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Diets and Seasonal Ingestion Rates of *Aurelia coerulea* (Cnidaria: Scyphozoa) Polyps by *in situ* Feeding Experiments in Jiaozhou Bay, China

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The benthic scyphopolyp population is an important stage in the scyphozoan lifecycle. Nevertheless, few studies have detailed the natural feeding and quantified the energy flux of polyps based on field research. To better understand the scyphopolyp natural diet and seasonal variation patterns in the ingestion rate, *in situ* feeding experiments were conducted on *Aurelia coerulea* polyps in Jiaozhou Bay, China from August 2018 to April 2019. The diet of *A. coerulea* polyps was determined by gut content analysis. Digestion rates were also measured. Ingestion rates, based on the gut contents and digestion rates, were assessed monthly. Copepods, copepod nauplii, and ciliates were identified in the guts of *A. coerulea* polyps. Copepods with the bulk of total prey intake in number are an important source of nutrition for *A. coerulea* polyps in Jiaozhou Bay. Prey capture of *A. coerulea* polyps (prey polyp^{-1}) varied among months, and was highly dependent upon the abundance of planktonic prey in the habitat. Copepods and copepod nauplii were digested more rapidly as temperature increased. Carbon weight-specific ingestion rate exhibited an obvious seasonal change, with the mean value of 0.13 ± 0.12 μg C μg C^{-1} d^{-1}. More rapid digestion of prey at higher temperatures and larger prey availability would cause a higher ingestion rate in polyps. Scyphopolyps are widely distributed predators in littoral ecosystems and they may play an important role in plankton–benthos coupling by transferring energy from the water column to the benthos. Massive scyphopolyps blooms may influence pelagic ecosystems.

Keywords: jellyfish bloom, Scyphozoa, feeding, scyphopolyp, Copepoda, prey capture, pelagic ecosystem

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INTRODUCTION

Interest in the importance of jellyfish in the material cycle and the energy flow of marine ecosystems has increased as outbreaks of jellyfish populations attract public and scientific attention (Dong et al., 2010; Uye, 2011; Condon et al., 2013; Duarte et al., 2013). Previous studies have reported the potential causes and consequences of jellyfish population fluctuations, focusing on the trophic relationships between the pelagic medusae and other marine organisms, as well as the effects of medusae blooms on marine ecosystems (Olesen et al., 1994; Purcell, 2003, 2009). Most jellyfish are important as gelatinous consumers of zooplankton and ichthyoplankton, and massive aggregation of pelagic medusae have

been shown to decrease populations of zooplankton as well as fish eggs and larvae (Schneider and Behrends, 1994; Purcell, 1997; Hansson et al., 2005; Uye, 2011).

Common bloom jellyfish, *Aurelia* spp., are offshore scyphomedusae with worldwide distributions (Olesen et al., 1994; Purcell et al., 2009; Dong et al., 2010). Mass occurrences of *Aurelia* medusae have been reported from many parts of the world (Möller, 1980; Olesen et al., 1994; Omori et al., 1995; Dong et al., 2010). This jellyfish has metagenic life cycles, with pelagic stages (ephyra, medusa, and planula) and benthic stages (polyp, strobila, and podocyst) (Arai, 1997; Lucas et al., 2012). The benthic polyps can generate additional polyps through asexual reproduction and release abundant ephyrae (small medusae) by strobilation. Thus, the polyp is an important stage in the *Aurelia* lifecycle (Lucas et al., 2012) and recruitment success is critical for maintaining jellyfish population (Gröndahl, 1988b; Lucas, 2001; Purcell, 2007). For polyp ecology of the jellyfish *Aurelia*, previous studies have documented the metamorphosis of planula larvae into polyps, the expansion of polyp *via* asexual propagation, and the strobilation and recruitment of polyps of this jellyfish under laboratory conditions (e.g., Purcell, 2007; Han and Uye, 2010; Wang N. et al., 2015). The majority of field studies have been confined to the population dynamics and locations of polyp, the timing and rate of strobilation, and the substrates of polyp colonization (e.g., Lucas and Williams, 1994; Uye and Shimauchi, 2005; Purcell et al., 2009; Ishii and Katsukoshi, 2010; Feng et al., 2017).

However, the relative importance of food conditions for natural polyp population is controversial, and few data exist on potential seasonal variation in ingestion rates *in situ* (Lucas et al., 2012; Ikeda et al., 2017). Previous studies have shown that scyphozoan polyps consume a wide variety of prey, including copepods, copepod nauplii, rotifers, planula larvae of scyphomedusae, dinoflagellates, ciliates, and fish larvae (Gröndahl, 1988b; Östman, 1997; Kamiyama, 2011; Huang et al., 2015; Ikeda et al., 2017). Kamiyama (2011) estimated the feeding rates of *Aurelia aurita* polyps on ciliates as prey and speculated that planktonic ciliates likely serve as a major food for *A. aurita* polyps. In contrast, Ikeda et al. (2017) speculated that the most appropriate prey for polyps might be large copepod nauplii by examining the effect of prey characters on the ingestion rate of *A. aurita* polyps. They also constructed an energy budget model for *A. aurita* polyp and estimated the ingestion rates of polyps based on the biomass of mesozooplankton in Fukuyama Harbor, Japan. However, most studies on the feeding ecology of polyps have been laboratory-based. Few studies have detailed the natural feeding and quantified the energy flux of polyps based on field research (Mills, 2001; Lucas et al., 2012; Ikeda et al., 2017). Thus, quantitative descriptions of the natural diets and the potential seasonal variation patterns in ingestion rate of *Aurelia* polyps based on the field research are needed to characterize the feeding ecology of polyps in littoral benthic communities.

Aurelia coerulea blooms have also been reported in Jiaozhou Bay, China (Wan and Zhang, 2012; Wang et al., 2020). In this study, we performed *in situ* feeding experiments on *A. coerulea* polyps in Jiaozhou Bay from August 2018 to April 2019. This location provided a natural environment for the prey capture of *A. coerulea* polyps. Moreover, according to previous studies, strobilation of *A. coerulea* polyps, as indicated by the presence of ephyrae, occurs in Jiaozhou Bay as early as April (Wan and Zhang, 2012; Wang Y. T. and Sun, 2015); *A. coerulea* attain sexual maturity by mid-summer, and Wang Y. T. and Sun (2015) speculated that the metamorphosis of planula larvae into polyps might occur during August. Therefore, feeding ecology assessments of the *A. coerulea* polyp are most reasonable between August 2018 and April 2019 in Jiaozhou Bay. This covers the period from *A. coerulea* spawning to polyp strobilation. To estimate the diet of polyps in nature, prey types were identified based on gut content analysis. Additionally, we estimated polyp prey digestion rates. Consequently, seasonal variation patterns in polyp ingestion rates were estimated based on *in situ* surveys of prey abundance in gut contents and digestion rates. Finally, we used the study data to practically assess the potential role of scyphopolyp predators in the plankton–benthos energy transfer process within the littoral ecosystem.

MATERIALS AND METHODS

Study Area

Jiaozhou Bay is a semi-enclosed bay located on the southern side of the Shandong Peninsula, China (**Figures 1A,B**). Jiaozhou Bay is strongly influenced by human activities; industrial and agricultural businesses are found around the bay. Anthropogenic structures in Jiaozhou Bay, such as port installations and offshore platforms, are suitable settling surfaces for scyphopolyps, and the increasing numbers of these anthropogenic structures have provided new habitats (Miyake et al., 2002; Holst and Jarms, 2007). Underwater surveys have identified *A. coerulea* polyps on the bottom of a research vessel (the "Haiou" boat at the Station) in Jiaozhou Bay (Feng et al., 2017). To better understand the scyphopolyp diet and seasonal variation in ingestion rate in the field, *in situ* feeding experiments were conducted on *A. coerulea* polyps in Jiaozhou Bay between August 2018 and April 2019 next year; this provides a realistic environment for the prey capture of polyps.

Temperature, Salinity, and Zooplankton

Temperature and salinity at 2–3 m depth (the depth where base plates carrying the polyps were submerged, see below) were measured monthly using an AAQ1183-1F CTD (Alec Electronics Co., Japan) at the station in Jiaozhou Bay. Zooplankton samples were also collected monthly to study plankton variation concurrent with polyp analysis using a II plankton net (mesh size: 160 μm, diameter: 50 cm). The plankton nets were towed a short distance (ca. 30–50 cm) from the polyp-settling plastic plates. Zooplankton samples were stored in 5% formalin in 1-L bottles, classified into different taxonomic groups, and counted. The abundance of each zooplankton group (A, ind m^{-3}) was determined on a per unit volume (m^3).

In situ Experiment Procedures and Sampling

Aurelia coerulea polyps were obtained by previously described artificial asexual reproduction methods (Holst and Jarms, 2007;

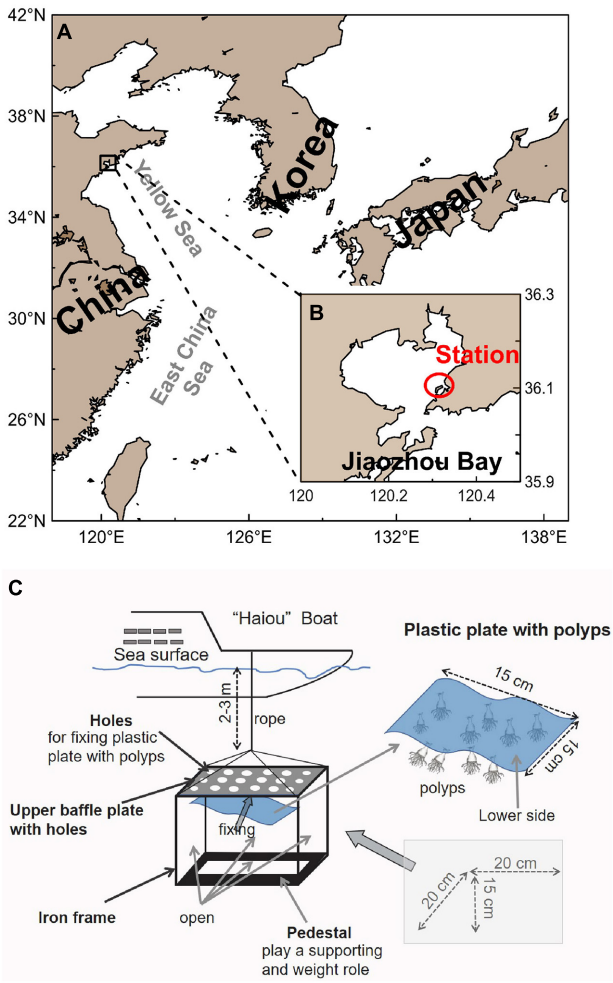

FIGURE 1 | Study area and schematic diagram *of Aurelia coerulea* polyps *in situ* feeding experiment. **(A)** Map of Jiaozhou Bay. **(B)** Station in Jiaozhou Bay where the plastic plates carrying polyps were deployed. **(C)** A roof (20 cm × 20 cm × 15 cm) with four open sides was used to support the plastic plate carrying the polyps; the upper side was a baffle plate to simulate the bottom of "Haiou" boat, and the holes were used to fix plastic plate and tie a rope; the lower side was a pedestal that played a supporting and weight role. Polyps were attached to the lower side of the plastic plate (15 cm × 15 cm).

Feng et al., 2017). Six mature females and four mature males (*A. coerulea* medusae) collected in Jiaozhou Bay were cultured in a 200-L aquarium at a water temperature of 21–23°C in our jellyfish laboratory (Institute of Oceanology, Chinese Academy of Sciences). Corrugated plastic plates (15 cm × 15 cm) were deployed as bases for *A. coerulea* polyp attachment. Before *in situ* experiments, these polyps were cultured in 120-L aquariums filled with filtered seawater (20-μm filter) at a water temperature of 21–23°C and salinity of 31–32. Adequate *Artemia* nauplii were supplied daily (7×10^3 ind L^{-1}), and the water was then replaced with newly filtered seawater. Fully developed 16-tentacle polyps were selected for the following *in situ* feeding experiments between August 2018 and April 2019. Although the experimental polyp ages after asexual reproduction were different between different months, the sizes of polyps (calyx diameter, μm) used for *in situ* experiments were similar between different months (the mean size of polyps for the following gut contents across 9 months was 965.86 ± 289.50 μm).

A floating dock, the "Haiou" boat (50-m long, 8-m wide) in Jiaozhou Bay (36.07°N, 120.34°E), was used as the experimental platform. The water depths ranged between 5 and 6 m at the station. Before deployment, each plastic plate carrying polyps was fixed on a roof with four open sides (20-cm long, 20-cm wide, 15-cm high, **Figure 1C**) to support the plastic plate and to reduce possible physical damage caused by movements. The polyps were then acclimated for at least 48 h with the *in situ* filtered seawater (20-μm filter) before the experiments. The *A. coerulea* polyps used for the *in situ* feeding experiments appeared healthy, extending tentacles fully. Each month (from August 2018 to April 2019), five base plates carrying the polyps (mean density was about 3 polyps cm^{-2}) were submerged at the station and secured by ropes at a depth of 2–3 m, and the mean size of polyps was similar between different base plates. Five new plastic plates were deployed in the next month following the above processes. The rooves carrying plastic plates were all horizontally moored with the polyps' attachment side facing downward (**Figure 1C**), mimicking the natural state in Jiaozhou Bay and avoiding sedimentation effects (Feng et al., 2017).

All samplings for gut content analysis were conducted during the day (8:00 a.m. to 6:00 p.m.), and the seasonal variations in the gut contents of *A. coerulea* polyps sampled diurnally were compared. The plastic plates with polyps were sampled a minimum of 15 days after deployment to ensure that polyps were adequately acclimated to the field environment. Before polyp sampling, the rooves carrying the plates were slowly pulled out (pulling speed no more than 0.1 m s^{-1}). A bucket (40-cm diameter, 32-cm high) was used to take the rooves out when the rooves were about to leave the water. Polyps were divided into two parts: one part was sampled for gut content analysis, and the other part was used for the digestion experiment (see below).

Gut Content Analysis and Estimation of Prey Carbon Content

Gut contents of polyps were analyzed monthly. A total of 50 visually undamaged polyps from one plastic plate were randomly collected for gut content analysis each month. The selected plate carrying the polyps was cut with scissors. Then they were immediately placed in a glass Petri dish (9-cm in diameter) with 5% buffered formaldehyde to prevent further digestion. The polyps' attachment side faced upward to protect these polyps from damage. The sampled polyps were immediately examined under a stereo microscope (Nikon Corporation, Shinagawa-ku, Tokyo, Japan). At the same time, the sizes of these polyps (calyx diameter, μm) were measured by the NIS-Elements D software (Ver. 5.01). The waters in the Petri dishes for the preservation of polyps were also checked. Prey items including copepods (including copepod adults and copepodites), copepod nauplii, and ciliates (Tintinnids) were identified in polyps' guts. Crustacean carapaces and tentacles were also found in polyps'

guts. Each prey item was enumerated. The numbers of polyps with prey in the gut were also recorded.

The mean carbon contents of copepods and copepod nauplii found in the guts of polyps were estimated by volume biomass of prey referring to the methods described by previous studies (**Table 1**). The copepods and copepod nauplii isolated from polyps' guts were selected to measure the lengths (prosome length for copepods and carapace length for copepod nauplii) by the NIS-Elements D software. Then, the mean carbon contents of copepods and copepod nauplii captured by polyps were determined by methods used in the studies of Uye (1982) and Berggreen et al. (1988), respectively (**Table 1**).

Digestion Experiments

Polyp digestion rates were determined by examining the decrease in the number of prey in polyps' guts over time (h). Digestion rates of copepods were measured monthly by *in situ* experiments. However, it was impossible to determine how long prey had been in the gut prior to sampling. Therefore, we assumed that copepods were captured by the polyps shortly before collection. Polyps for digestion experiments were collected from 2 to 5 plates, depending on the digestion rates and sampling times during experiments in different months. The base plates carrying polyps for the digestion experiments were dipped in a 50-L container with natural filtered seawater (20-μm filter). The time when the base plates were transferred to the container was considered as the initial time. To follow the digestion process, 50 visually undamaged polyps (16-tentacle) were collected per hour, and the selected polyps were immediately preserved in a glass Petri dish with 5% buffered formaldehyde to stop digestion. Then the selected polyps were dissected under a stereo microscope and the remaining numbers of copepods in polyp guts at each sampling time were recorded. The length of time at which no prey could be detected (the solid matter and tissues of prey disappeared or only carapaces and tentacles were left, the ending time) was used in the calculation of the following prey-capture rates (Martinussen and Båmstedt, 1999; Purcell, 2003).

Gut content analysis indicated that polyps' guts contained a small number of copepod nauplii at the start of the digestion experiments; therefore, the digestion rate of copepod nauplii could not be measured directly *in situ*, but under laboratory conditions. Copepod nauplii (mean carapace length: 204.7 μm) were obtained by the reproduction of mature copepods (*Pseudodiaptomus annandalei*, Calanoida) cultured in our laboratory at a water temperature of about 21°C and salinity of 31–32, and two diatoms, *Phaeodactylum tricornutum* and Chrysophyta, were offered as prey for copepods daily. Before experiments, copepod nauplii (about 500 ind L^{-1}) were offered as prey for polyps feeding for about 0.5–1 h (mean 1.2 prey $polyp^{-1}$ after feeding). Then these polyps were transferred into filtered seawater (20-μm filter) and were cultured in constant-temperature incubators. To study the effect of temperature on digestion rates, digestion experiments were conducted in constant-temperature incubators at 5, 7, 12, 18, 22, and 26°C (according to the natural temperatures), respectively. A total of 20 polyps were collected per hour, and the selected polyps were immediately preserved in 5% buffered formaldehyde. They were then dissected under a stereo microscope to follow the digestion process.

We did not measure the digestion rate of ciliate due to the difficulty in detecting the variation in the number of ciliates in polyp gut over time by laboratory test.

TABLE 1 | Estimation of carbon weight of different prey items (copepods and copepod nauplii) found in the gut of polyp.

Prey	Body length (*L*, mean ± SD, μm)	*n*	Carbon weight (*C*, μg)	References
Copepod	485.47 ± 134.34[a]	112	0.750	Uye, 1982[c]
Copepod nauplii	237.96 ± 45.13[b]	24	0.234	Berggreen et al., 1988[d]

"n" means the numbers of prey in polyps guts selected for the measurement of body length.
[a] *Prosome length.*
[b] *Carapace length.*
[c] *Calculated using* $\log C = 3.07 \log L - 8.37$.
[d] *Calculated using* $C = 3.18 \times 10^{-9} \times L^{3.31}$.

Prey Capture and Ingestion Rate

The mean number of copepods and copepod nauplii found in the gut of each sampled polyp (50 polyp specimens on each sampling date) was recorded as prey capture (*N*, prey $polyp^{-1}$). The prey-capture rate (*C*) of *A. coerulea* polyp was expressed as the number of prey captured per polyp per day (prey $polyp^{-1}$ d^{-1}) and was calculated monthly following Coma et al. (1994):

$$C = N[\sum_{t=0}^{D} 1 - (t/D)]^{-1} \times 24, \quad (1)$$

where t is time (in hours), and *D* is the digestion time (in hours).

Then the ingestion rate of polyp (*I*, μg C $polyp^{-1}$ d^{-1}) was calculated based on the carbon content weight of copepods and copepod nauplii (*PW*, μg C; **Table 1**). However, differences in the size of polyps collected on the same sampling date may affect the prey capture of polyps. To eliminate the effect of polyp size on ingestion rate, we converted polyp size to polyp carbon weight (*W*, μg C) using the relationship between polyp body volume (*BV*, μm^3) and carbon weight as given in Ikeda et al. (2017): $W = BV \times 27.4 \times 10^{-9}$. The contracted polyps were photographed with a digital camera-equipped stereo microscope to determine their body volumes (Ikeda et al., 2017). The ingestion rates were converted to carbon weight-specific ingestion rates (I_w, μg C μg C^{-1} d^{-1}; copepods and copepods nauplii as prey): $I_W = I / W$.

Statistical Analyses

OriginPro8.0 and SPSS16.0 were used to organize and statistically analyze the data in this study. One-way analysis of variance (ANOVA) was used to determine the differences in polyp size for gut content analysis and digestion rate on different sampling dates; normality and equal variances were checked before ANOVA analysis. The Spearman correlation test was used to evaluate the relationship between both the number of polyps with prey in gut and prey capture (prey $polyp^{-1}$) and

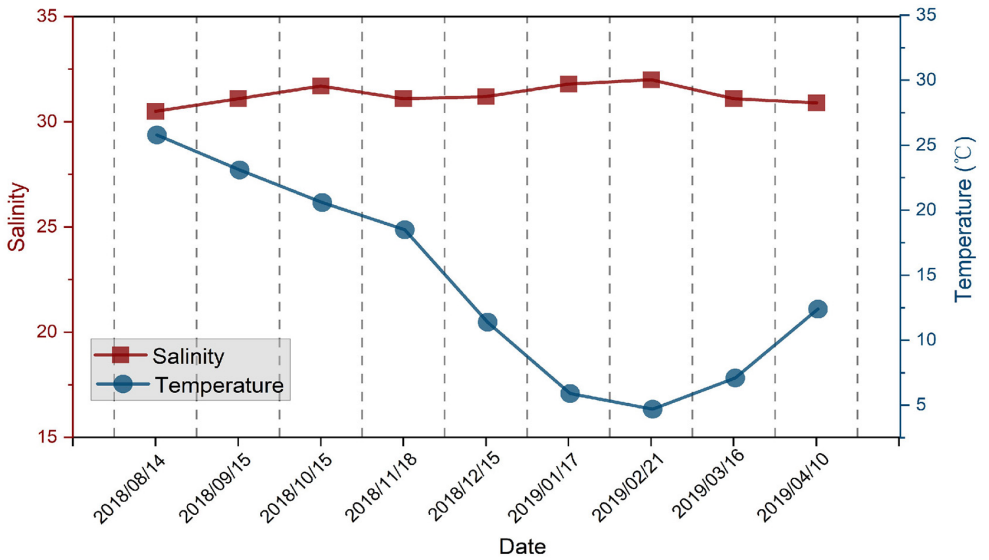

FIGURE 2 | Temperature and salinity at the Station in Jiaozhou Bay (**Figure 1B**) from August 2018 to April 2019.

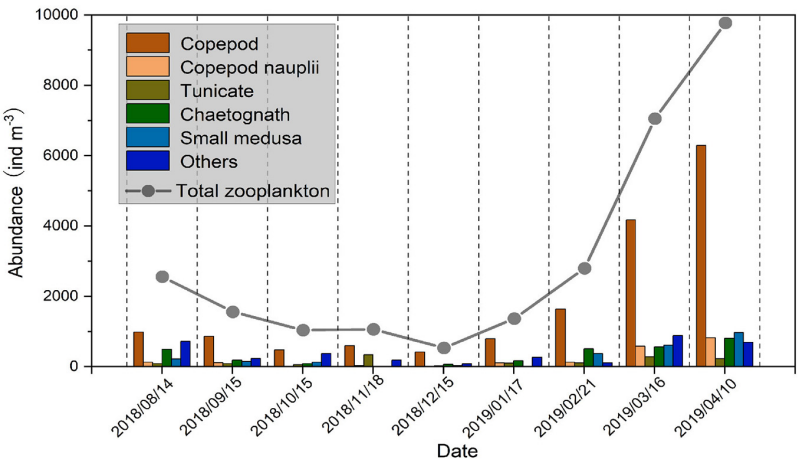

FIGURE 3 | Zooplankton abundance (ind m^{-3}) collected by a II plankton net at the Station in Jiaozhou Bay from August 2018 to April 2019.

zooplankton abundance (ind m^{-3}). We considered $P < 0.05$ to be statistically significant.

RESULTS

Temperature, Salinity, and Zooplankton Abundance

During the study, the temperature at the sampling station ranged from 4.8 to 25.8°C, while salinity ranged from 30 to 32 (**Figure 2**). Zooplankton collected by a II plankton net (160-μm mesh size) within the study area were comprised of 54.04 ± 9.60% copepods (including copepods adults and copepodites), 4.82 ± 3.34% copepod nauplii, 7.20 ± 8.43% tunicates, 10.53 ± 5.61% chaetognaths, 7.17 ± 4.71% small medusae, and 16.23 ± 9.18% others in abundance. Copepods formed the dominant zooplankton community in the present study area (**Figure 3**). Abundance of total zooplankton had significant seasonal variation, which decreased from August to December 2018 and then increased from January to April 2019, with an average abundance of 3157.11 ± 3164.90 ind m^{-3}, and the highest value in this study was recorded in April 2019 (**Figure 3**).

Gut Content and Prey Capture

The mean size (±SD) of *A. coerulea* polyps for gut content analysis in the 9-month study was 965.86 ± 289.50 μm. There were no significant differences in polyp sizes between different months (one-way ANOVA: $F = 0.264$, $P = 0.976$) (**Figure 4**). A total of 50 polyps were sampled for gut content analysis each

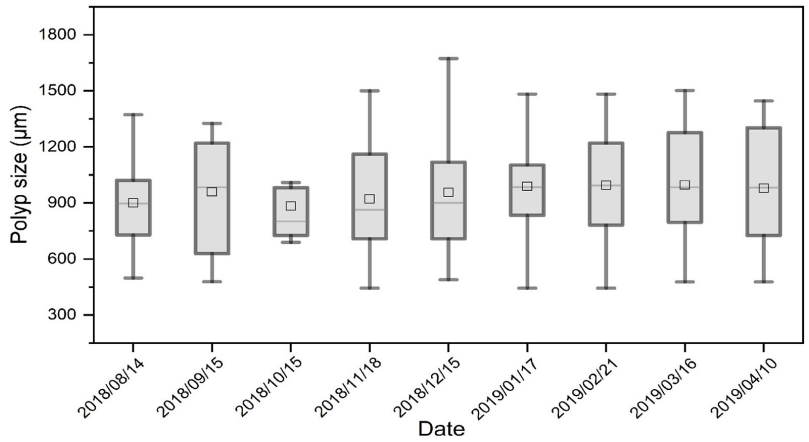

FIGURE 4 | Boxplot of the size diversities of *A. coerulea* polyps used for gut content analysis for each sampling date. One-way ANOVA analysis indicated that there were no significant differences in polyp sizes between different months ($F = 0.264$, $P = 0.976$). The lower whisker, lower hinge, horizontal line, upper hinge, and upper whisker show minimum, lower quartile, median, upper quartile, and maximum size diversity, respectively. The squares in the boxplot indicated the mean values of polyp size.

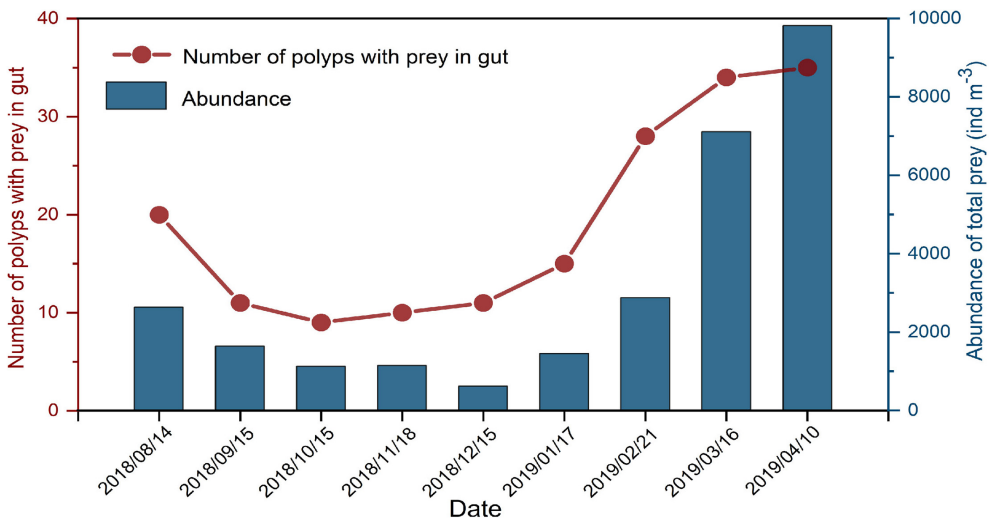

FIGURE 5 | The relationship between the number of polyps with prey in gut (50 polyps were collected on each sampling date) and abundance of zooplankton (ind m^{-3}) during the study period. A Spearman correlation test showed that the number of polyps with prey in gut was significantly correlated with zooplankton abundance ($R^2 = 0.904$, $P = 0.001$, $n = 9$).

month, and the number of polyps with prey in the gut varied in different months (**Figure 5**). The Spearman correlation test showed that the number of polyps with prey in the gut was significantly correlated with zooplankton abundance ($R^2 = 0.904$, $P = 0.001$, $n = 9$).

Copepods (copepod adults and copepodites), copepod nauplii, and ciliates (Tintinnids) were identified in the guts of polyps in Jiaozhou Bay during the study period. The gut content analysis indicated that copepods represented the bulk of the total prey intake in number (88.02 ± 10.58%), followed by copepod nauplii (11.34 ± 10.03%) and ciliates (0.65 ± 1.31%; only three ciliates were found in three polyps' guts during February and March 2019) (**Figure 6**). However, numbers of prey in the gut of polyps had significant seasonal variations: the number of total prey (copepods, copepod nauplii, and ciliates together) in the gut of polyps on each sampling data (50 polyps) decreased from August 2018 to November 2018, and then increased from December 2018 to April 2019 (**Figure 6**).

The mean values of prey capture (N, prey $polyp^{-1}$) on copepods and copepod nauplii were 0.49 ± 0.32 and 0.10 ± 0.11 prey $polyp^{-1}$, respectively. The maximum values of N both on copepods and copepod nauplii occurred in April 2019, with the maximum of 1.06 and 0.30 prey $polyp^{-1}$, respectively (**Figure 7**). Prey capture was significantly affected by zooplankton abundance (**Figure 7** and **Table 2**).

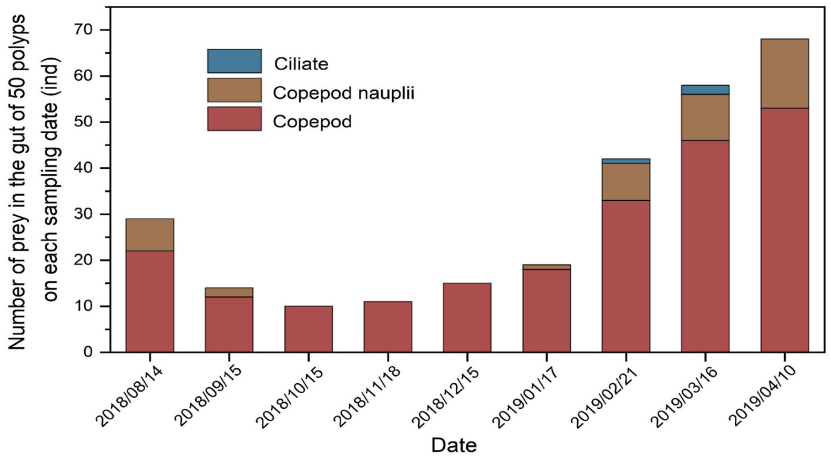

FIGURE 6 | Number of prey (copepods, copepod nauplii, and ciliates) in the gut of 50 polyps on each sampling date (50 polyps were detected on each sampling date). Sampling period ranged from August 2018 to April 2019.

Digestion Rate

The sizes of polyps sampled for the digestion experiments did not differ significantly among different months (one-way ANOVA: $F = 0.588$, $P = 0.785$), and were not significantly different from the polyps collected for gut content analysis (one-way ANOVA: $F = 2.699$, $P = 0.102$). Thus, the size of *A. coerulea* polyps was unlikely to be an influencing factor on the digestion experiment results, nor an influence in the use of these results for calculations of prey-capture rates.

Digestion processes indicated that an exponential decrease in the number of prey per polyp occurred over time in all digestion experiments (**Figure 8**); as temperature increased, both copepods (**Figure 8A**) and copepod nauplii (**Figure 8B**) in polyps' guts were digested more rapidly by *A. coerulea* polyp. Digestion of polyps was significantly affected by water temperature. The linear regressions for the digestions of copepods and copepod nauplii were as follows: $y = 34.56 - 1.31x$ [$P < 0.001$, $R^2 = 0.977$; y = digestion time (h), x = temperature (°C)] and $y = 12.78 - 0.45x$ ($P = 0.001$, $R^2 = 0.931$), respectively (**Figure 9**).

Prey-Capture Rate and Ingestion Rate

The prey-capture rate (C, prey polyp^{-1} d^{-1}) in each month (**Table 3**) was calculated directly from the mean value of prey capture (prey polyp^{-1}) and the digestion rate (D, h). Our results indicated that each *A. coerulea* polyp would consume, on average, 1.87 ± 1.44 copepods and 0.68 ± 0.83 copepod nauplii daily during the study period (**Table 3** and **Figure 10A**). Values of C varied in different months (**Figure 10A**), and the maximum C-value of 7.52 total prey (copepods and copepods nauplii together) polyp^{-1} d^{-1} happened in August 2018 (**Figure 10A**).

The carbon weight-specific ingestion rates of *A. coerulea* polyps (I_w, μg C μg C^{-1} d^{-1}, copepods and copepods nauplii as prey) showed a large seasonal variation, which decreased from 0.43 μg C μg C^{-1} d^{-1} in August 2018 to 0.04 μg C μg C^{-1} d^{-1} in December 2018, then increased to 0.17 μg C μg C^{-1} d^{-1} in April 2019 (**Figure 10B**). The mean (±SD) value of I_w was 0.13 ± 0.12 μg C μg C^{-1} d^{-1} during the study period (**Table 4**).

DISCUSSION

Prey Capture of *A. coerulea* Polyps

We cultured *A. coerulea* polyps *in situ* (Jiaozhou Bay) during August 2018 to April 2019 and evaluated their diet by analyzing gut contents; the results indicated that copepods, copepod nauplii, and ciliates were all captured by *A. coerulea* polyps. Compared to copepod nauplii and ciliates, copepods were frequent in polyps' guts comprising 88.02 ± 10.58% in number of the total prey in this study. Consistent with our study result, a previous study by Östman (1997) indicated that the main prey for scyphopolyps (*Aurelia* and *Cyanea*) from the Gullmar Fjord on the Swedish west coast appeared to be small copepods, which occurred abundantly in water.

Previous studies have reported that the main food of the medusa stage of *Aurelia* is meso-zooplankton (Arai, 1997); for example, studies by Ishii and Tanaka (2001) and Uye and Shimauchi (2005) both found that copepods, which often dominate zooplankton biomass in eutrophic embayments, were an important food source for *A. aurita* medusae. The medusa can swim, concentrate prey around their oral parts, and excrete mucus to retain food items around their oral opening (Southward, 1955); polyps cannot actively move toward prey, and cannot accumulate prey particles by themselves (Kamiyama, 2011). The most important method of polyp predation is using their tentacles as a trap and capturing their prey with the help of nematocysts located on the tentacles (Kamiyama, 2011). For scyphopolyps, as a benthic suspension-feeding predator, the success of tentacle entrapment feeding is mainly based on the prey encounter rate (Kamiyama, 2011; Ikeda et al., 2017), implying that prey capture appeared to be determined by zooplankton availability. This was demonstrated by our study: the prey capture of *A. coerulea* polyp was highly dependent

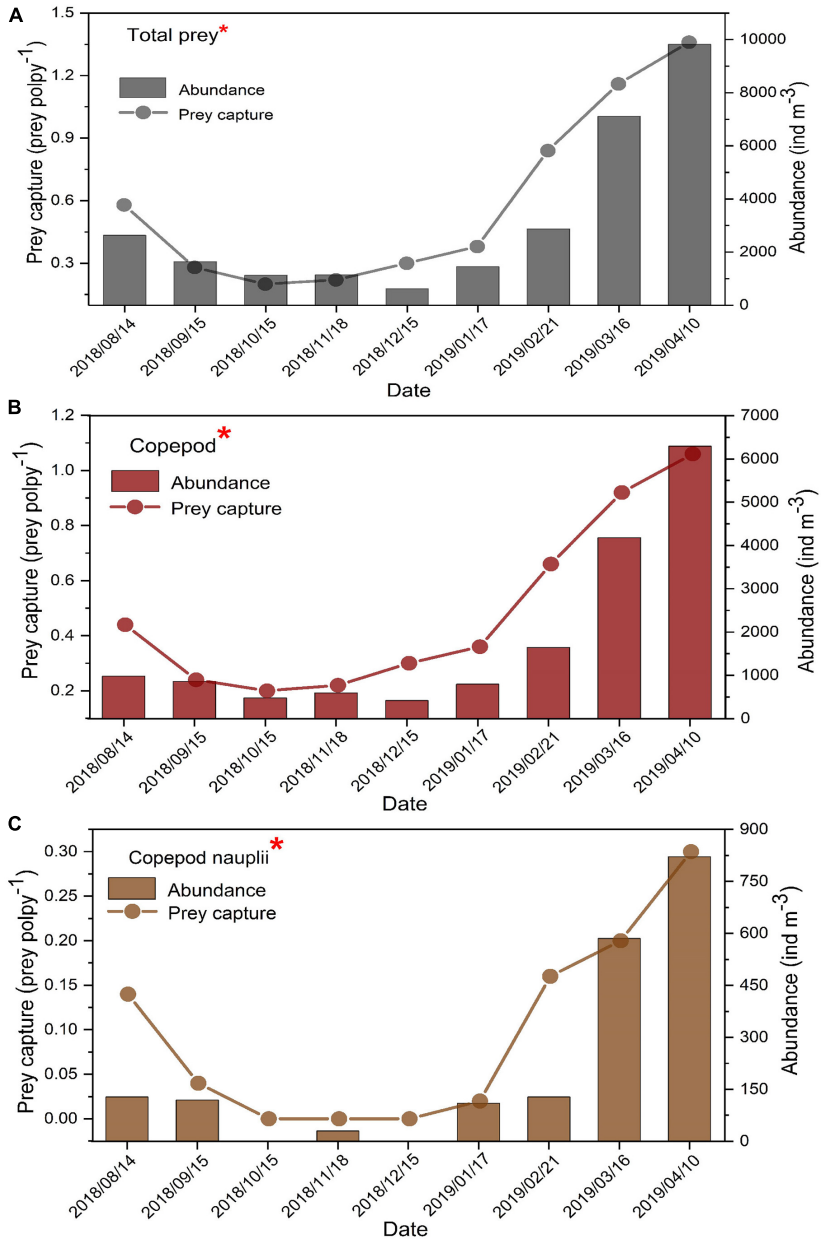

FIGURE 7 | The relationship between prey capture (prey polyp^{-1}) and zooplankton abundance (ind m^{-3}) [total prey **(A)**, copepods **(B)**, and copepod nauplii **(C)**] during August 2018 to April 2019 sampling period. *Spearman correlation tests showed that the prey capture was significantly correlated with zooplankton abundance. **Table 2** shows the results of the Spearman correlation tests.

upon the abundance and frequency of planktonic prey in the polyp habitat (**Figure 7** and **Table 2**). A similar correlation was observed between zooplankton abundance in the surrounding environment and the number of polyps containing prey items, which indicated that an increased higher zooplankton abundance was reflected by an increase in the number of polyps containing prey (**Figure 5**). This relationship also was reported by Coma et al. (1994) with the study of the prey capture of gorgonian *Paramuricea clavata*. Thus, the relatively high abundance of copepods in surrounding water (54.04 ± 9.60%; **Figure 3**) might increase prey availability and the opportunity to encounter *A. coerulea* polyps. However, Ikeda et al. (2017) speculated that the most appropriate prey for polyps might be large copepod nauplii. Copepod nauplii only comprised a small part of the polyp diet in this study (**Figure 6**). Perhaps the relatively low prey capture of copepod nauplii was due to the low population abundance in our study area (4.82 ± 3.34%; **Figure 3**). For benthic suspension-feeding predators, a previous study has indicated that their prey capture may be influenced by hydrodynamic processes (Tsounis et al., 2006). The plastic

TABLE 2 | The results of Spearman correlation test for the relationship between zooplankton abundance and prey capture (prey polyp^{-1}).

Prey capture (prey polyp^{-1})	Abundance (ind m^{-3})		
	Total prey	Copepods	Copepod nauplii
Total prey	R^2 = 0.867, ***P*** = 0.002*		
Copepods		R^2 = 0.867, ***P*** = 0.002*	
Copepod nauplii			R^2 = 0.983, ***P*** < 0.001*

**P-values given in bold are significant at 5% level.*

plates carrying polyps were fixed on rooves (simulation of a vessel bottom) *in situ*; the rooves, with four open sides, were horizontally moored with the polyps' attachment side facing downward (**Figure 1C**), mimicking the natural state in Jiaozhou Bay (Feng et al., 2017). Therefore, normal water-flow may not be disturbed.

Micro-zooplankton are also numerically important components of seawater zooplankton communities (Pierce and Turner, 1992). Kamiyama (2011) showed that planktonic ciliates, a main component of micro-zooplankton, served as food items for *A. aurita* polyps under laboratory conditions. However, in the present study, ciliates were found in the guts of *A. coerulea* polyps rarely (**Figure 6**). Östman (1997) also rarely found ciliates in the guts of polyps. This may because ciliates are fragile and readily destroyed by mechanical stress during polyp feeding (Östman, 1997; Kamiyama, 2011); the rapid digestion of ciliates may also cause a short retention time of ciliates in the gut of polyps. These factors may cause an underestimate of the contribution of ciliates to the diets of *A. coerulea* polyps in this study. According to one previous study, the abundance of ciliates has a great seasonal variation in our study area with the value of 300–2418 ind L^{-1} (Yu et al., 2011). However, previous studies have indicated that faster prey may encounter *A. aurita* polyps more frequently (Kamiyama, 2011; Ikeda et al., 2017), which was corroborated by the theoretical encounter model (Greene et al., 1986; Rothschild and Osborn, 1988). Therefore, the relatively low swimming speed of ciliates probably reduced the opportunity to encounter to scyphopolyps compared to mesozooplankton (Kamiyama, 2011). In addition, compared to larger prey, like copepods, ciliates only provide a small energy source from one prey.

In summary, copepods that were characterized by larger prey availability, faster swimming speed, and higher carbon weight might account for the majority of the diet of *A. coerulea* polyps in Jiaozhou Bay.

Ingestion Rate of *A. coerulea* Polyp

The carbon weight-specific ingestion rates of *A. coerulea* polyp estimated in this study were based on the prey capture of copepods and copepod nauplii, but not contained ciliates due to the lack of specific digestion time. Therefore, it is important to

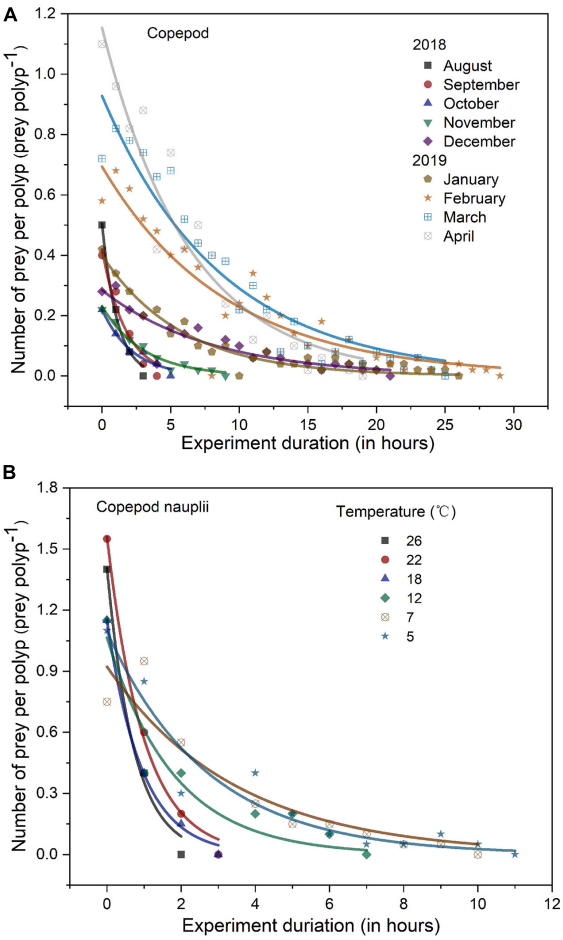

FIGURE 8 | Digestion processes of copepods **(A)** and copepod nauplii **(B)** in the gut cavity of *A. coerulea* polyp *in situ* experiment and laboratory experiment, respectively. Number of prey found in the gut of polyps at different points of the experiment expressed as prey polyp^{-1}, and the curves of different colors were the results of exponential fitting. Time 0 means the initial time.

acknowledge that the ingestion rate of *A. coerulea* polyp likely be even larger than presented in this study (ranging from 0.04 to 0.43 μg C μg C^{-1} d^{-1}). However, few ciliates were found in the polyps' guts in this study, whereas copepods represented the bulk of the total prey intake in number (88.02 ± 10.58%), followed by copepod nauplii (11.34 ± 10.03%) as indicated by the results of gut content analysis (**Figure 6**). Digestion rates of copepod nauplii could not be measured directly *in situ*, but were determined in laboratory conditions. The nauplii of *P. annandalei* (Calanoida) that was not a common species in Jiaozhou Bay were used as prey to determine the digestion time of copepod nauplii. The mean carapace length of these copepod nauplii was 204.7 μm, which was similar to the carapace length of copepod nauplii (237.96 ± 45.13 μm) detected in polyp guts. Thus, it is reasonable to use the results of the digestion of *P. annandalei* nauplii in the calculations of ingestion rate.

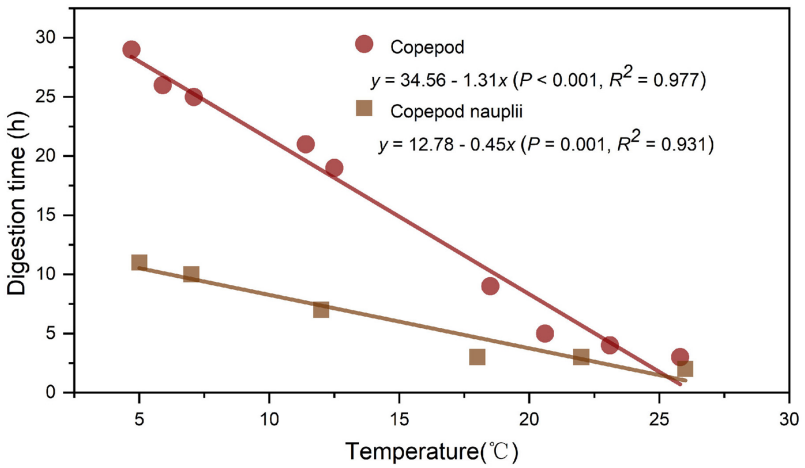

FIGURE 9 | The relationship between temperature and digestion time of copepods and copepod nauplii.

We compared the carbon weight-specific ingestion rates of *Aurelia* polyps (I_w, μg C μg C^{-1} d^{-1}) estimated in laboratory experiments by previous studies (Kamiyama, 2011; Ikeda et al., 2017). Kamiyama (2011) conducted feeding experiments using ciliates (*Favella ehrenbergii*, *Strombidium* sp., and *Myrionecta rubra*) as prey at 20°C, and indicated that ingestion rates of *A. aurita* polyps on all ciliates increased with increasing ciliate density up to ca. 300–500 μg C L^{-1}. I_w value of *A. aurita* polyp estimated by Kamiyama (2011) was 0.21 μg C μg C^{-1} d^{-1} (mean carbon content 38.1 μg of polyp). This estimated value of I_w was about twice as large as the I_w (copepods and copepod nauplii as prey) that we estimated at the same temperature (0.07–0.12 μg C μg C^{-1} d^{-1}, temperature of 18.5–20.6°C). However, the high ciliates densities in Kamiyama's experiments are unrealistic in Jiaozhou Bay, as the annual average biomass of ciliate generally ranges from 0.6 to 18.5 μg C L^{-1} (Yu et al., 2011). Under controlled laboratory conditions, Ikeda et al. (2017) constructed an empirical energy budget model for natural *A. aurita* polyp population. Based on the bioenergetic model (Ikeda et al., 2017): $I_W = 13 \times (0.026T - 0.11) \times P_c$ [T: water temperature (°C); P_c: prey carbon density (μg C mL^{-1})], we estimated the I_w of *A. coerulea* polyp of ciliates as prey (T = 20.6°C in October) using a ciliate biomass density of about 0.0011 μg C mL^{-1} (P_c) near our study station in Jiaozhou Bay (Yu et al., 2011). The evaluated I_w of ciliates (as prey) was about 0.006 μg C μg C^{-1} d^{-1}, which was far less than the I_w value estimated based on gut content in this study (0.12 μg C μg C^{-1} d^{-1} in October). According to the study of Ikeda et al. (2017), the respiration rate (R, ng O_2 μg C^{-1} d^{-1}) of polyps was significantly affected by temperature, and the metabolic rate (M, μg C μg C^{-1} d^{-1}) could be expressed as $M = 0.0055e^{0.066T}$. Therefore, the estimated metabolic rate of *A. coerulea* polyp at 20.6°C was approximately 0.021 μg C μg C^{-1} d^{-1}, which was more than three times larger than the estimated I_w of *A. coerulea* polyp of ciliates as prey. This also suggested that ciliates are not the main food source for *A. coerulea* polyp, but a supplement of polyp diet in Jiaozhou Bay.

Aurelia coerulea polyps had a large seasonal variation in I_w, ranging from 0.04 to 0.43 μg C μg C^{-1} d^{-1} within the study period, which was also indicated by the estimation of Ikeda et al. (2017). This was due to the temperature variations (effect on digestion) and the variations in prey availability in different months. The relatively high values of I_w for *A. coerulea* polyp were found in August 2018 and April 2019, with the values of 0.43 and 0.17 μg C μg C^{-1} d^{-1}, respectively (**Figure 10B**). The digestion time of copepods was 3 h measured in August 2018 (temperature = 25.8°C), and of copepod nauplii was 2 h measured at 26°C for *A. coerulea* polyp. The rapid digestion of prey might result in the highest I_w of *A. coerulea* polyp in August 2018. In addition, the relatively higher I_w measured in April 2019 might be due to the large zooplankton abundance, which increased prey availability for *A. coerulea* polyp. Thus, more rapid digestion of prey at higher temperature conditions and greater prey availability would cause higher ingestion rates in polyps.

The ingested carbon of *A. coerulea* polyp population might have different utilization patterns in different seasons because of the seasonal variation in eco-physiology or life cycle characteristics of *Aurelia* polyps in temperate offshore waters (Han and Uye, 2010; Thein et al., 2012), including Jiaozhou Bay (Wang N. et al., 2015; Feng et al., 2018). During the warm season (temperature >15°C, from August to November), the estimated I_w values were 0.07–0.43 μg C μg C^{-1} d^{-1} (**Table 4**). The estimated metabolic rates were 0.019–0.03 μg C μg C^{-1} d^{-1} during this period (according to $M = 0.0055e^{0.066T}$; Ikeda et al., 2017). Hence, the mean growth rate of *A. coerulea* polyp during August and November in Jiaozhou Bay was estimated to be 0.124 ± 0.123 μg C μg C^{-1} d^{-1} (assimilation efficiency assumed to be 0.8; Schneider, 1989). In this period, owing to the relatively large growth rate, the ingested carbon might be mainly used for somatic growth and population expansion through the budding pattern for *A. coerulea* polyp population in Jiaozhou Bay. This was also demonstrated by Feng et al. (2017). During the cold season (temperature <15°C, from December 2018 to April 2019), the estimated growth rate was 0.057 ± 0.042 μg C μg

TABLE 3 | Prey capture (*N*, prey polyp^{-1}) and prey-capture rate (*C*, prey polyp^{-1} d^{-1}) of copepod and copepod naupli on each sampling date.

Sampling date	14 August		15 September		15 October		18 November		15 December		17 January		21 February		16 March		10 April		Mean (±SD)	
	N	*C*	*N*	*C*	*N*	*C*	*N*	*C*	*N*	*C*	*N*	*C*	*N*	*C*	*N*	*C*	*N*	*C*	*N*	*C*
Copepod	0.44	5.28	0.24	2.31	0.20	1.60	0.22	1.06	0.30	0.66	0.36	0.64	0.66	1.06	0.92	1.70	1.06	2.54	0.49 ± 0.32	1.87 ± 1.44
Copepod naupli	0.14	2.24	0.04	0.48	–	–	–	–	–	–	0.02	0.08	0.16	0.64	0.20	0.87	0.30	1.80	0.10 ± 0.11	0.68 ± 0.83
Total prey	0.58	7.52	0.28	2.79	0.20	1.60	0.22	1.06	0.30	0.66	0.38	0.72	0.82	1.70	1.12	2.57	1.36	4.34	0.59 ± 0.42	2.55 ± 2.20

"–" means this prey was not found in polyp guts on this sampling date.

C^{-1} d^{-1}. Reproduction by budding and podocysts of *A. coerulea* polyps may greatly diminish during this period due to cold water temperature (Han and Uye, 2010; Feng et al., 2018). However, seasonal cooling may stimulate some physiological changes of *A. coerulea* polyps in preparation for metamorphosis into strobilae (Feng et al., 2018). Thus, the majority of carbon intake of polyps during this period may be incorporated into somatic growth in preparation for strobilation.

Potential Effects of Polyp Predation on Pelagic Ecosystem

In shallow water, benthic cnidarian feeders can affect pelagic plankton communities by significantly reducing plankton abundance (e.g., Coma et al., 1995, 1999; Gili and Coma, 1998; Tsounis et al., 2006). Much evidence has suggested that benthic cnidarians, including the Octocorallia (Coma et al., 1994; Ribes et al., 1999; Rossi et al., 2004), *Eudendrium* (Barange and Gili, 1988), and *Obelia* (Orejas et al., 2013), are important components of the benthic–pelagic-coupling processes of littoral marine ecosystems. A previous study has indicated that *Aurelia* polyps covered large areas of hard-bottom substrates between 1 and 20 m deep (Gröndahl, 1988b). *A. aurita* planulae may settle gregariously: polyp densities of 60,000–400,000 polyps m^{-2} have been reported on the west coast of Sweden (Gröndahl, 1988a,b); Purcell et al. (2009) found that *Aurelia labiata* polyps covered 58.3 ± 0.6% of the available surface area beneath marina floats in Cornet Bay, WA, United States, and the mean polyp density was 9.3 polyps cm^{-2}. Abundant scyphopolyps, with a predation strategy similar to other benthic suspension-feeding predators (Barange and Gili, 1988), may also play an important role in energy and matter exchange between the plankton and the benthos in littoral ecosystems, as Marcus and Boero (1998) emphasized that benthic–pelagic couplings determined the productivity and biological structures of coastal aquatic ecosystems. However, this energy and matter exchange has been ignored, perhaps because the polyp stage causes a lesser degree of ecosystem damage than does the medusa stage.

Han and Uye (2010) estimated that 4 μg C polyp^{-1} d^{-1} was the maximum ingestion rate of natural polyps on a diet of the copepod *Oithona davisae*. If the density of *A. aurita* polyps on the Swedish coast as estimated by Gröndahl (1988b) was used to approximate the effects of scyphopolyps predation on pelagic prey items, we found that the overall impact of the scyphopolyp population was between 240 and 1600 mg C polyps m^{-2} d^{-1}. This estimate is an initial approximation, because polyp densities and spatial and temporal variations in prey-capture rates differed. In view of the high spatial and temporal variability in prey-capture rates, grazing impact probably differs among populations in different environments. However, this suggests that scyphopolyps may play a significant role in plankton–benthos coupling. According to underwater surveys performed by our divers, the maximum density of *A. coerulea* polyps was approximately 3–6 polyps cm^{-2} on the bottom of marina floats and along the concrete walls of port installations in Jiaozhou Bay (unpublished data). The maximum grazing impact of the

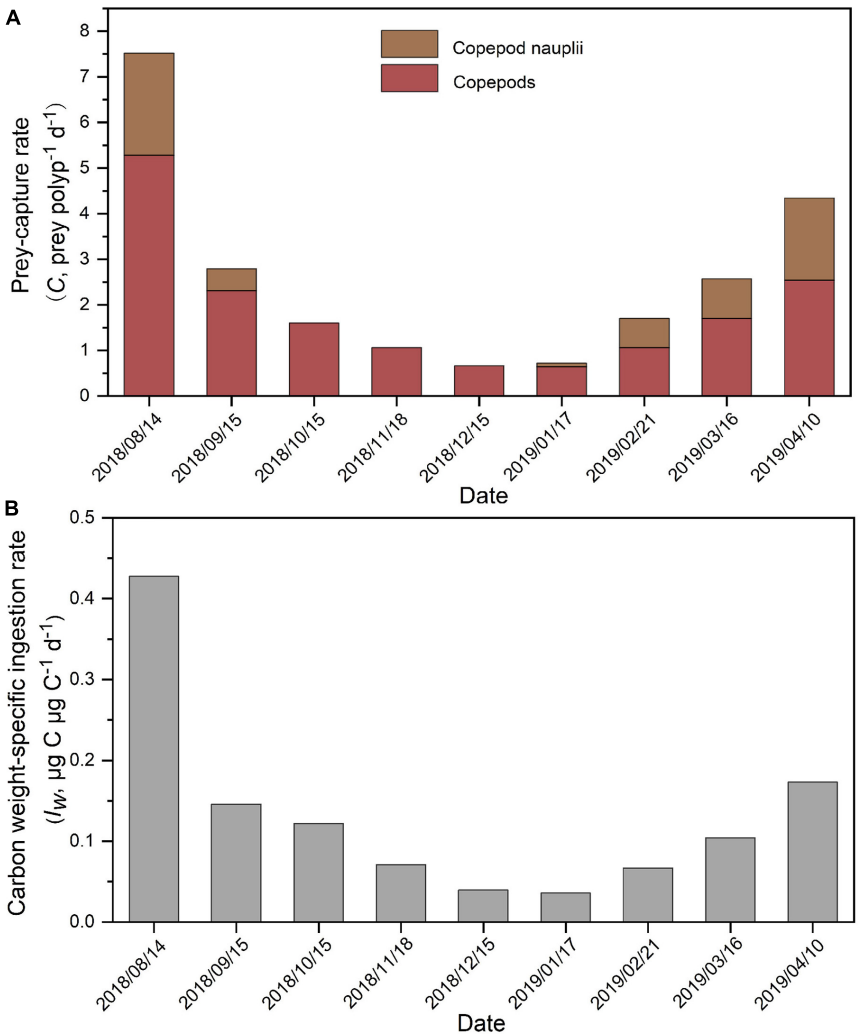

FIGURE 10 | Prey-capture rate (*C*, prey polyp^{-1} d^{-1}) of copepods and copepod nauplii **(A)** and seasonal variation in carbon weight-specific ingestion rates for *A. coerulea* polyps (I_w, µg C µg C^{-1} d^{-1}; **(B)**) during August 2018 to April 2019.

TABLE 4 | Ingestion rates (*I*, µg C polyp^{-1} d^{-1}) and carbon weight-specific ingestion rates (I_w, µg C µg C^{-1} d^{-1}) of *A. coerulea* polyps from August 2018 to April 2019.

Sampling date	14 August	15 September	15 October	18 November	15 December	17 January	21 February	16 March	10 April	Mean (±SD)
W (µg C)	10.49	12.66	9.87	11.20	12.57	13.87	14.13	14.19	13.45	12.49 ± 1.62
I (µg C polyp^{-1} d^{-1})	4.48	1.84	1.20	0.80	0.50	0.50	0.94	1.48	2.33	1.56 ± 1.25
I_w (µg C µg C^{-1} d^{-1})	0.43	0.15	0.12	0.07	0.04	0.04	0.07	0.10	0.17	0.13 ± 0.12

W (µg C) is the mean carbon weight of polyps on each sampling date.

A. coerulea polyp population in Jiaozhou Bay ranged from 44 to 88 mg C polyps m^{-2} d^{-1} (mean ingestion rate: 1.46 µg C polyp^{-1} d^{-1}). This abundant accumulation of polyps might create high feeding pressure on the pelagic ecosystem in Jiaozhou Bay. Marine waste (e.g., plastics, glass, and wood), mariculture rafts, and waterfront construction projects provide additional areas suitable for polyp attachment, facilitating habitat expansion, and supporting polyp population growth (Uye and Ueta, 2004; Holst and Jarms, 2007). Scyphomedusae polyp blooms might influence the pelagic ecosystem because polyps play an important predatory role in the plankton–benthos energy transfer process of littoral ecosystems.

CONCLUSION

Gut content analysis indicated that copepods, copepod nauplii, and ciliates could be captured by *A. coerulea* polyps. Copepods are an important source of nutrition for the polyp stage of *A. coerulea* population in Jiaozhou Bay. Prey capture of

A. coerulea polyp (prey polyp^{-1}) varied among months, and was positively influenced by abundance of planktonic prey in the surrounding water. Our results indicated seasonal variations in ingestion rates of *A. coerulea* polyp in Jiaozhou Bay, and the relatively high values of ingestion rates occurred in August 2018 and April 2019 with more rapid digestion of prey and greater prey availability. Massive scyphomedusae polyp blooms may contribute to the energy flow of littoral ecosystems.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/supplementary material, further inquiries can be directed to the corresponding authors.

ETHICS STATEMENT

This study was carried out in accordance with the current laws in China. There are no legal or ethical restrictions involving jellyfish and zooplankton populations.

AUTHOR CONTRIBUTIONS

WP, ZF, and SS contributed to conception and design of the study. WP and ZF led the writing of this study. WP and GD executed the sampling and samples analysis. WP organized the database and performed the statistical analysis. All authors contributed critically to the drafts and gave final approval for publication.

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