×10^5 ind. m ⁻³	IIR 2.2–21.8 mg C medusa ⁻¹ d ⁻¹	nd	[10]
2	<i>Aurelia aurita</i> s.l. Honjo District, Japan	Summer–fall	0.6–1.3 ind. m ⁻³ 20.6–120 mg C m ⁻³	ZP 4.4–23.4 $\times 10^4$ ind. m ⁻³ 1.3–150 mg C m ⁻³	IIR 0.06–29.8 mg C medusa ⁻¹ d ⁻¹ PIR 0.11–12.8 mg C m ⁻³ d ⁻¹	0.6–29% of ZP biomass 1.6–47% of ZP production rate	[11]
3	<i>Aurelia aurita</i> Kiel Bight/western Baltic	Summer	0.002–0.16 ind. m ⁻³ 2–44 mg C m ⁻³	ZP, production rate: ca. 100 mg C m ⁻² d ⁻¹	IIR 8–15 mg C medusa ⁻¹ d ⁻¹ FD 40–80 mg C medusa ⁻¹ d ⁻¹	Ca. 64% of ZP production rate estimated from FD	[46]
4	<i>Aurelia coerulea</i> Jiaozhou Bay, China	May–Aug	0.4–2.1 ind. m ⁻³ 5.8–528.1 g WW m ⁻³	Copepods, 1.15–7.38 $\times 10^3$ ind. m ⁻³	IIR copepods: 228–1054 medusa ⁻¹ d ⁻¹ PIR copepods: 33–2077 m ⁻³ d ⁻¹	1.17–95.98% d ⁻¹ of copepod abundance	[8]
5	<i>Aurelia aurita</i> Tokyo Bay, Japan	Spring–summer	4.8 ind. m ⁻² , 1.02 g C m ⁻² in 1995 43.8 ind. m ⁻² , 10.0 g C m ⁻² in 1996 3.2 ind. m ⁻² , 0.42 g C m ⁻² in 1997	Experimental prey, ZP, 63–234 ind. L ⁻¹	WSCL 0.16 L gWW ⁻¹ h ⁻¹	PCP 14.2% d ⁻¹ in 1995 PCP 162% d ⁻¹ in 1996 PCP 5.0% d ⁻¹ in 1997	[53]
6	<i>Aurelia aurita</i> Kertinge Nor, Denmark	Spring–fall	1–304 ind. m ⁻³	Experimental prey, <i>B. plicatilis</i> : 625–4000 ind. L ⁻¹	CL 0.01–2.3 L medusa ⁻¹ h ⁻¹	PCP 10–351% d ⁻¹	[5]

7	<i>Aurelia labiata</i> Puget Sound, USA	2019–2021	36–2310 g WW m ⁻³	Experimental prey, Calanoids 1.4×10^3 – 1.08×10^5 ind. m ⁻³ <i>D. anglicus</i> 5.42×10^3 – 1.57×10^5 ind. m ⁻³	CL calanoids 322 L medusa ⁻¹ d ⁻¹ CL <i>D. anglicus</i> 284 L medusa ⁻¹ d ⁻¹	PCP 4–228% d ⁻¹	[54]
8	<i>Aurelia aurita</i> Bornholm Basin, central Baltic	Jul–Oct	≤0.023 ind. m ⁻³	Copepods: 4.6 – 6.1×10^3 ind. m ⁻³ Cladocerans: 1.3 – 7.6×10^4 ind. m ⁻³	IIR copepods: 55–386 medusa ⁻¹ d ⁻¹ , IIR cladocerans: 1559–4815 medusa ⁻¹ d ⁻¹	+ 0–1.15% d ⁻¹ of copepod abundance + 0–7.87% d ⁻¹ of cladoceran abundance	[55]
9	<i>Aurelia labiata</i> Prince William Sound, USA	Summer	0.0022 ind. m ⁻³	Copepods: 1727.8 ind. m ⁻³ Cladocerans: 65.5 ind. m ⁻³	IIR copepods: 506 prey medusa ⁻¹ d ⁻¹ IIR cladocerans: 634 prey medusa ⁻¹ d ⁻¹	0.05% d ⁻¹ of copepod abundance 2.3% d ⁻¹ of cladoceran abundance	[56]
10	<i>Aurelia coerulea</i> Masan Bay, Korea	May–Sep	0.03–2.11 ind. m ⁻³ 0.17–23.65 g WW m ⁻³	ZP, 4.3 – 26.9×10^3 ind. m ⁻³ 6.9–20.6 mg C m ⁻³	IIR 0.31–5.31 mg C medusa ⁻¹ d ⁻¹ PIR 0.06–0.66 mg C m ⁻³ d ⁻¹	0.3–6.6% d ⁻¹ of ZP bio-mass 1.1–11.8% d ⁻¹ of ZP production rate	Pre-sent study

Notes: ZP = mixed zooplankton; IIR = individual ingestion rate; FD = food demand; CL = clearance rate; WSCL = weight-specific clearance rate; PCP = population clearance potential, expressed as water-column volumes cleared per day; PIR = population ingestion rate; nd = not determined or not reported; *B. plicatilis* = *Brachionus plicatilis*; *D. anglicus* = *Ditrichocorycaeus anglicus*. † Expressed as prey ind. medusa⁻¹ d⁻¹; not converted to carbon units owing to unavailability of prey-specific carbon content in the original study [55].

4.3. Population Ingestion Rate and Ecological Interpretation

Population ingestion rate of *Aurelia coerulea* in Masan Bay peaked in May at 0.66 mg C m⁻³ d⁻¹ (6.6% of mesozooplankton biomass and 11.8% of production) when medusa abundance was 2.11 ind. m⁻³, then dropped to 0.06 mg C m⁻³ d⁻¹ in June as abundance fell to 0.03 ind. m⁻³, despite the increase in ingestion rate with medusa growth (Figure 7). The seasonal decline in medusa abundance was therefore the primary determinant of population-level predation impact, placing Masan Bay in the lower range of values reported for *Aurelia* medusae (Table 2).

The dominant role of medusa abundance in driving population-level predatory impact is consistent with observations from other coastal systems (Table 2): in Jiaozhou Bay, increasing abundance of *A. coerulea* was accompanied by higher population-level ingestion, with predation pressure reaching 95.98% of copepod abundance during the medusa bloom period [8]; in the Honjo District, population ingestion rate ranged from 0.11 to 12.8 mg C m⁻³ d⁻¹ as medusa biomass varied from 20.6 to 120 mg C m⁻³ [11]; in Tokyo Bay, medusa biomass varied 24-fold among consecutive years (0.42–10.0 g C m⁻²), and population clearance potential changed accordingly from ≤14% to 162% d⁻¹ [53]; similarly, *Aurelia* medusa abundance or biomass can generate strong population clearance potential, as shown in Kertinge Nor and Puget Sound, where population clearance potential reached 10–351% d⁻¹ and 4–228% d⁻¹, respectively [5,54], whereas in Bornholm Basin and in Prince William Sound, predation remained weak throughout due to low medusa abundance [55,56].

Mesozooplankton abundance and biomass in Masan Bay are relatively low during spring and summer [57] (Figure 3a,b), when *Aurelia* medusae are present. Because mesozooplankton biomass is low relative to that in high-impact systems, even a moderate increase in medusa abundance would result in a disproportionately greater predation pressure on the community.

The digestion-time equation of FitzGeorge-Balfour et al. [37] was applied because it provides a temperature-dependent estimate for *A. aurita* s.l., a species complex within which Korean moon jellyfish were formerly treated before being identified as *A. coerulea* [17,18]. Although the medusae used in those laboratory experiments were cultured from polyps in London, the regression equation was fitted to a combined dataset that includes

published digestion-time data from *Aurelia* populations in Tokyo Bay [10] and the Inland Sea of Japan [45], both of which are now recognized as *A. coerulea* [17,18]. The application of this equation to *A. coerulea* therefore represents an approximation within the same species complex rather than a strict interspecific extrapolation. Nevertheless, digestion time may vary with prey type, prey size, temperature, and medusa size [35,37], and species-specific differences within the *Aurelia* complex cannot be excluded. Because a species-specific digestion-time equation for *A. coerulea* was not available, the present estimates should be interpreted as temperature-based approximations, and species-specific digestion-time studies of *A. coerulea* remain an important subject for future research.

The population ingestion rate described above was estimated using whole-water-column mean temperature and observed whole-water-column medusa abundance; however, medusa vertical distribution may be constrained during stratified periods. Previous studies have shown that *Aurelia* vertical distribution can be restricted by sharp pycnoclines and low dissolved oxygen during stratified summer periods [23,24]. In the present study, dissolved oxygen fell below 4 mg L⁻¹ at 4 m in June and 5 m in July, coinciding with a distinct density gradient (Figure 8a). Recalculating the population ingestion rate using the mean temperature of the upper layer above this boundary, together with the digestion-time equation of FitzGeorge-Balfour et al. [37], increased the estimated rate by 11.0% in June and by 13.5% in July (Figure 8b; Table 3). Because medusa vertical distribution was not directly observed, this recalculation retained the observed whole-water-column medusa abundance and modified only the digestion time using the upper-layer temperature. Therefore, it should be interpreted as a conservative temperature-based scenario rather than a direct estimate of layer-specific population ingestion rate. Although the magnitude of this correction was modest, these results indicate that potential vertical habitat restriction should be considered when estimating predatory impact during stratified periods.

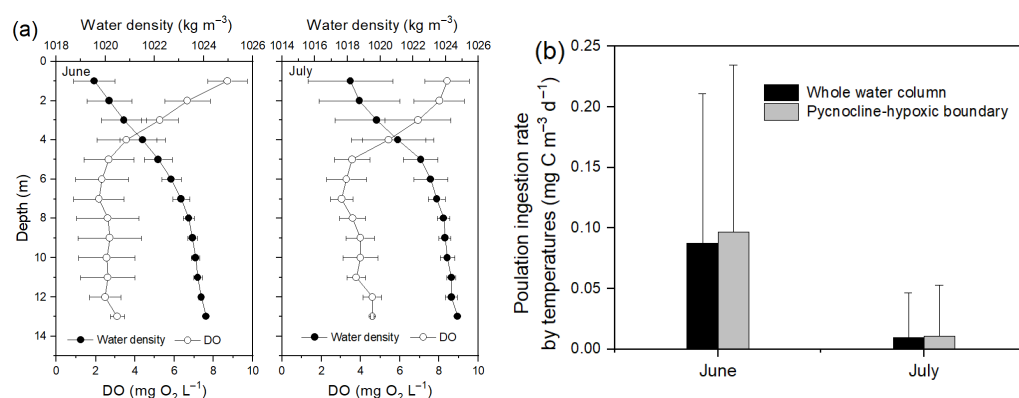


Figure 8. (a) Vertical profiles of water density and dissolved oxygen concentration in June and July and (b) population ingestion rates of *Aurelia coerulea* calculated using whole-water-column mean temperature and upper-layer mean temperature above the pycnocline–hypoxic boundary in Masan Bay. Vertical and horizontal lines denote SD.

Table 3. Population ingestion rates estimated using layer-specific digestion time based on mean temperature of the whole water column and the upper pycnocline–hypoxic boundary layer.

Date	Whole Water Depth	Pycnocline–Hypoxic Boundary Water Depth
8 May	0.66 ± 1.14 mg C m ⁻³ d ⁻¹ (15.1 °C, DT: 2.30 h)	-
25 Jun	0.06 ± 0.11 mg C m ⁻³ d ⁻¹ (20.1 °C, DT: 1.75 h)	0.07 ± 0.07 mg C m ⁻³ d ⁻¹ (22.0 °C, DT: 1.58 h)
16 Jul	0.16 ± 0.22 mg C m ⁻³ d ⁻¹	0.18 ± 0.18 mg C m ⁻³ d ⁻¹

	(20.9 °C, DT: 1.68 h)	(23.2 °C, DT: 1.48 h)
23 Sep	0.34 ± 0.71 mg C m ⁻³ d ⁻¹ (24.7 °C, DT: 1.37 h)	-

Note: DT = digestion time, calculated from the temperature-dependent equation of FitzGeorge-Balfour et al. [37].

5. Conclusions

This study provides the first gut-content-based estimate of the population-level predation impact of *Aurelia coerulea* on mesozooplankton in Masan Bay, a representative area where the jellyfish occur in large numbers. Population ingestion rate was highest in May, when medusa abundance peaked, reaching 0.66 mg C m⁻³ d⁻¹, equivalent to 6.6% of mesozooplankton biomass and 11.8% of production (Figure 7). After June, population ingestion rate declined sharply because medusa abundance decreased markedly, although individual medusae continued to grow and individual ingestion rate increased in the pooled data with body size (Figures 4 and 5). Gut contents indicated broadly opportunistic feeding of *A. coerulea*, while *Oithona similis* showed consistently positive selectivity during the warm season (Figure 6). In June and July, recalculation using upper-layer temperature above the pycnocline–hypoxic boundary increased estimated population ingestion rate by 11.0% and 13.5%, respectively (Figure 8), indicating that the vertical habitat actually occupied by medusae should be considered when estimating predation impact under stratified conditions. Overall, the ecological role of *A. coerulea* in Masan Bay depended primarily on seasonal variation in medusa abundance and was further modified in summer by hydrographic stratification and hypoxia-induced vertical habitat restriction.

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