Marine Pollution Bulletin xxx (2016) xxx–xxx

Contents lists available at ScienceDirect

Marine Pollution Bulletin

journal homepage: www.elsevier.com/locate/marpolbul

Selective suppression of *in situ* proliferation of scyphozoan polyps by biofouling

Song Feng [a,b,1], Shi-Wei Wang [c,1], Guang-Tao Zhang [c,*], Song Sun [a,b,c,**], Fang Zhang [a,b]

[a] *Key Laboratory of Marine Ecology and Environmental Sciences, Institute of Oceanology, Chinese Academy of Sciences, Qingdao 266071, China*
[b] *Laboratory for Marine Ecology and Environmental Science, Qingdao National Laboratory for Marine Science and Technology, Qingdao 266071, China*
[c] *Jiaozhou Bay Marine Ecosystem Research Station, Institute of Oceanology, Chinese Academy of Sciences, Qingdao 266071, China*

ARTICLE INFO

Article history:
Received 12 May 2016
Received in revised form 25 September 2016
Accepted 26 October 2016
Available online xxxx

Keywords:
Artificial constructions
Polyps
Biofouling
Competition
Predation

ABSTRACT

An increase in marine artificial constructions has been proposed as a major cause of jellyfish blooms, because these constructions provide additional substrates for organisms at the benthic stage (polyps), which proliferate asexually and release a large amount of free-swimming medusae. These hard surfaces are normally covered by fouling communities, the components of which have the potential to impede the proliferation of polyps. In this study, we report an *in situ* experiment of polyp survival of four large scyphozoan species found in East Asian marginal seas that were exposed to biofouling, a universal phenomenon occurring on marine artificial constructions. Our results showed that the polyps of three species (*Nemopilema nomurai*, *Cyanea nozaki*, and *Rhopilema esculentum*) attached to the artificial surfaces were completely eliminated by biofouling within 7–8 months, and only those of moon jellyfish (*Aurelia* sp.1) in the upper layers could multiply on both artificial materials and other organisms (*e.g.*, ascidians and bryozoans). Fouling-associated competition and predation and suppressed asexual reproduction of podocysts were observed to contribute to the loss of polyps. This study shows that the natural distribution of polyps is defined by the biofouling community that colonizes the surfaces of artificial constructions. Consequently, the contribution of marine constructions to jellyfish bloom is limited only to the ability of the jellyfish species to reproduce asexually through budding and inhabit solid surfaces of fouling organisms in addition to inhabiting original artificial materials.
We anticipate that fragile polyps will colonize and proliferate in harsh environments that are deleterious to biofouling, and we propose special attention to polyps in antifouling practices for excluding the possibility that they occupy the available ecological space.

1. Introduction

The topic on whether the abundance of global jellyfish is really increasing has been considerably debated (Condon et al., 2012; Purcell, 2012; Condon et al., 2013); yet, jellyfish blooms have recently increased in many coastal waters around the globe, including the Bering Sea, the Black Sea, and the South American Pacific and Atlantic coasts (Brodeur et al., 2002; Kideys, 2002; Decker et al., 2014; Mianzan et al., 2014). Analogously, East Asian marginal seas have also recently experienced disastrous jellyfish blooms, in which three nuisance species, namely *Aurelia* sp.1, *Cyanea nozaki*, and *Nemopilema nomurai*, and the edible species *Rhopilema esculentum* inhabited as the dominant scyphozoan species (Zhang et al., 2012; Dong et al., 2014; Uye, 2014; Sun et al., 2015; Yoon et al., 2014).

Enormous blooms of *Aurelia* sp.1, *C. nozaki*, and *N. nomurai* have frequently occurred in East China Sea, Yellow Sea, Bohai Sea, and Korean and Japanese coastal waters in recent decades (Ding and Cheng, 2005, 2007; Dong et al., 2006; Dong et al., 2010; Hong et al., 2013; Sun et al., 2015; Uye, 2011, 2014; Yoon et al., 2014; Zhang et al., 2012). High-density aggregations of *Aurelia* sp.1 have repeatedly caused the nuclear power plants to shut down through clogging of the cooling water intakes in China and Korea (Dong et al., 2010; Korean Nuclear Power Plant Operational Performance Information System, http://opis.kins.re.kr/). Frequent outbreaks of *C. nozaki* and *N. nomurai* have posed severe threats to local fisheries, including clogging and destruction of the nets, mortality of fish, reduction in fish catches, and stinging hazard to fishermen. (Kawahara et al., 2006; Dong et al., 2010; Uye, 2014). In the Changjiang estuary, *Cyanea* spp. accounted for 85.5% and 98.4% of the total fishery catch in November 2003 and May 2004, respectively (Xian et al., 2005). The blooms of *N. nomurai* in 2005 resulted in a monetary loss of USD 250 million to fisheries and >100,000 complaints from fishermen in Japan (Uye, 2014). In contrast, the annual catches of *R.*

* Corresponding author.
** Correspondence to: S. Sun, Key Laboratory of Marine Ecology and Environmental Sciences, Institute of Oceanology, Chinese Academy of Sciences, Qingdao 266071, China.
E-mail addresses: fengsong@qdio.ac.cn (S. Feng), wangshiwei@qdio.ac.cn (S.-W. Wang), gtzhang@qdio.ac.cn (G.-T. Zhang), sunsong@qdio.ac.cn (S. Sun).
[1] Song Feng and Shi-wei Wang contributed equally to this work and should be considered co-first authors. Song Feng wrote this manuscript. Song Feng and Shiwei Wang completed the *in situ* experiment together, dealt with the data, and drew the figure. Guang-Tao Zhang and Song Sun helped the accomplishment of the manuscript, and should be considered as co-corresponding authors.

http://dx.doi.org/10.1016/j.marpolbul.2016.10.062

esculentum, one of the most abundant fishery resources, have been sharply decreasing in Chinese waters in this decade (Dong et al., 2014). This situation has also exerted a deleterious influence on fishery economy. Moreover, as medusae compete for copepods with fish and even feed on their eggs and larvae (Hansson et al., 2005; Uye and Shimauchi, 2005; Uye, 2008), continually extensive jellyfish blooms may cause changes in the marine ecosystem, resulting in a shift from traditional fish-dominated ecosystem to jellyfish-dominated ecosystem (Uye, 2011).

Outbreaks of jellyfish are typically attributed to their unique ecological adaptation combined with a series of human-induced stresses to marine ecosystems and climate change (Richardson et al., 2009; Uye, 2011; Purcell, 2012). Among the multiple explanations for these outbreaks, an increase in artificial structures in coastal waters is included because of the potential contribution of these structures to the growth of benthic polyp stage of scyphozoan species. Submerged hard surfaces afford additional substrates for polyps, which can multiply through asexual reproduction, liberate abundant ephyrae by strobilation, and increase the likelihood of causing jellyfish blooms (Duarte et al., 2013). Evidence of links between medusa outbreaks and increased marine constructions has been given in several studies at various locations (Lo et al., 2008; Malej et al., 2012; Makabe et al., 2014). These hard surfaces are also usually occupied by fouling communities (Mineur et al., 2012). The effect of the organisms fouling these structures on the polyps has rarely been reported. High polyp survival in *Aurelia* spp. and *Cyanea* spp. was recorded in environments with low biomass of fouling organisms (Watanabe and Ishii, 2001; Colin and Kremer, 2002; Willcox et al., 2008; Ishii and Katsukoshi, 2010). Moreover, some predators of fouling communities, such as nudibranchs, are known to include polyps in their diets (Hoover et al., 2012; Takao et al., 2014). Thus, to evaluate the actual contribution of artificial structures to jellyfish blooms, it is necessary to understand how polyps interact with other fouling organisms.

Compared with other explanations of jellyfish blooms occurring in planktonic stages through complex trophic cascading, the contribution of artificial structures restricted to benthic polyps has been investigated through indoor experiments and by diving observations. In the laboratory, many artificial materials commonly used in marine constructions have been proved to be suitable substrates for polyps of a range of scyphozoan species (Holst and Jarms, 2007; Hoover and Purcell, 2009). In natural environments, polyps co-existing with other fouling organisms have been observed on submerged structures, but dense population of polyps has usually been found limited to *Aurelia* species (Miyake et al., 2002; Willcox et al., 2008; Purcell et al., 2009; Di Camillo et al., 2010; Ishii and Katsukoshi, 2010; Toyokawa et al., 2011; Makabe et al., 2014). There is no indication on why the habitats of polyps of other species have remained unknown. As biofouling was absent in all controlled experiments, it is still unclear whether proliferation of polyps of the four abovementioned species can be suppressed by biofouling, including in particular whether such interactions are species specific and how the difference occurs in the field.

To illustrate the numerical change in polyps with the development of biofouling communities under *in situ* conditions, these four species of newly settled polyps on settling plates were deployed at different depths in Jiaozhou Bay, where the blooms of *Aurelia* sp.1, *C. nozaki*, and *N. nomurai* have massively occurred in recent years, replacing the *R. esculentum* population that was once abundant. Quantitative parameters of polyp growth; asexual reproduction; and the abundance of polyps, fouling organisms, and predators were continuously monitored for 8 months to test the null hypothesis that biofouling did not significantly affect the proliferation of polyps of the four species.

2. Methods

2.1. Establishment of laboratory polyp populations

Artificial asexual reproduction methods described in previous reports were adopted in our study (Pit, 2000; Morandini et al., 2004; Holst et al., 2007; Holst and Jarms, 2007), with minor modifications to accommodate the target species. Using a pneumatic boat, medusae were captured from nearshore waters of Jiaozhou Bay in July (*Aurelia* sp.1) and September (*C. nozaki*, *N. nomurai*, and *R. esculentum*) 2012. The living medusae were transported to the laboratory in individual bucket, and the maturity of gonads was examined using a stereomicroscope. Six mature females and four mature males were incubated in 200 L aquarium (for *Aurelia* sp.1) and 30 m^3 ponds (for the other species). Two-thirds of the water was renewed with newly filtered seawater (dissolved oxygen (DO) > 7 mg L^{-1}) once every 2 days, and the water temperature was 25 °C and 21 °C. During the incubation, 1 L of seawater sample in the aquarium or ponds was collected twice per day, and a small aliquot of the sample was observed under the dissecting microscope. Once planula larvae were detected, corrugated plastic plates were deployed in the aquariums or ponds, and the medusae were discarded. Millions of planulae were observed settling on the plastic plates. Adequate *Artemia* nauplii were supplied at 1–2 h intervals every 3 days. The water was then replaced with newly filtered seawater. Polyps grew as the seawater temperature changed. Mature polyps with 16 tentacles were simultaneously developed 1 month later, when asexual production started to appear. Only fully developed 16-tentacle polyps were selected for the following *in situ* experiments.

2.2. Experiment site and incubation procedures

A floating dock, referred to as "Haiou," in Jiaozhou Bay (36.07°N, 120.16°E; length: 50 m, width: 8 m), with water depths ranging between 4.5 and 6 m, was selected as our experiment platform (Fig. 1). To reduce possible physical damages caused by movements and to avoid the loss of polyps, the plates carrying polyps were incubated in

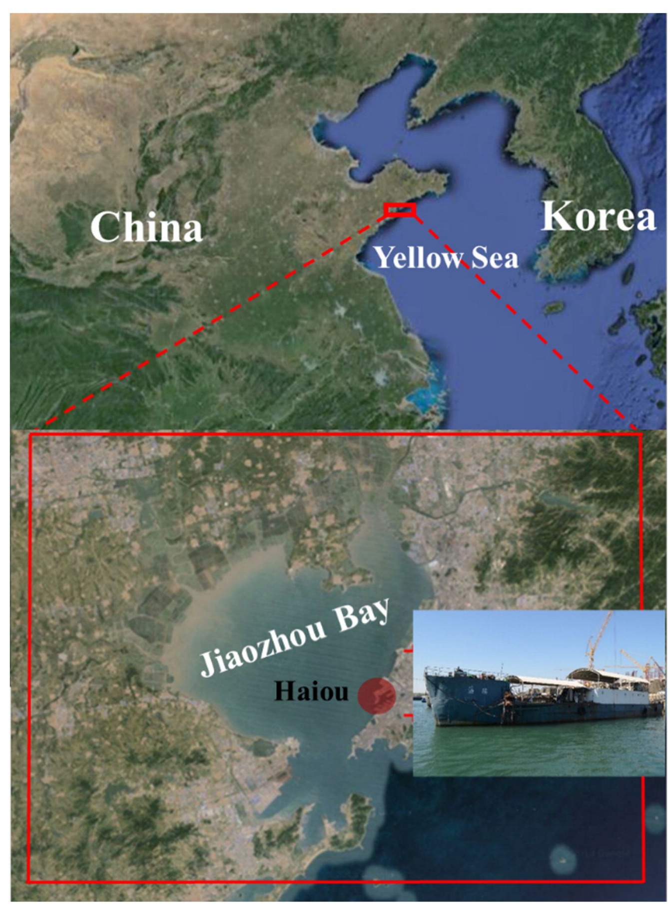

Fig. 1. Location of Jiaozhou Bay and the *in situ* experiment sites. The inlet image shows the floating dock (Haiou; 36.07°N, 120.16°E) for *in situ* polyp deployment.