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Feeding behaviour of a serpulid polychaete: Turning a nuisance species into a natural resource to counter algal blooms?

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ABSTRACT

Occurrence of algal blooms in coastal waters is predicted to be more prevalent in future. To minimize their occurrence, manipulating the grazing pressure by suspension feeders is a potential management strategy, but its effectiveness may depend on their feeding preference. Therefore, we assessed the clearance rate of a widespread serpulid polychaete *Hydroides elegans* in larval and adult stages on various coastal phytoplankton. Additionally, the growth and development of *H. elegans* after consuming these phytoplankton were determined to reflect its sustainability to counter algal blooms. Results showed that *H. elegans* can consume and utilize different phytoplankton, except diatom *Thalassiosira pseudonana*, for growth and development in both life stages. Given the fast-colonizing ability which allows easy manipulation of abundance, *H. elegans* is considered practically and biologically ideal for tackling algal blooms. Other suspension feeders with different feeding niches could be used in combination to maximize the versatility of the top-down control.

1. Introduction

Eutrophication is one of the major human-induced disturbances on coastal ecosystems worldwide (Smith and Schindler, 2009; Kitsiou and Karydis, 2011), usually leading to exponential proliferation of phytoplankton (e.g. diatoms and dinoflagellates) in coastal waters, known as algal blooms (phytoplankton density > 2×10^4 cells ml^{-1}; Graham et al., 2008). While only a few (~2%) can produce toxins, algal blooms *per se* can pose deleterious effects on coastal ecosystems, especially mortality of marine organisms, and incur huge economic losses (Smith and Schindler, 2009). Algal blooms are predicted to be more prevalent in future because of increased agricultural activities and atmospheric carbon dioxide concentration (Crossland et al., 2005; Rost et al., 2008). Therefore, how to minimize the occurrence and impacts of algal blooms becomes an important issue in coastal management.

It is noteworthy that ecosystems have an inbuilt capacity to resist the disturbance caused by increased primary production through trophic compensation (Leising et al., 2005; Ghedini et al., 2015). In coastal waters, microzooplankton (e.g. ciliates, rotifers and planktotrophic larvae) are the primary grazers of phytoplankton, consuming 60–75% of primary production (Landry and Calbet, 2004). Sessile suspension feeders (e.g. oysters and mussels) can also pose huge grazing pressure on phytoplankton (Karatayev et al., 2015). As such, manipulating the grazing pressure on phytoplankton (i.e. top-down control) may be a promising management strategy to preclude or even counter algal blooms in coastal waters. This strategy has been evaluated using a modelling approach (Fulford et al., 2007, 2010; Richards and Chaloupka, 2015), but some technical problems remain, such as selective feeding of suspension feeders. To improve the effectiveness of this strategy, more studies on feeding behaviour are required for choosing ideal suspension feeders.

Since algal blooms can be caused by any phytoplankton species (Leising et al., 2005), ideal suspension feeders to cope with algal blooms should have the following biological features: (1) high clearance rate on phytoplankton at high concentration; (2) little or no feeding preference; (3) ability to utilize food sources to improve fitness. The last two features, which indicate versatility and sustainability to counter algal blooms, are critical but often overlooked. Indeed, many suspension feeders exhibit strong selective feeding towards preferred phytoplankton species and reject undesirable ones, largely depending on their size, quality (e.g. nutritional value) and palatability (e.g. texture and chemical cues) (Ward and Shumway, 2004). Although selective feeding is an adaptive behaviour, it implies that those suspension feeders with strong feeding preference would be impaired in the algal bloom event if the causative phytoplankton is an undesirable food item. Therefore, studying feeding preference and its relationship with fitness is critical for choosing ideal suspension feeders to tackle algal blooms.

Among various sessile suspension feeders in coastal waters, serpulid polychaetes are extremely abundant owing to their opportunistic life history. Whilst they have been regarded as nuisance species because

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of their fast-colonizing and reef-building ability on man-made structures (Nedved and Hadfield, 2009), their ecological roles are substantially overlooked. In fact, serpulid polychaetes can reduce water turbidity, enhance nutrient recycling and regulate the abundance of phytoplankton (Davies et al., 1989; Bruschetti et al., 2008; Pan and Marcoval, 2014). Since serpulid polychaetes are able to rapidly colonize many man-made structures, their grazing pressure on phytoplankton in coastal waters can be easily manipulated, meaning that they are practically ideal for tackling algal blooms. Yet, their feeding behaviour at high concentration of phytoplankton remains largely unexplored.

In this study, a serpulid polychaete *Hydroides elegans* was selected as a model species because of its worldwide distribution in coastal waters (Nedved and Hadfield, 2009). We examined the feeding preference of this suspension feeder by measuring clearance rate, in both larval and adult stages, on various common coastal phytoplankton of different sizes, nutritional values and textures at high concentration so that its capability and versatility to cope with algal blooms can be evaluated. The fitness after consuming the phytoplankton was determined by the growth and development of larvae as well as the tube growth of adults to indicate their sustainability to counter algal blooms. If the fitness of serpulid polychaetes can be enhanced by consuming phytoplankton at high concentration, they may be considered as the natural "resources" for minimizing the occurrence of algal blooms.

2. Materials and methods

2.1. Collection of H. elegans

Adult *H. elegans* were collected from a fish farm in Yung Shue O (22°19′N, 114°16′E), Hong Kong. They were maintained under laboratory conditions (temperature: 22.0 ± 1.0 °C, dissolved oxygen concentration: 8.5 ± 0.2 mg O_2 l^{-1}, salinity: 33.0 ± 0.5 ppt and pH: 8.11 ± 0.04) and phytoplankton *Isochrysis galbana* was daily provided as food. Prior to experimentation, they were allowed to acclimate for one week.

2.2. Preparation of larval and algal cultures

To prepare the larval culture, adult *H. elegans* were induced to spawn by carefully breaking the calcareous tube near the abdominal region under a stereomicroscope. The sperm and eggs were then mixed in a Petri dish filled with ~10 ml filtered seawater (FSW). Following fertilization, indicated by the first cleavage ~ 35 min after adding the sperm suspension, the embryos were gently rinsed with FSW in a 38 μm sieve and then transferred into a glass bottle filled with 150 ml FSW. The larvae hatched the next day.

Four species of common coastal phytoplankton, namely *Chaetoceros gracilis* (CG), *Dunaliella tertiolecta* (DT), *Isochrysis galbana* (IG) and *Thalassiosira pseudonana* (TP), were used as food for *H. elegans* in this study. Their characteristics are shown in Table 1. As algal blooms can be caused by multiple phytoplankton species, an assorted suspension (Mixed) was prepared by mixing these four phytoplankton species with equal volume and concentration, except that the concentration of DT was 8-fold lower than those of other species due to larger cell volume. The concentration of phytoplankton was determined using a haemacytometer.

2.3. Clearance rate of larvae and adults

To estimate the clearance rate of larvae, approximately 10,000 individuals of unfed 2-day-old larvae were transferred into a glass bottle containing 100 ml FSW with phytoplankton at ~2.0×10^6 cells ml^{-1}, except DT at ~2.5×10^5 cells ml^{-1} due to larger cell volume ($n = 5$ replicate bottles per food type). These concentrations are commonly observed in the past algal bloom events (e.g. Buskey et al., 2001; Lomas et al., 2001). Seawater in the bottle was gently aerated with air to generate water flow and maintain dissolved oxygen concentration. The larvae were allowed to feed under the aforementioned laboratory conditions for ~2 h. Then, 0.5 ml seawater was collected from each bottle and the concentration of phytoplankton was estimated using a haemocytometer ($n = 6$ trials per bottle). Prior to counting, the phytoplankton were fixed by adding 1% Lugol's iodine. The clearance rate was calculated using the following formula (Coughlan, 1969):

$$CR = \frac{V}{nt} \times \ln\frac{C_o}{C_t}$$

where CR is the clearance rate (l ind^{-1} h^{-1}); V is the volume of seawater; n is the number of individuals; t is the feeding time; C_o and C_t are the initial and final concentrations of phytoplankton, respectively.

As for the adults, they were starved for one day before experimentation to standardize their hunger level. Then, 20 individuals (tube length: ~22 mm; body length: ~7 mm) were transferred into a glass bottle containing 200 ml FSW with phytoplankton at ~2.0×10^6 cells ml^{-1}, except DT at ~2.5×10^5 cells ml^{-1} ($n = 3$ replicate bottles per food type). The experimental conditions and procedures for estimation of clearance rate were described above.

2.4. Larval growth and development

Approximately 5000 individuals of unfed 1-day-old larvae were transferred into a glass bottle containing 200 ml FSW with phytoplankton at ~2.0×10^6 cells ml^{-1} (DT at ~2.5×10^5 cells ml^{-1}) on Day 1 ($n =$ 3 replicate bottles per food type). A control was done by not adding food. To determine larval growth, the body length of larvae was daily measured from Day 1 to Day 7 under a compound microscope (Axioplan 2 imaging, ZEISS, Germany) using software AnalySIS LS Professional 5.0 (Olympus Soft Imaging Solutions GmbH, Germany) ($n = 15$ individuals per bottle). As for larval development, at least 50 individuals were daily collected from each bottle from Day 3 to Day 7 to determine the proportion of each developmental stage ($n = 3$ replicate bottles per food type): trochophore stage, metatroch stage and competent stage (Nedved and Hadfield, 2009). Malformed larvae, characterized by the enlarged hyposphere, unclear segmentation or deformed shape (Shin et al., 2013), were also enumerated. On Day 4, seawater in the bottle was renewed and food was replenished.

Table 1
Characteristics of phytoplankton *Chaetoceros gracilis* (CG), *Dunaliella tertiolecta* (DT), *Isochrysis galbana* (IG) and *Thalassiosira pseudonana* (TP).

Species	Group	Motility	Cell size (μm)	Dry weight (pg $cell^{-1}$)[a]	Percentage weight (%)[a]		
					Protein	Carbohydrate	Lipid
CG	Diatom	No	5–7	74.8	12.0	2.67	6.95
DT	Dinoflagellate	Yes	10–11	99.9	20.0	12.2	15.0
IG	Dinoflagellate	Yes	5–6	30.5	28.9	12.8	23.0
TP	Diatom	No	4	28.4	34.2	8.80	19.4

[a] Lavens and Sorgeloos (1996).