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Journal of Experimental Marine Biology and Ecology 342 (2007) 15–29

Journal of EXPERIMENTAL MARINE BIOLOGY AND ECOLOGY

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Effects of small-scale disturbance on invasion success in marine communities

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Received 1 September 2006; received in revised form 1 October 2006; accepted 9 October 2006

Abstract

Introductions of non-indigenous species have resulted in many ecological problems including the reduction of biodiversity, decline of commercially important species and alteration of ecosystems. The link between disturbance and invasion potential has rarely been studied in the marine environment where dominance hierarchies, dynamics of larval supply, and resource acquisition may differ greatly from terrestrial systems. In this study, hard substrate marine communities in Long Island Sound, USA were used to assess the effect of disturbance on resident species and recent invaders, ascidian growth form (i.e. colonial and solitary growth form), and the dominant species-specific responses within the community. Community age was an additional factor considered through manipulation of 5-wk old assemblages and 1-yr old assemblages. Disturbance treatments, exposing primary substrate, were characterized by frequency (single, biweekly, monthly) and magnitude (20%, 48%, 80%) of disturbance. In communities of different ages, disturbance frequency had a significant positive effect on space occupation of recent invaders and a significant negative effect on resident species. In the 5-wk community, magnitude of disturbance also had a significant effect. Disturbance also had a significant effect on ascidian growth form; colonial species occupied more primary space than controls in response to increased disturbance frequency and magnitude. In contrast, solitary species occupied significantly less space than controls. Species-specific responses were similar regardless of community age. The non-native colonial ascidian *Diplosoma listerianum* responded positively to increased disturbance frequency and magnitude, and occupied more primary space in treatments than in controls. The resident solitary ascidian *Molgula manhattensis* responded negatively to increased disturbance frequency and magnitude, and occupied less primary space in treatments than in controls. Small-scale biological disturbances, by creating space, may facilitate the success of invasive species and colonial organisms in the development of subtidal hard substrate communities.

Keywords: Ascidians; Bioinvasion; Bryozoans; Disturbance; Fouling community; Long Island Sound

1. Introduction

Although species range expansions and contractions are intrinsic ecological processes, there has been an increased rate of range expansion by nonindigenous species primarily due to human activities (Mooney and Drake, 1986; Carlton, 1989; Ruiz et al., 1997). Second to habitat loss, introduced species are thought to be among the most important causes for the decline of

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doi:10.1016/j.jembe.2006.10.011

native species (Everett, 2000; Pimentel et al., 2000). The increased invasion rate has affected terrestrial, aquatic and marine systems promoting the potential for a global homogenization of species diversity (McKinney and Lockwood, 1999).

Coastal waters experience a heightened susceptibility to invasion and represent one of the most invaded systems on the planet as many bays, estuaries and nearshore waters are affected by stressors as a result of urbanization, exploitation of fisheries and shipping (Carlton and Geller, 1993; Carlton, 1989; Cohen and Carlton, 1998; Grosholz, 2002). Within a given region, estuarine invaders result in an increased variety of taxa and an increase in ecosystem impacts. The rate of range expansion for introduced coastal species appears to be more variable than that of terrestrial species and tends to show patterns of large range expansions over short time periods (Grosholz, 1996). This implies that introductions in coastal systems may have greater impacts on native communities than introductions in terrestrial systems.

Range expansions of invasive species may be affected by many factors including disturbance regimes within the invaded habitat. A number of classic studies have established the importance of natural disturbance and its effect on space allocation, recruitment, and subsequent interspecific competition and species composition in marine benthic communities (e.g., Dayton, 1971; Sousa, 1985; Connell and Keough, 1985; Sousa, 2001). Disturbance events typically lead to increased resources for potential colonizers. In hard substrate communities this is primarily in the form of increased available space for settlement and subsequent growth. While there is considerable variation in the frequency and magnitude of natural disturbance, small-scale events (eg., 1–100 cm^2) often occur more frequently than large-scale disturbances (e.g., 100 m^2 to km^2; Connell and Keough, 1985; Sousa, 1985, 2001). Given sufficient variation in recruit densities, disturbances that are large in size are more likely to lead to changes in community assemblage and succession than small-scale disturbances (Petraitis and Latham, 1999). Although it is clear that disturbance severity, with cascading effects on spatial resources and competition, affects settlement and patterns and rates of succession (Underwood, 1998; Airoldi, 1998; Sousa, 2001), most studies have been restricted to examining the effects of complete removal of residents and have not looked at multiple levels of disturbance frequency or magnitude.

The question of how disturbance affects invasibility has been examined through theoretical and correlative terrestrial studies. While theory repeatedly predicts that increased disturbance should lead to increased invader success, results from empirical studies do not always support this theory (Hobbs, 1989; DeFerrari and Naiman, 1994; Stachowicz et al., 1999; Seabloom et al., 2003; Gilbert and Lechowicz, 2005; Klein et al., 2005; Gross et al., 2005). The link between disturbance and invasion potential has rarely been studied in marine systems where dominance hierarchies, dynamics of larval supply, and resource acquisition may differ greatly from terrestrial systems (Sousa, 2001). While there is an abundance of evidence that disturbances can facilitate the invasion of non-native species in terrestrial and aquatic ecosystems (Sousa, 2001), only a few studies have focused on the influence of disturbance in promoting successful invasion in marine communities. After major storm-induced freshwater flow into San Francisco Bay in which native populations were reduced, Meng et al. (1994) and Nichols et al. (1999) found increased invasion rates of fish and non-native bivalves, respectively. In another study, fragmented eelgrass meadows were found to facilitate the growth of a non-indigenous mussel (Reusch and Williams, 1999), implying that disturbances resulting in fragmentation of eelgrass beds would increase the success of the invasive mussel. The majority of these studies focused on the effects of large-scale environmental disturbances and did not investigate the effect of small-scale disturbances on the susceptibility of communities to invasion.

Hard substrate assemblages provide an ideal system to study questions related to invasion dynamics because these communities can be manipulated over a range of different frequencies and magnitudes of disturbance. Highly localized, small-scale disturbances are typically driven by biological (e.g., predation by fish and crabs) processes, while low frequency, high magnitude disturbances are typically driven by physical (e.g., storms) processes (Hall et al., 1994, Sousa, 2001).

The present study focuses on the effect of disturbance on invasion success in shallow water fouling communities in eastern Long Island Sound, USA, an urbanized estuary invaded by a number of species over the past 150 years. In this study, we examined the effects of small-scale disturbance magnitude and frequency on the successful space occupation by members of the fouling assemblage. To determine whether invaders that are relatively new to the system respond to disturbance in a similar manner to resident species, we addressed the effect of disturbance on the resident species and recent invaders. Once settled, fouling organisms fall into two growth forms — colonial and solitary. The two forms often differ in life history characteristics and growth strategy and their capacity to respond to disturbance and occupy open space may also differ. To address these potential differences, we examined the effect of