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Predator–prey interaction between muricid gastropods and mussels under ocean acidification

X-Y. Xu [a], K.R. Yip [a], P.K.S. Shin [a,b], S.G. Cheung [a,b,*]

[a] Department of Biology and Chemistry, City University of Hong Kong, Tat Chee Avenue, Kowloon, Hong Kong, China
[b] The State Key Laboratory in Marine Pollution, City University of Hong Kong, Tat Chee Avenue, Kowloon, Hong Kong, China

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ABSTRACT

Predation of the muricid gastropod *Thais clavigera* on two-sized groups of the mussel *Brachidontes variabilis* was studied under three pCO_2 levels, 380, 950, and 1250 μatm. At 950 μatm pCO_2 level, the prey handling time decreased significantly and large-sized *B. variabilis* were preferred by *T. clavigera*. However, the prey consumption rate was independent of pCO_2 levels, although the prey searching time increased significantly at elevated pCO_2. These findings indicated that the predator–prey interaction between *T. clavigera* and *B. variabilis* was altered under ocean acidification, which will have a long-term impact on the population dynamics of the interacting species.

1. Introduction

Increasing carbon dioxide levels in the atmosphere due to anthropogenic activities increase its dissolution in the ocean and hence decrease pH of the ocean surface. A decrease in pH of 0.1–0.4 units is predicted by the end of this century (Hoegh-Guldberg et al., 2014), which will result in ~50% reduction in the carbonate ion concentration of seawater. As several marine organisms possess external skeleton made up of calcium carbonate, reduction in the carbonate ion concentration will decrease calcification (Kroeker et al., 2010). Ocean acidification (OA) can induce physiological stresses not directly related to calcification in marine organisms. These include reduction in soft body growth, respiration, energy turnover, and energy metabolism (Pörtner et al., 2004; Doney et al., 2009). Calcium- and other ion-transport-based phenomena such as muscle contraction and neurosensory functions are sensitive to pH (Whittaker, 2008), and a reduction in pH was found to result in the loss of predator detection and impairment of anti-predatory responses in fish and gastropods (Dixson et al., 2010; Watson et al., 2014), reduction of visual risk assessment (Ferrari et al., 2012) in marine fishes, and the inability in locating food source and a decline in locomotory activity in hermit crabs and mud crabs (de la Haye et al., 2012; Dodd et al., 2015). Some studies have shown that behavioral disturbances can be completely restored by treatment with gabazine, a gamma-aminobutyric acid (GABA) antagonist of nervous systems, indicating potential interference of neurotransmitter receptor function by elevated CO_2 levels (Nilsson et al., 2012).

Studies on tolerance of individual taxonomic groups and life stages to ocean acidification provide little clues to predict long-term consequences of ocean acidification at population and community levels as their structures are determined not only by individual species tolerance but also through biological interactions such as predation and interspecific competition. Landes and Zimmer (2012) showed that ocean acidification negatively affected the closer muscle length of the crusher chela in *Carcinus maenas* and weakened the shells of their prey, the snail *Littorina littorea*, but they found no evidence that predator–prey interactions will change in the future. Ferrari et al. (2011) found that the predation rate on juvenile damselfish by the predatory dottyback was higher under elevated CO_2. The number of bigger damselfish consumed was not affected by CO_2 levels, but species preference was reversed at high CO_2 levels. Predation impact on a prey species is determined by the abundance and behavior of predators. If ocean acidification lowers the metabolism and impairs the muscular contraction and neurosensory functions of a predator, it may reduce the efficiency of foraging and consumption, thereby affecting the size and number of prey consumed (Sanford et al., 2016).

Thais clavigera is the commonest muricid gastropod found on Hong Kong rocky shores with barnacles and mussels as its preferred prey (Tong, 1986). Muricid gastropods can recognize the presence of a prey at a distance through chemical cues released from the prey (Carriker, 1981). *T. clavigera* uses chipping or boring for handling mussels. Larger mussels such as *Septifer virgatus* are side-bored, whereas smaller ones such as *Brachidontes variabilis* are chipped at the edges ventrally or posteriorly and then the valves are pulled apart (Taylor, 1980) after the proboscis is inserted at a point where the edges are chipped (Tong, 1986). Prey size preference has been demonstrated in muricid gastropods

* Corresponding author at: Department of Biology and Chemistry, City University of Hong Kong, Tat Chee Avenue, Kowloon, Hong Kong, China.
E-mail address: bhsgche@cityu.edu.hk (S.G. Cheung).

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feeding on barnacles and mussels in field and laboratory studies (Hughes and Dunkin, 1984), with larger prey being preferred as prey profitability (yield per unit handling time), which increases with the size of the prey (Hughes and Burrows, 1990). The present study investigated the effect of ocean acidification on prey detection and handling and prey size preference of *T. clavigera* on *B. variabilis*. We hypothesized that ocean acidification may disrupt the ability of *T. clavigera* to locate or consume prey; hence, smaller individuals of *B. variabilis* are preferred, which eventually reduces predation impact on *B. variabilis* population.

2. Materials and methods

2.1. Study organisms

Both *T. clavigera* (shell length: 30–33 mm) and *B. variabilis* (shell length: 7–18 mm) were collected from a rocky shore near the Wu Kai Sha Pier, Hong Kong (22.25°N, 114.14°E). The two species were maintained in the laboratory separately in seawater at 28 °C and a salinity of 30 psu. *B. variabilis* were fed twice a week with the green alga *Dunaliella tertiolecta*, whereas *T. clavigera* were fed with *B. variabilis*. Seawater was changed once a week to avoid the accumulation of metabolic wastes. *T. clavigera* were kept in the chambers at either one of three different CO_2 levels during the whole experiment. Prior to experimentation, *T. clavigera* were exposed to experimental pCO_2 for at least 1 month. As *B. variabilis* were sparsely populated and occurred at low abundance, they were collected in a number of occasions and therefore exposed to experimental pCO_2 for only about 1 week before the experiment started.

2.2. Experimental set up

Three CO_2 concentrations, 380 μatm, 950 μatm, and 1250 μatm, representing the present-day situation and the scenarios for 2100 and 2300, respectively, as predicted by the fourth assessment report of the Intergovernmental Panel on Climate Change (IPCC, 2007) were used in this experiment. Air was pumped into a conical flask, where it was mixed with CO_2 at a known flow rate. To achieve the desired CO_2 concentrations, the flow rate of CO_2 was controlled by a digital flow meter (GCR-B9SA-BA15, Vogtlin, Sweden), and the flow rate of air was controlled by a mechanical flow meter. The CO_2 concentration of the mixed gas was checked by a CO_2 analyzer (LT-260, Li-Cor Company, Switzerland). The mixed gas was dried in another conical flask containing silica gel before it was bubbled into individual experimental glass bottles. Temperature, pH_{NBS}, and salinity were measured once a week during the experiment. Ten individuals of *T. clavigera* were used as replicates for every pCO_2 level and maintained in separate small glass bottles, which were supplied with the mixed gas individually. An additional small glass bottle containing *B. variabilis* only was used to estimate the non-predation mortality. All the bottles were placed in a water bath maintained at 28 °C (Fig. 1).

2.3. Effect of OA on prey searching time

Prey searching time was investigated using a Y-maze design (Fig. 2). Water at a desired pCO_2 level was pumped from a reservoir tank into the two arms of a Y-maze. The water leaving the maze passed through a filter containing filter sponge and activated charcoal before returning to the reservoir tank. There were four sets of experiment for every pCO_2 level. In Set 1 and Set 2, the same amount of live *B. variabilis* was placed near to the entrance of one arm, while the other arm empty was left empty. *B. variabilis* were placed in the left arm in Set 1 but in the right arm in Set 2. Set 3 and Set 4 were similar to Set 1 and Set 2, except that empty shells of *B. variabilis* were used instead of leaving the arm empty. All the experiments were repeated 10 times, with a new individual of *T. clavigera* being used each time that was placed at the end of the long arm of the Y-maze (Fig. 2). The movement of *T. clavigera* was videotaped, and the time required for it to reach the live *B. variabilis* or empty shells was measured.

2.4. Prey handling time

Prey handling time of *T. clavigera* of the two-sized groups of *B. variabilis* (shell length: 12–13 mm and 10–12 mm) was measured, and 10 individuals of *T. clavigera* were studied for each pCO_2 level. According to the feeding habit of *T. clavigera*, they were fed once every 4 days. For the whole experiment, the handling time on two larger sized and two smaller sized *B. variabilis* was measured for every individual of *T. clavigera*. The handling time was measured as the time elapsed between *T. clavigera* in contact with *B. variabilis* and when it finished consuming *B. variabilis*, leaving behind the empty shell valves. The prey handling procedure was videotaped when real-time observation was not allowed.

2.5. Effect of OA on prey size preference and consumption rate

Prey size preference experiment was conducted according to Hughes and Dunkin (1984) and Rodrigues et al. (1987) under three pCO_2 levels. Two larger sized (shell length: 14–18 mm) and three

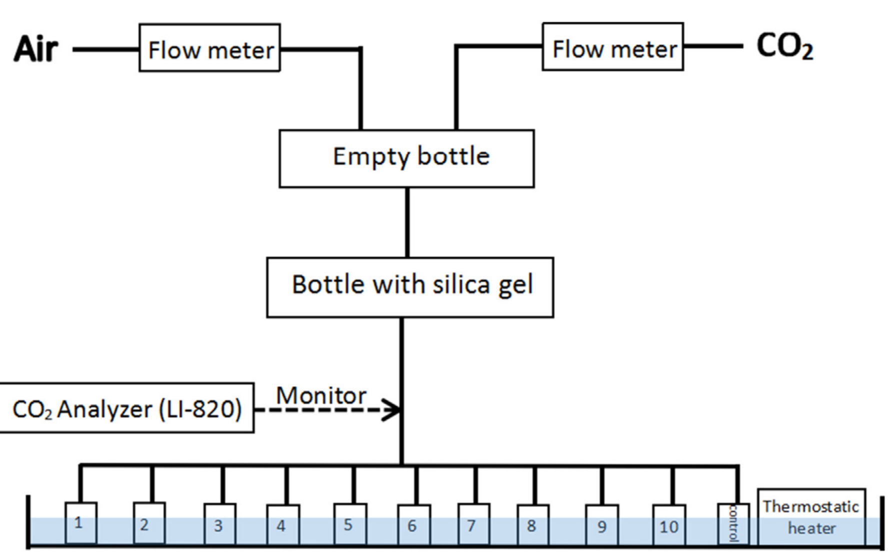

Fig. 1. Schematic diagram of the experimental set up.

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