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Seasonal heterogeneity provides a niche opportunity for ascidian invasion in subtropical marine communities

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ABSTRACT

Implications of changes in environmental conditions caused by seasonality and human alterations on the recruitment of non-native species and their biotic resistance to predation are poorly understood. Here, through the use of experimental recruitment panels and predation exclusion cages, we examined 1) whether a subtropical seasonality (i.e., tropical and temperate conditions) affects the recruitment and abundance of the non-native ascidian *Ciona intestinalis*, the cryptogenic *Styela plicata* and *Ascidia sydneiensis*, and native *Hermandia momus* in fouling communities in Hong Kong, 2) whether human environmental alterations (i.e., typhoon shelters and sheltered bays with different habitat alteration and seawater quality) affect the abundance of the ascidians, and 3) whether predation reduces the abundance of ascidians under different environmental conditions caused by seasonality and human alteration. Our experimental results indicate that seasonality provides a temporal niche for the recruitment of the ascidians; *C. intestinalis* and *S. plicata* recruited mostly in winter, whereas *A. sydneiensis* and *H. momus* recruited in summer. *Ciona intestinalis* was the only ascidian that prospered in anthropogenically altered environments where it monopolized communities. The marked seasonal recruitment of the ascidians obscured the effect of predation between seasons, whereas human alteration did not affect predation. The recruitment of the ascidians in subtropical communities appeared to correspond to their original temperate or tropical distributions, hence *Ciona intestinalis*, with a temperate native distribution, benefits from a temporal niche opportunity during winter conditions. We argue that seasonality, as an important ecological factor for recruitment and community ecology dynamics, must also be considered in the context of biological invasion.

1. Introduction

The environmental heterogeneity hypothesis proposes that environments with temporal and spatial heterogeneity promote invasibility of non-native species and also their coexistence with native species (Melbourne et al., 2007). Seasonal environmental fluctuations (e.g. temperature) are known to have implications for species responses such as abundance, survival, reproduction, growth, behavior, etc. (Coma et al., 2000; Vieira et al., 2012; Andrews et al., 2014). Therefore these seasonal variations affect the biotic interactions within a community (Vieira et al., 2012). Abundance of non-native species is affected by seasonality with implications for resource competition (Blum et al., 2007), however, our knowledge regarding the effect of seasonality (i.e. temporal heterogeneity) on the recruitment of non-native species and predation remains largely unexplored.

Environmental and biological seasonality has been considered important in structuring marine communities at all latitudes (Clarke, 1988; Coma et al., 2000; Afeworki et al., 2013; Andrews et al., 2014). The recruitment and abundance of marine invertebrates (including non-native species) through seasons is a result of species-specific interactions with the environment (Tracy and Reyns, 2014). Therefore, in temperate regions, where seasonal changes are stronger with a larger range of temperature

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fluctuations, species recruitment and abundance patterns are apparently marked (Stachowicz and Byrnes, 2006; Freestone et al., 2009). Tropical regions also present seasonal events (e.g. upwelling and monsoon rainfall events) that change environmental conditions and communities (Witman and Smith, 2003). In subtropical regions, where environmental seasonality varies between temperate and tropical conditions, the recruitment and abundance of marine species clearly respond to seasonal changes (Morton and Morton, 1983; Lam, 2001; Huang, 2003). Studies have reported that some non-native species recruit under seasonal and local spatial conditions in which native species recruitment is lower (Osman et al., 2010; Tracy and Reyns, 2014), suggesting that non-native species may use available temporal niches according to their abilities to respond to environmental changes.

It is well documented that marine communities under environmental stress (e.g. estuaries and urban areas with habitat alteration and pollution) become more susceptible to invasions (Occhipinti-Ambrogi and Savini, 2003; Floerl et al., 2004; Dafforn et al., 2009). One explanation is that some non-native species are more tolerant of stressors such as extreme temperature, salinity, low oxygen and pollution than native species (Jewett et al., 2005; Piola and Johnston, 2009; Lenz et al., 2011). Such tolerance differences could be due to a selection of individuals with higher phenotypic plasticity during unfavorable conditions in transportation and establishment during the invasion process (Richards et al., 2006; McKenzie et al., 2011). Environmental stress could decrease local biodiversity or the activity of the species and therefore the intensity of biotic interactions within the communities (Occhipinti-Ambrogi and Savini, 2003; Piola and Johnston, 2008; Cheng and Hovel, 2010), providing a niche opportunity (e.g. more resources and lower predation pressure) for the establishment of non-natives species that can tolerate these conditions (Shea and Chesson, 2002).

Predation studies have demonstrated that generalist native predators play an important role in biotic resistance to non-native species in marine communities (de Rivera et al., 2005; Dumont et al., 2011a; Freestone et al., 2013; Rius et al., 2014). Predators can limit the abundance and distribution of non-native marine species that may lack effective defenses (de Rivera et al., 2005; Dumont et al., 2011a). Non-native species may then find predation refuge in habitats that predators cannot access due to spatial isolation (Dumont et al., 2011b) or unfavorable environmental conditions (Byers, 2002a; Cheng and Hovel, 2010). Low salinity has been shown to reduce predation on non-native species in estuaries (Cheng and Hovel, 2010). A similar mechanism has been suggested to occur in anthropogenically disturbed environments (Byers, 2002b; Osman et al., 2010) and could potentially operate in seasonal ecosystems. In this case, environmental heterogeneity caused by temporal and spatial conditions that reduce the abundance or activity of native predators can release the predation pressure on the recruitment of non-native species.

Subtropical regions present an interesting overlap of species with tropical and temperate distributions (Morton and Morton, 1983; Schiel et al., 1986). The marine environment of Hong Kong is influenced by the warm-tropical Hainan current from the South China Sea during the summer season, whereas during the winter season seawater is replaced by the cold Taiwan current from East China Sea and by the warm Kuroshio current from the Luzon Straits (Morton and Morton, 1983). Heavy rainfall in summer reduces salinity in estuaries and enclosed systems (Morton and Morton, 1983). Sedentary subtidal taxa can persist through both seasons, but their recruitment and abundance respond to seasonal changes (Hon, 1978; Mak, 1983; Lam, 2001; Huang, 2003). For example, in Hong Kong three main general groups of species can be found in fouling communities, those that recruit and dominate in winter (e.g. *Bugula neritina*, *Ulva* spp, *Styela plicata* and *Ciona intestinalis*), in summer (e.g. *Saccostrea cucullata*, *Alectryonella* sp. *Perna viridis*) and those species that remain invariable and dominant throughout the seasons (e.g. *Hydroides elegans* and *Balanus* spp., Hon, 1978; Mak, 1983; Lam, 2001; Huang, 2003). Studies on native fish and crab assemblages in Hong Kong indicate that most predator species have a tropical distribution, and their abundance and feeding activity decrease under temperate conditions in winter (Lai, 1996; Cornish, 2000). A similar pattern occurs in subtidal predatory gastropods with low abundance and feeding activity in winter (Morton and Blackmore, 2009). These antecedents suggest that recruitment and abundance of fouling species as well as predator activities could be determined by seasonality and the original distribution of the species (i.e. tropical and temperate distribution).

In the present study, we explored the role of seasonality on the recruitment and predation of the non-native ascidian *Ciona intestinalis* (Linnaeus, 1767), the cryptogenic (i.e., unclear origin) *Styela plicata* (Lesueur, 1823) and *Ascidia sydneiensis* (Stimpson, 1855) and the native *Hermandia momus* (Savigny, 1816) in fouling communities from environments with different intensities of human alteration. *Ciona intestinalis* is a common and widely distributed temperate non-native species in human facilities (Carver et al., 2006). In Hong Kong, *C. intestinalis* was introduced probably in the 1970's but its distribution remains restricted to fouling communities in areas with high habitat alteration and pollution, showing higher recruitment in winter season (Morton, 1987; Astudillo et al., 2014). *Ciona intestinalis* is also highly vulnerable to generalist predators (Dumont et al., 2011a), such that it could be expected that its recruitment would be higher in winter and in environments with low predation. We, therefore, examined 1) whether the recruitment of *C. intestinalis* and the other ascidians is regulated by seasonal conditions, 2) whether environments with different human alterations (i.e., habitat alteration and low seawater quality) affect the abundance of the ascidians, and 3) whether predation reduces the abundance of the ascidians under different environmental conditions caused by seasonality and human activities. Taken together, we address here how seasonality and habitat alteration affect the recruitment of the ascidians and the integrity of biotic resistance by predation in marine fouling communities.

2. Materials and methods

2.1. Study sites

We conducted the experiments in six piers in Hong Kong (Appendix A). Three piers were located in sheltered bays with low human alteration (i.e., habitat alteration caused by reclamation and low seawater quality) and the other three were located in typhoon shelters with high human alterations. Typhoon shelters are marine systems artificially enclosed by breakwater barriers to protect vessels against rough sea conditions during typhoons. Human alterations in Joss House Bay (JHB), Sok Kwu Wan (SKW) and Chi Ma Wan (CMW) sheltered bays are restricted to small fish mariculture rafts and fisherman villages. On the contrary, Yau Ma Tei (YMT), Kwun Tong (KT) and Aberdeen (AB) typhoon shelters are in highly populated and developed areas in Hong Kong with almost complete shore reclamation. Aberdeen has numerous fishing boats, marinas and shipyards. Yau Ma Tei is one of the container cargo ports in Hong Kong. Kwun Tong is located in an industrial area enclosed by the former airport of Hong Kong and receives contaminated discharges from Kai Tak River. All piers are based on sediment bottoms with depths between 4 and 7 m.