

Experimental clearance rates of *Aurelia coerulea* ephyrae and medusae, and the predation impact on zooplankton in Jiaozhou Bay*

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Abstract The population explosion of jellyfish *Aurelia coerulea* occurred in Jiaozhou Bay, China in 2009. The potential predation impact of *A. coerulea* on zooplankton was investigated. Population clearance potential and residence time ($t_{1/2}$) for copepods were calculated from laboratory clearance rates and measurements of jellyfish size and abundance from May to August 2009 in Jiaozhou Bay. Clearance rates varied widely with prey organisms, but they were not significantly different among various prey concentrations. Medusae captured rotifers, fish larvae and hydromedusae more efficiently than fish eggs, copepods and chaetognaths. Ephyrae captured rotifers and hydromedusae more efficiently than fish larvae and copepods. Clearance rate linearly increased with the cross sectional area of *A. coerulea* (size from 0.3 to 7.1 cm). Water temperature also had a marked effect on clearance rate and this was related to the increased beat frequency as water temperature increased. In early May 2009, *A. coerulea* potentially cleared the volume of water in the Bay less than 0.001 times a day, but this value was estimated to be more than 0.3 times a day in July. The $t_{1/2}$ for copepods was less than 6 d in June and July. Abundances of copepods, hydromedusae and chaetognaths were extremely low in 2009 compared to 2008 and 2010 (jellyfish non-bloom years). Large predation pressure by the *A. coerulea* population occurred to control zooplankton communities in Jiaozhou Bay. *A. coerulea*, when present at a high population level, can be a keystone species in Jiaozhou Bay and control the trophic structure here.

Keyword: scyphomedusae; predation pressure; prey selection; zooplankton control; jellyfish bloom

1 INTRODUCTION

Jellyfish are gelatinous zooplanktonic organisms, which play an important role in the material cycle and energy flow of marine ecosystems (Möller, 1984; Purcell, 1997). Dramatic changes in the distributions and abundances of some jellyfish, such as ctenophores and cnidarians (hydromedusae, siphonophores and scyphomedusae) (Båmstedt et al., 1994; Purcell and Cowan Jr., 1995; Purcell et al., 1999), have increased discussion about the impact of these organisms on

pelagic food webs (Purcell, 1985; Purcell et al., 1999; Pitt et al., 2009).

Common bloom jellyfish, *Aurelia* are offshore scyphomedusae with worldwide distributions (Olesen

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et al., 1994; Olesen, 1995; Purcell, 2009). Global populations of *Aurelia* species have increased significantly in the past half-century (Kogovšek et al., 2010). Mass occurrences of *Aurelia* species have been reported from many parts of the world, including Japan (Yasuda, 1976; Omori et al., 1995), Sweden (Hernroth and Gröndahl, 1983), China (Dong et al., 2010), and Greece (Papathanassiou et al., 1987). *Aurelia* species are voracious predators, consuming a broad range of prey (Purcell, 1997; Hansson et al., 2005), including fish eggs and larvae, copepods, barnacles, gastropods, bivalves and polychaetes (Purcell, 1985, 1997; Ishii and Tanaka, 2001; Purcell and Arai, 2001). High densities of *Aurelia* species can seriously deplete populations of zooplankton and ichthyoplankton, both by direct predation and competition for the same resources (Purcell, 1997). For example, during high-density blooms, *Aurelia aurita* medusae consumed about 2/3 of all daily secondary production in Kiel Bight Bay, Germany, leading to a noticeable decline of meso-zooplankton (Schneider and Behrends, 1994). Intraguild predation is also common in jellyfish, including *Aurelia* species (Purcell, 1991; Titelman and Hansson, 2006). Gut content analyses indicated that *Aurelia*, including its small medusae and ephyrae, consumed many hydromedusae (Sullivan et al., 1997).

Jiaozhou Bay is a semi-enclosed bay and locates on the southern side of the Shandong Peninsula that is strongly influenced by human activities (Wang and Sun, 2015). This bay is therefore an ideal system for studying the influence of ecological disasters on a marine ecosystem, with a particular focus on jellyfish blooms and the impact of these blooms on the compositions and quantities of zooplankton communities. Population explosions of *Aurelia coerulea* have been recorded in Jiaozhou Bay, with an especially large population outbreak in 2009 (Wan and Zhang, 2012; jellyfish bloom year, JBY). Jellyfish did not bloom in 2008 and 2010 (jellyfish non-bloom years, NJBYs). The explosions of *A. coerulea* population might cause imbalances to marine food webs and have negative effects on the marine ecology of Jiaozhou Bay (Wan and Zhang, 2012; Wang and Sun, 2015). Therefore, information on its trophic relationships with other zooplankton groups is required; we also wanted to know how this jellyfish functions within marine ecosystems.

Wan and Zhang (2012) observed *A. coerulea* ephyrae in Jiaozhou Bay during April, and reported that the population of *A. coerulea* medusae increased sharply in May, peaking in June. Wang and Sun

(2015) found that *A. coerulea* strobilation occurs in early spring in Jiaozhou Bay as the water temperature begins to increase. In late May, young medusae (size: 9.74 ± 1.7 mm) were observed. These medusae attained sexual maturity in mid-summer; in August, medusae numbers decreased, and reached zero by September (Wan and Zhang, 2012; Wang and Sun, 2015). It is likely that the *A. coerulea* population had its largest impact on zooplanktonic taxa from May to August in 2009. Previous studies found the highest abundances of *A. coerulea* in northern Jiaozhou Bay near the Hongdao (Fig.1) (Wan and Zhang, 2012; Wang and Sun, 2015). In the present study, to investigate the influence of *A. coerulea* population on zooplankton, the abundances of each zooplankton group at a fixed station in northern Jiaozhou Bay from May to August were compared between NJBYs (2008, 2010) and JBY (2009). Clearance rates of *A. coerulea* medusae and ephyrae for different prey items were measured in laboratory experiments. The population clearance potential of *A. coerulea* was calculated in Jiaozhou Bay during mass occurrence of *A. coerulea* in May to August 2009. This was done by combining clearance experiments in the laboratory with field measurements of medusae size and abundance and the surface water temperature during the study period. The influences of *A. coerulea* blooms on the numbers and compositions of zooplankton communities in Jiaozhou Bay were determined.

2 MATERIAL AND METHOD

2.1 Experimental animal

Aurelia coerulea ephyrae and medusae used in this experiment were cultivated in our jellyfish laboratory (Institute of Oceanology, Chinese Academy of Sciences, Qingdao, China). Ephyrae (inter-rhopalia diameter 2.5 ± 0.5 mm) were released by polyps, and then they were transferred to a cylindrical glass incubator (70-cm diameter, 50-cm high) with water volume of 120 L, and given *Artemia* nauplii twice a day. Experiments were conducted as the *A. coerulea* medusae grew.

Prey items, including *Artemia* nauplii, rotifers, fish eggs and larvae, small copepods, large copepods, hydromedusae and chaetognaths, were used in feeding experiments. The main species and size of each prey item are shown in Table 1. Copepods, hydromedusae and chaetognaths were captured in Jiaozhou Bay using shallow water II type plankton nets (net mesh: 160 μ m; net mouth area: 0.08 m²) between early May

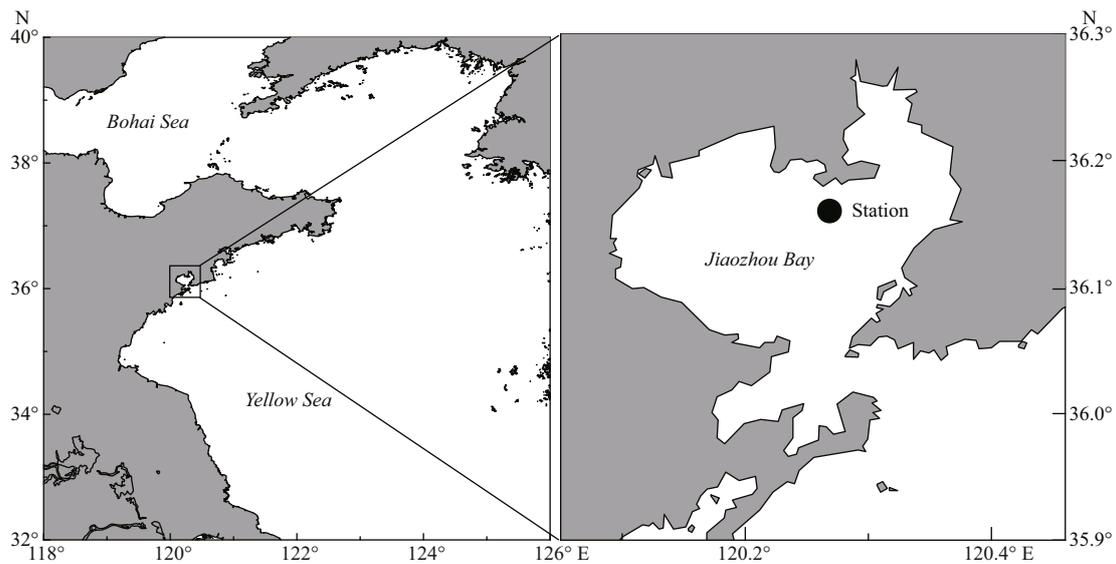


Fig.1 Map of the study area

Black dot in the right panel shows the fixed station that zooplankton samples being collected in Jiaozhou Bay.

Table 1 Details of prey organisms

Prey item	Species	Prey size (mm)
Rotifer	<i>Brachionus plicatilis</i>	0.25±0.05
<i>Artemia</i> nauplii	–	0.50±0.10
Small copepods	<i>Acartia bifilosa</i>	1.05±0.15
	<i>Paracalanus parvus</i>	0.55±0.05
Large copepods	<i>Calanus sinicus</i>	2.00±0.50
Fish eggs	<i>Scophthalmus maximus</i>	1.20±0.10
Fish larvae	<i>S. maximus</i>	2.00±0.30
Hydromedusae	<i>Rathkea octopunctata</i>	3.00±0.55
	<i>Podocoryne minima</i>	1.50±0.05
Chaetognaths	<i>Sagitta crassa</i>	11.50±0.50

For each prey item, body lengths of 10 individuals were measured. These results are shown in mean±SD.

and early June 2017. Captured zooplankton were immediately transported to the laboratory; small copepods (mean body length: 0.6 ± 0.1 mm), large copepods (mean body length: 2 ± 0.5 mm), hydromedusae, and chaetognaths were selected, respectively. Then these prey items were held in plastic buckets containing 20-L filtered seawater (20- μ m mesh) with an air pump.

Artemia nauplii, rotifers, and fish eggs and larvae (turbot, *Scophthalmus maximus*) were also offered as prey in feeding experiments. *Artemia* nauplii and rotifers were maintained in the laboratory at 18°C and salinity of 31. Fish used in the experiment were obtained from Jiaozhou Farm, Qingdao, China. To raise fish larvae, we incubated artificially fertilized fish eggs in artificial seawater at 18–19°C and salinity

of 31. After hatching, fish larvae were incubated in a tank with 1 000-L filtered seawater (20- μ m mesh) and an air pump; the fish offered rotifers daily. Approximately one third of the tank water was exchanged daily.

2.2 Feeding experiment

Aurelia coerulea ephyrae and medusae that were visually undamaged and actively pulsing were used in the experiments. Selected specimens were starved for 24 h, and then transferred to experimental containers (30-cm diameter, 30-cm height) with 20-L filtered seawater (20- μ m mesh). One *A. coerulea* medusa and ten ephyrae were placed in each experimental container. All jellyfish were allowed to acclimatize to experimental containers for at least 1 h under observation to ensure that their free-swimming behavior was normal. To know the exact number of each prey organisms, *Artemia* nauplii, copepods, and fish eggs were collected using a pipette; big drops of water with prey from the cultivation bucket were placed into a Petri dish and the number of prey in each drop was counted. Fish larvae, hydromedusae and chaetognaths were individually sorted out with a small handled sieve (0.1-mm mesh size), and transferred into 2-L beakers, respectively. Rotifer was counted under a dissecting microscope (Nikon, SMZ745, Japan).

Clearance rate was determined by measuring the volume of water cleared of prey organisms used in the present experiments per unit time. Thirteen containers (including the control) were employed in each

Table 2 Details of clearance experiments on *A. coerulea* medusae and ephyrae

Exp.#	Predator	V (L)	d (cm)	T (°C)	N	n	t (h)	Prey type	Mean prey size (mm)	C ₀ (ind./L)
Medusae										
1		20	6.90±0.40	18.8	4	1	1.5	Rotifers	0.25±0.05	10
2		20	6.90±0.40	18.3	5	1	2	<i>Artemia</i> nauplii	0.50±0.10	10
3		20	6.90±0.40	18.3	7	1	6	Small copepods	0.60±0.10	36
4		20	6.90±0.40	18.3	9	1	4	Fish eggs	0.90±0.10	0.5
5		20	6.90±0.40	18.9	7	1	3	Fish larvae	2.00±0.30	0.5
6		20	6.90±0.40	18.5	13	1	24	Large copepods	2.00±0.50	0.4
7		20	6.90±0.40	18.5	7	1	3	Hydromedusae	2.00±0.50	0.7
8		20	6.90±0.40	18.5	9	1	16	Chaetognaths	11.50±0.50	2.7
Ephyrae										
9		20	0.25±0.05	18.8	7	10	2	Rotifers	0.25±0.05	10
10		20	0.25±0.05	18.8	7	10	6	<i>Artemia</i> nauplii	0.50±0.10	10
11		20	0.25±0.05	18.8	13	10	24	Small copepods	0.60±0.10	36
12		20	0.25±0.05	18.5	13	10	24	Large copepods	2.00±0.50	0.4
13		20	0.25±0.05	18.8	7	10	6	Hydromedusae	2.00±0.50	0.7
14		20	0.25±0.05	18.7	13	10	24	Fish larvae	2.00±0.30	0.5
15		20	0.25±0.05	18.5	13	10	24	Chaetognaths	11.50±0.50	2.7
Medusae										
16		20	6.90±0.40	18.3				Small copepods	0.60±0.10	5, 20, 36, 60, 100
17		20	6.90±0.40	18.3				Fish larvae	2.00±0.30	0.5, 5, 10, 20, 60
18		20	6.90±0.40	18.3				Chaetognaths	11.50±0.50	0.5, 2.7, 10, 20, 60
19		20	0.30, 2.00, 4.20, 6.00, 7.10	18.5				Small copepods	0.60±0.10	36
20		20	4.50±0.30	5, 7, 10, 15, 20, 25, 30, 35				Small copepods	0.60±0.10	36

V: volume of water in experimental containers; d: size of predators, and inter-rhopalia diameter for ephyrae; T: water temperature; N: number of containers used in clearance experiment (including the control without medusa); n: number of *A. coerulea* medusae or ephyrae in each given container; t: incubation period; C₀: initial prey concentration.

experiment. The measurements of clearance rates were based on time series. Incubation time should be from the beginning of the experiment until the prey is completely cleared. However, rates of *A. coerulea* varied with different prey, the incubation time of different prey varied between 1 h and 24 h (Table 2), and the maximum incubation time was 24 h in this study. Sampling frequencies of different prey depended on the rate on which prey organisms were removed from the water by the predation of *A. coerulea*. The concentration of prey organisms in our laboratory experiment was determined according to the maximum densities of different zooplankton groups in the field (the maximum densities of zooplankton in the field: large copepods, 320.5 inds./m³; small copepods, 35 200.0 inds./m³; hydromedusae: 640.0 inds./m³; chaetognaths, 2 560.0 inds./m³). Fish larvae and eggs were not found in this field zooplankton survey, but according to previous study, densities of fish larvae

and eggs were very low in Jiaozhou Bay (maximum density: fish egg, 5.02 inds./m³; larvae, 16.34 inds./m³, Huang et al., 2007). It is reasonable that the concentrations of fish larvae and eggs were determined to be 0.5 inds./L. Concentrations (100 small copepods/L, 60 fishes/L, 60 chaetognaths/L) used to study the relationship between prey concentration and clearance rate are higher than the average density of populations in natural to demonstrate that *A. coerulea* were not saturated at these high prey densities. Details of the specific conditions for each experiment are shown in Table 2.

The experiments were started by carefully adding the prey organisms to each container with jellyfish. As time went on, the number of prey organisms gradually declined, and the reduction in the number of prey organisms as a function of time was followed by removing the jellyfish from one container at periods of time intervals and filtering (20- μ m mesh) all the water

(i.e. data for each container represents 1 time). The retained prey organisms were counted by using stereomicroscope (Nikon, SMZ745). Feeding experiments were performed in triplicate. For each experiment, a container without jellyfish served as a control. All experiments were conducted at 18–19°C and salinity of 31. The clearance rate (CI, in L/h) was determined based on the exponential reduction in prey concentration (C_t , the prey concentration at time t):

$$CI = -a \times V/n, \quad (1)$$

where a is the slope of the fitted regression line of $\ln C_t$ versus time t ; n is the number of jellyfish in each experimental container; and V is the volume of seawater of the given water.

Four clearance experiments were conducted: (1) clearance rate of different prey organisms for medusae and ephyrae (Table 2, #1–15); (2) the relationship between prey concentration and clearance rate (Table 2, #16–18); copepods (small copepods), fish larvae and gelatinous organisms (chaetognaths) with different concentrations were offered as prey; (3) the effects of predator size on clearance rate (Table 2, #19); the cross-sectional area of *A. coerulea* (A , cm²) was used to represent the predator size, which was defined as π multiplied by the square of the radius of *A. coerulea* bell because of the round medusae body; and (4) the relationship between water temperature and clearance rate, and medusae were adapted to the specified experimental temperature over 3 h prior to incubation (Table 2, #20). Zooplankton was comprised of 71% copepods in Jiaozhou Bay. Therefore, copepods were selected as the prey for experiments (3) and (4).

2.3 Frequency of bell contraction

The relationship between temperature and frequency of bell contractions (beats/min) was measured with 10 inds. medusae (mean size: 4.5±0.3 cm) and temperatures (°C) of 5, 7, 10, 15, 20, 25, 30, and 35. *A. coerulea* medusae were placed in 20-L water volume (30-cm container diameter, 30-cm height), containing filtered seawater (20- μ m mesh, salinity of 31). The number of pulses was counted for 10 min. Prior to the measurement, all medusae were allowed to acclimatize to experimental temperatures for 1–3 h under observation to ensure that their free-swimming behaviors were normal. Two series of these experiments were carried out. In the first series, the frequency of bell contractions was measured without any prey added. In the second series, small copepods were offered as prey, and the frequency of

bell contractions of *A. coerulea* medusae was measured after the capture of 1 prey. We also observed the swimming directions of medusae. These experiments were conducted in a constant temperature incubator.

2.4 Population clearance potential

The population clearance potential of *A. coerulea* (PCP, /d) in Jiaozhou Bay was estimated from May to August 2009. PCP is defined as the number of times per day that the water volume the total population of jellyfish could clear relative to the whole water column (Olesen, 1995). The effect of *A. coerulea* predation on zooplankton communities was further illustrated by calculating the theoretical mean residence time ($t_{1/2}$) for copepods (referred to Olesen, 1995). The dominant group, copepods, can occupy more than 70% of total zooplankton in the Jiaozhou Bay (our field surveys). Thus, PCP and $t_{1/2}$ were calculated for this dominant group, which could exactly reflect the effect of jellyfish predation on zooplankton. PCP and $t_{1/2}$ were calculated from experimental clearance rates, and information obtained from Wan and Zhang (2012) and unpublished data on *A. coerulea* density and mean size and water temperature from May to August 2009. Clearance experiments on the relationship between medusae size and clearance rate were conducted at 18.5°C, whereas the *in situ* temperature ranged from 11 to 26°C. Corrections for all medusae sizes (0.3–7.1 cm) were made to be proportional with the trend with temperature measured for 4.5-cm *A. coerulea*. A temperature correction factor (t_k) due to differences between temperatures in the laboratory and *in situ* was defined as: $t_k = CR_k/CR_{18.5}$, therefore, CI (L/h):

$$CI = (a(A) + b) \times t_k. \quad (2)$$

The population clearance potential of *A. coerulea* (PCP, /d) was defined as:

$$PCP = CI \times m \times 24/1000, \quad (3)$$

where CR_k and $CR_{18.5}$ are the clearance rate (L/h) for 4.5 cm *A. coerulea* at *in situ* temperature (k , °C) and 18.5°C, respectively; and A (cm²): the cross area of *A. coerulea*; m (inds./m³): abundance of *A. coerulea* in Jiaozhou Bay. Theoretical mean residence time of copepods $t_{1/2}$ was calculated as:

$$t_{1/2} = \ln 2/PCP. \quad (4)$$

It is assumed that the feeding rates were constant day and night, and the relations between individual sizes and clearance rates used in the present study were also valid for medusae larger than those used in the clearance experiments.

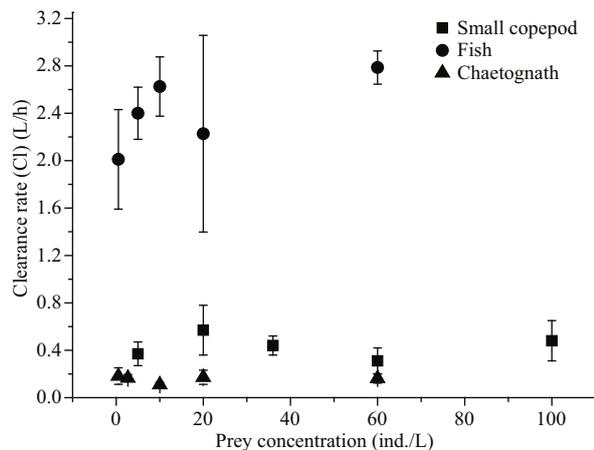


Fig.2 Clearance rates as a function of prey concentrations during incubations

Small copepods, fish larvae and chaetognaths were offered as prey. The mean size of *A. coerulea* medusae in these experiments was 6.9 ± 0.4 cm. Data points are the mean values of three replicates. Error bars indicate SD. An ANOVA on raw data showed no significant change in clearance rate was associated with prey concentration (small copepods: $F=0.454$, $n=15$, $P=0.767$; fish larvae: $F=1.433$, $n=15$, $P=0.293$; chaetognaths: $F=1.039$, $n=15$, $P=0.434$).

2.5 Zooplankton variation in Jiaozhou Bay

Zooplankton samples from May to August at a fixed location in northern Jiaozhou Bay ($36^{\circ}15'45''N$, $120^{\circ}25'04''$; Fig.1) were compared between NJBYs (2008, 2010) and JBY (2009). Zooplankton samples were collected by a shallow water II type plankton net (the net mesh: $160 \mu\text{m}$; net mouth area: 0.08 m^2) throughout the water column from bottom to surface; then zooplankton samples were immediately preserved in 5% neutral formalin. A Motoda sampler (Motoda, 1963) was used to subsample our zooplankton collection. Then each subsample was placed in a scan cell ($11 \text{ cm} \times 24 \text{ cm}$), and scanned the subsamples at 4 800 dpi with ZooScan (ZooScan, HYDROPTIC, France, $L \times W \times H$: $60 \text{ cm} \times 54 \text{ cm} \times 36 \text{ cm}$), following manufacturer instructions. Zooplankton samples in Jiaozhou Bay were classified into the organismal groups according to Sun et al. (2008). These were copepods, chaetognaths, medusae, appendicularians, *Noctiluca scintillans* and others. The “total zooplankton” included all organisms except *N. scintillans*, because there were large interannual variations in *N. scintillans* abundance. To study the effects of jellyfish on different zooplankton organisms in greater detail, total zooplankton (including copepods) and copepods alone were classified into three groups based on size: $<0.5 \text{ mm}$, $0.5\text{--}1 \text{ mm}$, and $>1 \text{ mm}$. The abundance (D , inds./m^3) of each zooplankton group was determined on a per unit volume (m^3) basis, which was calculated as: $D=N/v$,

where N is the number of each zooplankton group; v ($v=s \times h$) is the volume of water filtered by the plankton net; s is the area of the plankton net mouth; and h is the sampling depth.

2.6 Statistical method

SPSS v16.0 was conducted to statistical analysis of processing data. One-way analysis of variance (ANOVA) was used to determine the differences in clearance rates among different prey concentrations; normality and equal variances were checked before ANOVA analysis. The differences in clearance rates of different prey items and the variations in frequency of bell contraction at different feeding conditions were analyzed by the non-parametric Kruskal-Wallis test. Statistical significance was set at $P < 0.05$.

3 RESULT

3.1 Clearance rate and bell contraction of *A. coerulea*

3.1.1 Effects of prey type and predator size on the clearance rate

Clearance rates were not significantly different among the various prey concentrations, whether small copepods, fish larvae, or chaetognaths were offered as prey (ANOVA, small copepods: $F=0.454$, $n=15$, $P=0.767$; fish larvae: $F=1.433$, $n=15$, $P=0.293$; chaetognaths: $F=1.039$, $n=15$, $P=0.434$) (Fig.2). Prey type has significant effect on clearance rate; for *A. coerulea* medusae of similar size (6.9 ± 0.4 cm; Table 2), the estimated mean clearance rates were $4.78 \pm 1.34 \text{ L/h}$ for rotifers, $1.12 \pm 0.29 \text{ L/h}$ for *Artemia*, $2.55 \pm 0.29 \text{ L/h}$ for fish larvae, $0.67 \pm 0.04 \text{ L/h}$ for fish eggs, $1.58 \pm 0.03 \text{ L/h}$ for hydromedusae, $0.37 \pm 0.03 \text{ L/h}$ for small copepods, $0.04 \pm 0.01 \text{ L/h}$ for large copepods, and $0.17 \pm 0.04 \text{ L/h}$ for chaetognaths (Fig.3a). Clearance rates for rotifers, fish larvae, hydromedusae, and *Artemia* were significantly higher than clearance rates for fish eggs and small copepods, followed by chaetognaths and large copepods ($H=19.636$, $P=0.003$). Ephyrae could not capture large copepods or chaetognaths. For ephyrae, the estimated mean clearance rates were $0.064 \pm 0.005 \text{ L/h}$ for rotifers, $0.026 \pm 0.015 \text{ L/h}$ for *Artemia*, $0.007 \pm 0.001 \text{ L/h}$ for small copepods, $0.05 \pm 0.017 \text{ L/h}$ for hydromedusae, and $0.001 \pm 0.0003 \text{ L/h}$ for fish larvae. Clearance rates for rotifers and hydromedusae were significantly higher than the other prey ($H=12.700$, $P=0.013$) (Fig.3b).

Predator size also had a significant effect on clearance rate. The relationship between the cross

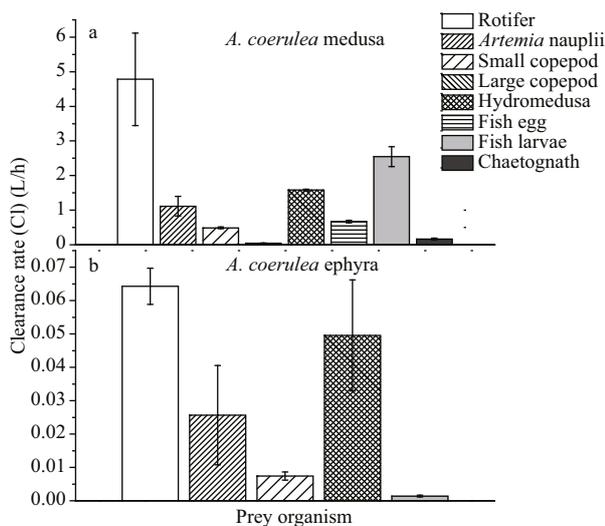


Fig.3 Clearance rates of *A. coerulea* feeding on different prey organisms

a. *A. coerulea* medusae (mean size: 6.9±0.4 cm); b. *A. coerulea* ephyrae (mean inter-rhopalia diameter: 0.25±0.05 cm). Error bars indicate SD. Experimental conditions are shown in Table 2.

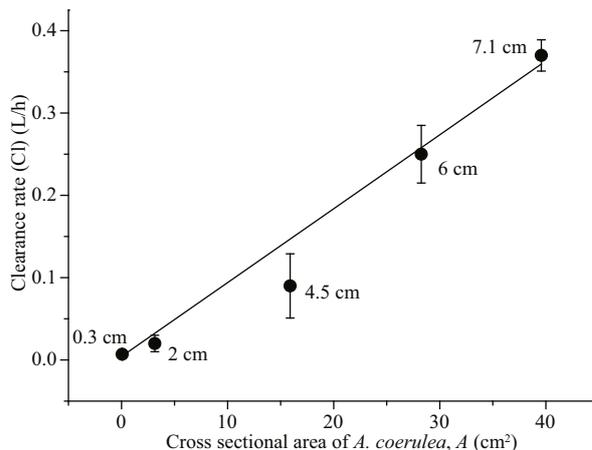


Fig.4 Relationship between the cross sectional area of *A. coerulea* and the clearance rates of the experiments with small copepods as prey organisms ($F=271.107$, $P<0.001$, $R^2=0.985$)

A (cm^2): the cross sectional area of *A. coerulea*; Cl (L/h): clearance rate. The numbers with “cm” next to the data points indicate the size of experimental *A. coerulea*.

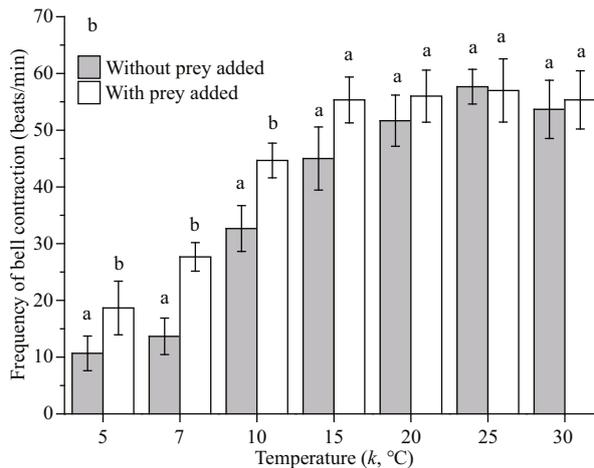
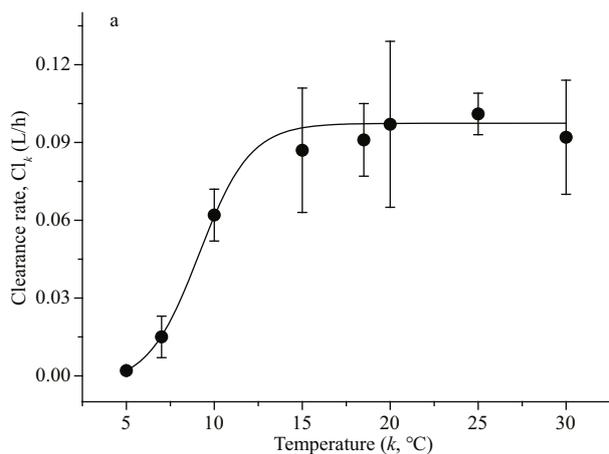


Fig.5 Relationship between clearance rate, bell contraction, and temperature

a. relationship between temperature and clearance rate for 4.5±0.3 cm medusae ($F=481.23$, $P<0.001$, $R^2=0.984$). Cl_k : clearance rate at temperature k ($^{\circ}C$); b. relationship between temperature and mean frequency of bell contraction for 4.5±0.3 cm medusae with prey and without prey; different letters in (b) mean significant differences ($P<0.05$) at the same temperature. Error bars indicate SD.

sectional area of *A. coerulea* and clearance rates in experiments with small copepods as prey is shown in Fig.4. The clearance rate increased from 0.007 L/h for 0.3-cm *A. coerulea* to 0.37 L/h for 7.1-cm *A. coerulea*. By linear regression, clearance rate (Cl) linearly increased with the cross sectional area of *A. coerulea* (A): $Cl=0.009A+0.0042$ ($F=271.107$, $P<0.001$, $R^2=0.985$; Fig.4).

3.1.2 The effect of temperature on clearance rate and bell contraction

The relationship between temperature and clearance rate for *A. coerulea* medusae (mean size: 4.5±0.3 cm)

with small copepods as prey is shown in Fig.5a. The sigmoidal curve fit shows that clearance rate increased from 0.002 L/h at 5 $^{\circ}C$ to 0.093 L/h at 15–16 $^{\circ}C$, and clearance rate was constant at 17 $^{\circ}C$ to 30 $^{\circ}C$. When the temperature was raised above 33 $^{\circ}C$, the medusae died. The relationship is described by the following equation:

$$CR_k = -0.0075 + 0.102 / (1 + 10^{((8.878 - k) \times 0.269)})$$

($F=481.230$, $P<0.001$, $R^2=0.984$).

The frequency of bell contraction as a function of water temperature is shown in Fig.5b. The mean beat frequency of *A. coerulea* medusa without prey increased from 11±3 beats/min at 5 $^{\circ}C$ to 45±6 beats/min at 15 $^{\circ}C$, and did not increase further as the

Table 3 Population clearance potential (PCP, /d) and residence time for copepods ($t_{1/2}$, day) in Jiaozhou Bay, 2009

Date (2009)	Temperature (k , °C)	Mean abundance (mean±SD, inds./m ³)	Mean size (mean±SD, cm)	Clearance rate (Cl, L/h)	PCP (/d)	$t_{1/2}$
05 May	16.3	6.0±1.7	0.58±0.11	0.007	0.001	>30
11 May	17.2	10.1±1.2	0.66±0.17	0.008	0.002	>30
24 May	18.5	11.3±2.1	5.99±3.27	0.258	0.070	9.90
08 June	21.5	8.7±4.5	8.74±1.72	0.562	0.117	5.92
20 June	21.9	7.3±1.7	12.53±5.74	1.111	0.195	3.56
29 June	22.8	6.4±3.2	15.21±4.29	1.635	0.251	2.76
04 July	23.5	4.0±1.7	16.72±1.14	2.101	0.202	3.44
15 July	24.7	6.9±2.8	16.62±3.19	1.951	0.323	2.15
25 July	25.3	4.9±2.1	17.26±1.36	2.110	0.118	5.87
10 August	25.5	0.2±0.3	12.12±2.61	1.099	0.005	>30

Data on medusae abundances, sizes, and temperature were obtained from Wan and Zhang (2012) and our unpublished data.

temperature increased above 15–16°C. The mean beat frequency with prey was significantly higher than the frequency with no prey at 5°C, 7°C, and 10°C, and there was no significant difference above 15°C.

3.2 Population clearance potential in Jiaozhou Bay

The surface water temperature varied from May to August in 2009. Temperature ranged from 16.3°C to 25.5°C during the survey period. The size of *A. coerulea* increased from 0.58±0.11 cm in early May to 17.26±1.36 cm in July, and decreased to 12.12±2.61 cm in August (Table 3). The water column PCP for *A. coerulea* in Jiaozhou Bay during May to August in 2009 is shown in Table 3 and Fig.6. PCP was low in early May, but increased from late May to July, then decreased in August (Fig.6). At the beginning of May, the population of *A. coerulea* could potentially clear the volume of water in the bay less than 0.001 times each day, and the theoretical mean residence time ($t_{1/2}$) for copepods was more than 30 days. The PCP increased gradually at the end of May, and the $t_{1/2}$ was relatively low (9.9 days). The maximum PCP was measured on 15 July, when the population of *A. coerulea* could clear a volume of water in the bay 0.323 times per day, and the $t_{1/2}$ for copepods was only 2.15 days in this period. The theoretical mean residence time for copepods was estimated to be less than 6 days in June and July. In August, PCP was less than 0.01 times per day, and the $t_{1/2}$ was greater than 30 days (Fig.6; Table 3).

3.3 Zooplankton variation in Jiaozhou Bay

On average, the zooplankton abundance at the sampling site was comprised of 71% copepods in abundance. Copepods are the dominant zooplankton

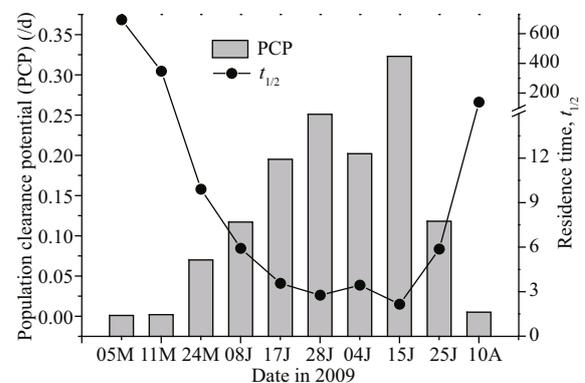


Fig.6 Population clearance potential (PCP, /d) and residence time ($t_{1/2}$) for copepod

Data obtained from Table 3. M: May; 08J, 17J, and 28J: June; 04J, 15J, and 25J: July; A: August.

community in Jiaozhou Bay. In NJBYS (2008 and 2010), the abundances of total zooplankton (<1 mm) and copepods (<1 mm) were relatively high during May to July, whereas they were significantly less in JBY (2009; Fig.7a & b). In addition, the abundances of hydromedusae and chaetognaths also decreased in the JBY compared to the levels in the NJBYs (Fig.7c & d).

4 DISCUSSION

4.1 Clearance rate

The clearance rates of *Aurelia* species on different prey items have been well studied (Table 4). It is therefore of interest to compare our obtained clearance rates for different prey organisms with those of previous studies. Previous and present studies all indicate that the *Aurelia* clearance rates for fish larvae and hydromedusae were higher than the other prey items, and there was a lower clearance rate of

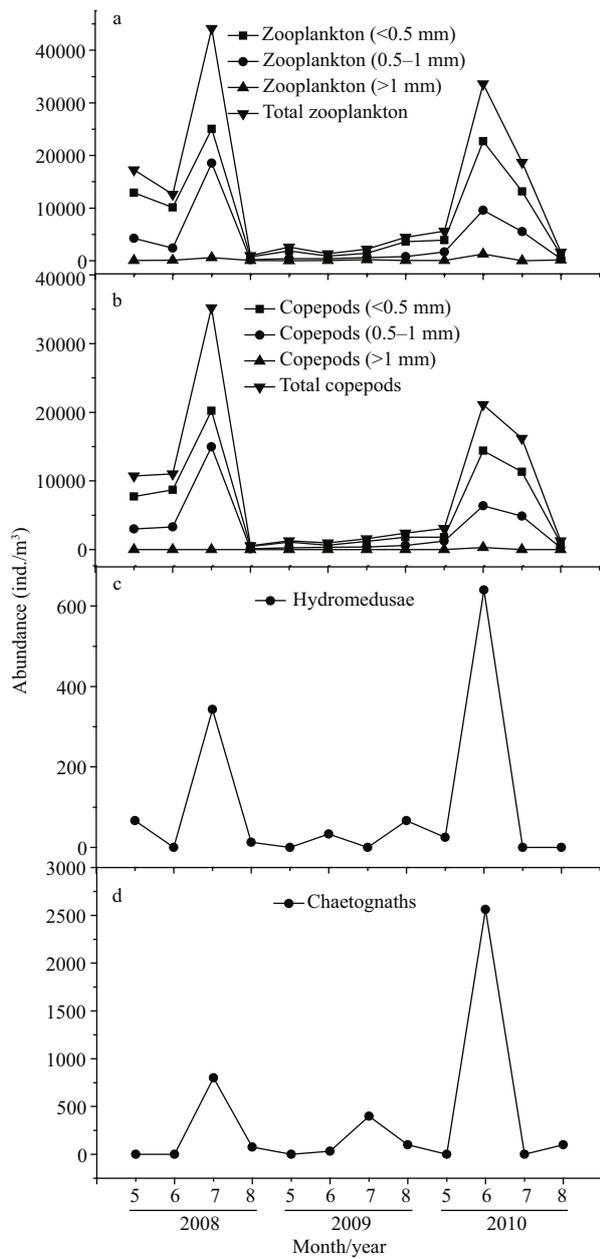


Fig.7 Abundances of total zooplankton (a), copepods (b), hydromedusae (c), and chaetognaths (d) between May and August 2008, 2009, and 2010 in Jiaozhou Bay, at the fixed station shown in Fig.1

Total zooplankton (including copepods) and copepods alone were divided into three groups in size: <0.5 mm, 0.5–1 mm, and >1 mm.

copepods (Fig.8). Predatory jellyfish have selective feeding behaviors that are based on several factors, including prey size, swimming speed and escape ability, predator tentacle length, width and spacing, predator swimming behavior and the resulting bell-margin water flow (Båmstedt, 1990; Purcell, 1992; Ford et al., 1997; Purcell et al., 1999; Suchman and Sullivan, 2000). Here, the clearance rate of hydromedusae was higher than the rate of copepods.

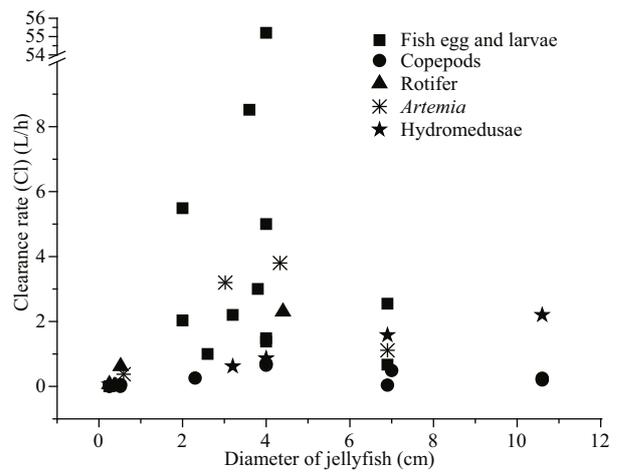


Fig.8 Clearance rate of different prey types

This figure combines the data from the present study and previous publications (Table 4).

This suggests that the low swimming speeds and poor escape abilities of hydromedusae increased their vulnerability to be attacked by both medusae and ephyrae. Although Anderson (1974) indicated that fast swimming copepods were more vulnerable to be ambushed by jellyfish, copepods have a characteristic escape jump (Hartline et al., 1996). Their rapid and vigorous escape behaviors are important adaptations for avoiding predation (Buskey et al., 2002; Waggett and Buskey, 2008). Fancett (1988) found that *Cyanea capillata* preferentially preyed upon fish eggs and larvae, whereas copepods were least preferred. We also found that the clearance rates of *A. coerulea* for fish larvae were generally higher than the rates for other prey. This result was consistent with previous studies, which suggested that fish larvae have relatively poor escape abilities compared to copepods (Purcell and Arai, 2001; Titelman and Hansson, 2006). Chaetognaths also have a characteristic escape jump, and the ‘jumping’ chaetognaths often escaped predation by *A. coerulea* in our study. Consequently, even if a successful encounter between these prey (copepods and chaetognaths) and *A. coerulea* (as a predator) happened, the stronger escape ability of copepods and chaetognaths, compared to fish larvae and hydromedusae, reduced the predation efficiency of *A. coerulea*.

Water temperature is an important factor that influences the clearance rate for *Aurelia* (Olesen, 1995). Clearance rate for 4.5-cm *A. coerulea* medusae at 5°C was only 2.2% of the clearance rate at 15°C (Fig.5a). The relationship between water temperature and clearance rate in our study can be explained by the increased beat frequency as water temperature

Table 4 Summary of clearance rates (CI) of *Aurelia* species on various prey organisms (fish, copepods, rotifers, *Artemia*, and hydromedusae) reported by this and previous studies

Prey type	<i>d</i> (cm)	<i>T</i> (°C)	Prey size (mm)/stage	CI (L/h)	Reference
Fish					
<i>Claupea harengus</i>	2.0	10–12	Yolk sac	5.490	Bailey, 1984
<i>C. harengus</i>	2.0	10–12	First feeding	2.030	Bailey, 1984
Capelin	3.6	10–15	Yolk sac	8.520	de Lafontaine and Leggett, 1988
Capelin	8.8	10–15	Yolk sac	21.900	de Lafontaine and Leggett, 1988
<i>Mallotus villosus</i>	2.6	8.2	Yolk sac	1.000	de Lafontaine and Leggett, 1988
<i>M. villosus</i>	3.2	7.4	Yolk sac	2.200	de Lafontaine and Leggett, 1988
<i>M. villosus</i>	3.8	8.7	Yolk sac	3.000	de Lafontaine and Leggett, 1988
<i>Gadus morhua</i>	4.0	8.0	Yolk sac	5.000	Titelman and Hansson, 2006
<i>Paralichthys olivaceus</i>	4.0	15±1	3.3±0.3	1.483	Liu et al., 2016
<i>Sebastes schlegeli</i>	4.0	15±1	6.0±0.5	1.380	Liu et al., 2016
Turbot	0.25±0.5	18.7	2.0±0.3	0.001	This study
Turbot	6.9±0.4	18.3	0.9±0.1	0.671	This study
Turbot	6.9±0.4	18.3	2.0±0.3	2.546	This study
Copepods					
Copepods	4.0	15.0	–	0.654	Båmstedt, 1990
<i>Acartia tonsa</i>	2.3	15.0	–	0.258	Olesen, 1995
Copepodites	10.6	11.0	–	0.250	Hansson, 2006
Copepods	10.6	11.0	Nauplii	0.200	Hansson, 2006
<i>A. tonsa</i>	4.0	15.0	–	0.700	Møller and Riisgård, 2007
Copepods	0.52±0.01	15.0	Nauplii	0.054	Riisgård and Madsen, 2011
	0.51±0.06	15.0	Adults	0.001	Riisgård and Madsen, 2011
	0.25±0.5	18.8	0.6±0.1	0.008	This study
	6.9±0.4	18.3	0.6±0.1	0.488	This study
	6.9±0.4	18.3	2.0±0.5	0.041	This study
Rotifers					
Rotifers	0.4	15.0	–	0.010	Olesen, 1995
	0.36	15.0	–	0.011	Olesen, 1995
	4.4	15.0	–	2.300	Olesen, 1995
	0.52±0.02	12.4	0.2	0.622	Riisgård and Madsen, 2011
	0.25±0.05	18.8	0.2±0.1	0.068	This study
	6.9±0.4	18.8	0.2±0.1	4.782	This study
<i>Artemia</i>	0.59±0.02	12.4	0.5	0.377	Riisgård and Madsen, 2011
	3.02±0.01	15.0	0.7	3.200	Riisgård and Madsen, 2011
	4.33±0.01	15.0	0.6–0.7	3.800	Riisgård and Madsen, 2011
	6.9±0.4	18.3	0.5±0.1	1.115	This study
Hydromedusae					
Hydromedusae	10.6	11.0	–	2.200	Hansson, 2006
	0.2–0.3	18.8	2.0±0.5	0.061	This study
	3.2±0.2	18.9	2.0±0.5	0.619	This study
	4.0±0.1	18.9	2.0±0.5	0.865	This study
	6.9±0.4	18.9	2.0±0.5	1.580	This study

d (cm): size of the predator. – means no data.

increased (Fig.5b). An increase in the frequency of bell contraction means an increase in the swimming speed of the same size medusa. Increased swimming speed allows the medusae to search more area, which

causes the encounter rate of prey organisms to increase (Bailey and Batty, 1983); higher clearance rate was reasonable. In addition, compared to the frequency of bell contraction when no prey was added, the

frequency of bell contraction increased when prey added (Fig.5b). We speculated that this was related to *A. coerulea* feeding behaviors. *Aurelia* capture prey with external surface mucus or wrap prey through the constriction of bell (Costello and Colin, 1994). *A. coerulea* medusae capture small copepods after contact with their exumbrella surface, and small copepods would attempt to escape by making violent thrashing motions. These prey escape responses stimulate the constriction of bell more frequently, which was propitious to increase the success of predation. Bailey and Batty (1983) indicated that *Aurelia* medusae were relatively more active after capture of one fish larva and their “searching” path was altered. We found that an increase in beat frequency allowed medusa to swim vertically, rather than remaining at the bottom or top of the incubator when no prey were added. Hence, these responses allowed medusae to scan larger volumes of water and to increase encounter rates with prey.

4.2 Predation impact of *A. coerulea* in Jiaozhou Bay

Accurate assessment of the potential predation effects of *A. coerulea* bloom on zooplankton communities is important for understanding the plankton dynamics in marine ecosystems with mass occurrences of jellyfish. Predation by *Aurelia* during blooms can substantially affect the species composition and abundance of zooplankton in pelagic systems (Möller, 1980; Hansson et al., 2005; Möller and Riisgård, 2007). For example, Möller (1980) reported that increased *A. aurita* abundance was accompanied by a sharp decrease in copepod standing stock; Hansson et al. (2005) indicated that *A. aurita* was the main predator on zooplankton communities, and the mean half-life time ($t_{1/2}$) of cirripede larvae in May was just hours to a few days; Möller and Riisgård (2007) indicated that *A. aurita* had a high potential for preying on *Acartia tonsa* from mid-May to August in Skive Fjord, and the $t_{1/2}$ of *Acartia tonsa* only ranged from 1 to 6 d. The density of *A. coerulea* in Jiaozhou Bay was extremely high in 2009 and *A. coerulea* undoubtedly reduced zooplankton stocks. When the population explosion of jellyfish *A. coerulea* occurred in Jiaozhou Bay, the numbers and compositions of zooplankton communities were significantly changed.

The theoretically calculated PCP for *A. coerulea* in Jiaozhou Bay varied seasonally as a result of variation in medusae density, size and water temperature. PCP was high during June and July 2009 (0.12–0.32 times a day) indicating that *A. coerulea* exerted high

predation pressure on zooplankton during this period (Table 3; Fig.6). This came a time when a high number of relatively larger *A. coerulea* medusae (mean bell size from 8.74 ± 1.72 cm to 17.26 ± 1.36 cm) was present with a higher surface water temperature ($21.5\text{--}25.5^\circ\text{C}$) (Table 3). In the present study, clearance rates increased linearly with the cross-sectional area (Fig.4), which was consistent with the results of Olesen (1995). This suggests that large medusae have stronger predation ability because large jellyfish have a high prey encounter rate and high prey capture success (Bailey and Batty, 1983; Titelman and Hansson, 2006). The clearance rate also increased with temperature ($<15^\circ\text{C}$; Fig.5a). Consequently, a stronger capture ability of *A. coerulea* occurred during this period, and the *A. coerulea* population was able to clear the water volume of the bay 0.12–0.32 times per day during June and July 2009 (Table 3). *A. coerulea* predation exerted high predation pressure on copepods population in this period. The mean residence time ($t_{1/2}$) for copepods typically ranged from 2–10 d, and the minimum $t_{1/2}$ value of 2.15 d was found on 15 July. Estimated residence time for copepods was considerably shorter than the time that these copepodites spend as larvae in the water column, which is in several weeks. Although the abundance of *A. coerulea* was high in early May, the mean size was 0.66 ± 0.17 cm. Ephyrae and metamedusae have a lower clearance for preying on copepods (Figs.3b & 4). In August, a high proportion of *A. coerulea* was deteriorated and the mean size had decreased (Wang and Sun, 2015). Therefore, PCP was low in early May and August 2009, and the estimated mean $t_{1/2}$ of copepods was more than 30 d (Table 3; Fig.6). This indicated a lower level of jellyfish predation on copepods during these times. The *A. coerulea* population controlled the amounts of copepods in late May, June and July, but not during the other months in 2009.

The *A. coerulea* population control of zooplankton communities is supported by field zooplankton investigations. Zooplankton abundances varied in different seasons between JBY (2009) and NJBYs (2008 and 2010) (Fig.7). Mean abundances of total zooplankton and copepods sharply decreased in the JBY compared to the NJBYs, especially small copepods (<1 mm; Fig.7a & b). The high predation pressure exerted by *A. coerulea* reduced the copepod community standing stock. This was also demonstrated by Wan and Zhang (2012). In addition, low abundances of hydromedusae and chaetognaths were observed in

the field surveys whenever the abundance of *A. coerulea* medusae was high. Zooplankton organisms, in addition to copepods, might also be controlled by *A. coerulea* in Jiaozhou Bay, as *Aurelia* medusae are usually considered as voracious predators with high feeding efficiency (Purcell and Arai, 2001; Titelman and Hansson, 2006). Our feeding experiments indicated that hydromedusae were captured by *A. coerulea* ephyrae and medusae with considerably high efficiency (Fig.3). Therefore, high predation pressure by *A. coerulea* on hydromedusae occurred during population outbreaks of *A. coerulea* in Jiaozhou Bay. Although the predation efficiency was lower on chaetognaths (Fig.3), the high capture pressure by *A. coerulea* on the other zooplankton organisms, like copepods, would generate food competition with chaetognaths as a predator. Competition for prey between both planktivorous zooplankton and fish and jellyfish has been suggested in previous studies (Möller, 1980; Purcell and Arai, 2001; Hansson et al., 2005). This may also exist in Jiaozhou Bay when jellyfish population explodes. Variations in the zooplankton populations were probably not due to environmental changes, because of the stable environments in Jiaozhou Bay during 2008 and 2010 (temperature and salinity; Fig.9). However, the concentration of chlorophyll *a* was obviously high with the mean value of 7.4 $\mu\text{g/L}$ in July 2009 (Fig.9). The peak concentration reached nearly 10 $\mu\text{g/L}$ (Wan and Zhang, 2012). This was significantly higher than the normal concentration of chlorophyll *a* in Jiaozhou Bay. The function of *A. coerulea* as a key organism may manifest itself not only as affecting the great variations in zooplankton communities, but also in the abundance of phytoplankton in Jiaozhou Bay. Release of phytoplankton from the control of zooplankton grazing due to the predation pressure by *A. coerulea* may result in a pronounced phytoplankton increase. Möller and Riisgård (2007) also suggested this effect of *A. aurita* in Skive Fjord. Thus, *A. coerulea* bloom can change the structure of the marine ecosystems in Jiaozhou Bay.

The population clearance potential by *A. coerulea* on fish eggs and larvae has not been established in this study, but the feeding experiments indicated the effectiveness of *A. coerulea* in capturing fish eggs and larvae compared to other prey items (Fig.3). Clearance rates of fish larvae and eggs were up to 7 times and 2 times greater, respectively, compared to small copepods. This implies that *A. coerulea* bloom could

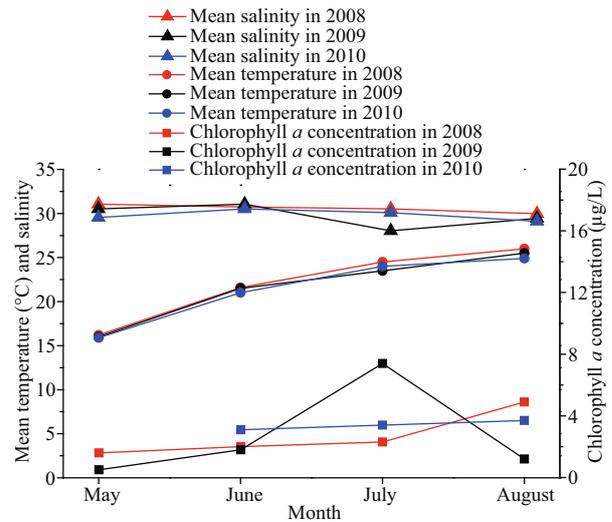


Fig.9 Variation in monthly mean temperature, salinity, and chlorophyll *a* concentration in Jiaozhou Bay during May to August 2008–2010

Data of environments in 2008 were obtained from Sun et al. (2011). Data of environments in 2009 were obtained from Wan and Zhang (2012). Data of environments in 2010 were obtained from Wang et al. (2012).

cause high mortality to fish eggs and larvae in Jiaozhou Bay, as was also indicated by Hansson et al. (2005) in Limfjorden, Denmark.

Like other studies that extrapolate empirical laboratory results to processes at the ecosystem level, this study assumes that the measurements of laboratory clearance rate with monospecific diets yield clearance rate values comparable to a field situation where the medusae experience a variety of prey species. The mixed prey assemblage might generate an effect that one prey species reacts to the presence of another species with changed swimming behaviors, leading to a modified encounter rate with jellyfish predator (Hansson et al., 2005). However, total zooplankton at our sampling site was mainly comprised of 71% copepods and this likely generated only a minor effect on the clearance rate of copepods at low densities of the rest of prey items. Hence, the copepod population was used as a model prey group to estimate the collective predation impact by *A. coerulea*, and the predation effects on other zooplankton populations were not calculated in the present study. Moreover, when comparisons of results among containers sizes have been made, feeding has always been lower in the smaller containers (de Lafontaine and Leggett, 1987; Purcell, 1997). Thus, clearance rates of *A. coerulea* in the present study should be considered as conservative estimates, and the population clearance potentials may be underestimated.

5 CONCLUSION

Prey type and predator size both have significant effects on clearance rate. *A. coerulea* captured rotifers, fish larvae, and hydromedusae more efficiently than fish eggs, copepods, and chaetognaths. Clearance rate linearly increased with the cross sectional area of *A. coerulea*. Water temperature also had marked effect on clearance rate and this may due to the increased beat frequency of *A. coerulea* as the water temperature increased. The *A. coerulea* population potentially cleared the volume of water in the Bay more than 0.3 times a day in July, and the residence time ($t_{1/2}$) for copepods was less than 6 d; the minimum $t_{1/2}$ -value was only 2.15 d in June and July in 2009. Abundances of copepods, hydromedusae, and chaetognaths were extremely low in 2009 compared to 2008 and 2010. Large predation pressure by *A. coerulea* population occurs to control zooplankton in Jiaozhou Bay, at least during June and July.

6 DATA AVAILABILITY STATEMENT

The authors declare that the data supporting the findings of this study are available within the article.

7 ACKNOWLEDGMENT

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