Journal of Experimental Marine Biology and Ecology 448 (2013) 162–170

Contents lists available at ScienceDirect

Journal of Experimental Marine Biology and Ecology

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

Effects of seaweed canopies and adult barnacles on barnacle recruitment: The interplay of positive and negative influences

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ARTICLE INFO

Article history:
Received 15 February 2013
Received in revised form 30 June 2013
Accepted 1 July 2013
Available online 2 August 2013

Keywords:
Ascophyllum
Barnacle
Intertidal
Seaweed
Semibalanus

ABSTRACT

Barnacles are dominant sessile invertebrates on many rocky shores worldwide. Hence, investigating the factors that affect their recruitment is important. Through field experiments done on the Atlantic coast of Canada, we investigated interspecific and intraspecific relationships affecting intertidal barnacle recruitment. Specifically, we evaluated the effects of seaweed canopies (*Ascophyllum nodosum*) and adult barnacles (*Semibalanus balanoides*) on the density of barnacle recruits at the end of the recruitment season. The effects of three canopy treatments on barnacle recruitment and understory environmental conditions allowed us to identify positive and negative effects of canopies. At mid-intertidal elevations subjected to a moderate wave action, we found that, during high tides, the flexible algal fronds damage wire sensors established on the substrate (whiplash effect) and limit barnacle recruitment. However, at low tide, algal canopies limit water loss and temperature extremes and enhance barnacle recruitment in understory habitats. The net effect of algal canopies on barnacle recruitment, however, was neutral, as the positive and negative influences balanced out. By manipulating the abundance of adult barnacles under the seaweed canopies, we found that adult barnacles enhance barnacle recruitment, likely due to the known attraction that adults exert on larvae seeking settlement and to the absence of post-settlement events that could otherwise have blurred such effects by the adults. The presence of adult barnacles, however, did not protect developing recruits from canopy whiplash effects. By understanding the contrasting influences that intertidal algal canopies have on understory abiotic conditions and barnacle recruitment, our ability to predict net canopy effects depending on the relative degree of physiological (e.g., high vs. low intertidal zone) and physical (e.g., sheltered vs. exposed shores) stresses should increase. This study also suggests that recruitment, considered as an important external factor in environmental models of community organization, can also be affected by components of the community itself, potentially triggering local feedbacks.

1. Introduction

Barnacles are common organisms in rocky intertidal habitats worldwide. They are often the dominant sessile invertebrates because of their high resistance to emersion stress. As filter-feeders, barnacles convert pelagic biomass into benthic biomass, which eventually sustains upper trophic levels in benthic food webs. Hence, their ecological role is often important (Anderson, 1994; Foster, 1987). To understand how barnacle populations persist on the shore, several studies have investigated their recruitment. For intertidal sessile invertebrates with planktonic larvae, recruitment refers to the appearance of new individuals that have developed after larval settlement and have reached an arbitrary size that allows them to be counted (Cole et al., 2011). The transition from settler to recruit takes between a few days and weeks, depending on the species and abiotic conditions (Pineda et al., 2009). For such species, recruitment is an important life-history step that affects population persistence (Bertness et al., 1992; Broitman et al., 2008; Menge, 2000).

Intertidal barnacle recruitment can be affected by non-trophic interspecific interactions. In particular, seaweeds that produce extensive canopies have a variety of positive and negative effects. Tides regularly expose intertidal habitats to aerial conditions, subjecting sessile organisms to abiotic stresses such as desiccation and temperature extremes (Eckersley and Scrosati, 2012; Raffaelli and Hawkins, 1999). Flexible macroalgal canopies lay mostly flat during low tides, limiting water loss and temperature variability in understory habitats. Thus, while seaweed canopies facilitate the performance of many understory species (Bertness et al., 1999; Watt and Scrosati, 2013), it has been suggested that canopies may also enhance barnacle recruitment by improving conditions for developing recruits during low tides (Dayton, 1971). During high tides, intertidal habitats are subjected to water movement caused by waves (Denny and Wethey, 2001). Thus, at high tide, flexible algal fronds hit and scour the substrate repeatedly (Dayton, 1975). Such a whiplash effect is considered to negatively affect barnacle

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0022-0981/$ – see front matter © 2013 Elsevier B.V. All rights reserved.
http://dx.doi.org/10.1016/j.jembe.2013.07.001

recruitment, because developing recruits would be smashed or dislodged by algal fronds (Hancock and Petraitis, 2001; Hawkins, 1983; Jenkins et al., 1999; Leonard, 1999; Lewis, 1964; Menge, 1976).

For those reasons, understanding canopy effects on barnacle recruitment requires an evaluation of the balance between the positive and negative influences. Through a factorial design, a field study applied clearing and caging treatments aiming to disentangle the positive and negative effects of algal canopies on barnacle recruitment, concluding that negative effects prevailed over facilitative effects in the studied system (Leonard, 1999). However, treatment effects on understory water retention, temperature extremes, and abrasion on the substrate were not evaluated. In fact, that has commonly been the case in studies of algal canopy effects on understory organisms (Cervin et al., 2004; Dayton, 1971, 1975; Hancock and Petraitis, 2001; Hawkins, 1983; Ingólfsson, 2008; Jenkins et al., 1999; Kiirikki, 1996; Lewis, 1964; Menge, 1976). Clearly, determining how canopy manipulations affect understory abiotic conditions in addition to barnacle recruitment would establish the environmental basis of canopy effects on recruitment more conclusively. Thus, our first objective was to investigate the positive and negative effects of algal canopies on barnacle recruitment by testing effects on recruitment as well as on understory abiotic conditions. Our hypotheses were that whiplash effects would be related to decreased recruitment and that limitation of water loss and temperature extremes would be related to increased recruitment.

Intertidal barnacle recruitment may also be affected by intraspecific interactions. Cyprid larvae often settle near adult barnacles, which produce chemical cues that cyprids detect by contacting the adults when exploring a substrate for settlement (Gabbott and Larman, 1987; Hadfield and Paul, 2001; Raimondi, 1991). A waterborne cue released by the adults may initially orient cyprids towards the adults (Clare, 2011). Such an attraction is thought to have evolved to indicate to larvae that habitat conditions are suitable for development. Gregarious settlement is also considered to favor future reproductive success, because barnacle fertilization is internal and requires the proximity of mating individuals (Anderson, 1994; Foster, 1987). Whether the positive adult–settler relationship persists to the recruitment stage is unclear, but it is theoretically possible if post-settlement events do not modify the initial effects of the adult cues. Thus, our second objective was to investigate adult barnacle effects on barnacle recruitment, under the hypothesis that the presence of adults would locally enhance recruitment. In canopy-covered intertidal habitats, adult barnacles might further favor barnacle recruitment by protecting developing recruits from the whiplash effect of seaweed canopies, since adults are taller than recruits. Thus, our third objective was to test the hypothesis that the whiplash effect of canopies on barnacle recruitment would decrease when adult barnacles are present. We evaluated our hypotheses through field experiments done in rocky intertidal habitats on the NW Atlantic coast.

2. Materials and methods

2.1. Study system

We did the field work along a 27 km stretch of coastline in Chedabucto Bay, Nova Scotia, Canada, between Halfway Cove (45° 21′ 0.5″ N, 61° 21′ 32.2″ W) and Fox Island (45° 20′ 43.8″ N, 61° 5′ 53.7″ W; Fig. 1A). Rocky intertidal habitats with stable substrate (bedrock) are common on this coast. Maximum water velocity measured using dynamometers (see design in Bell and Denny, 1994) in the autumn of 2012 in intertidal habitats from this coast was 5.3 ± 0.3 m s^{-1} (mean ± SE, n = 15, range = 2.9–7.1 m s^{-1}). Thus, this coast is subjected to moderate levels of wave exposure, since maximum water velocity reaches 12 m s^{-1} on shores directly facing the open ocean in Nova Scotia (Hunt and Scheibling, 2001). The tidal amplitude (vertical extent between the highest and lowest tide marks) is approximately 1.8 m on this coast. Between 0 m (chart datum, or lowest normal tide in Canada) and 1.2 m of elevation, rocky intertidal habitats are covered by dense canopies of the fucoid seaweed *Ascophyllum nodosum* (Linnaeus) Le Jolis (hereafter *Ascophyllum*; Fig. 2). This is the norm for sheltered rocky intertidal habitats on the NW Atlantic coast (Adey and Hayek, 2005; Longtin et al., 2009). Fronds of this macroalga can locally reach 1.6 m in length and 10 years of age. Fronds stay upright at high tide owing to their gas bladders, but they lay on the substrate at low tide because of their high flexibility. On the studied coast, the barnacle *Semibalanus balanoides* (Linnaeus, 1767) is by far the most abundant sessile invertebrate and the only intertidal species of barnacle (Fig. 3). Barnacle recruitment occurs during the spring on this coast (Cole et al., 2011).

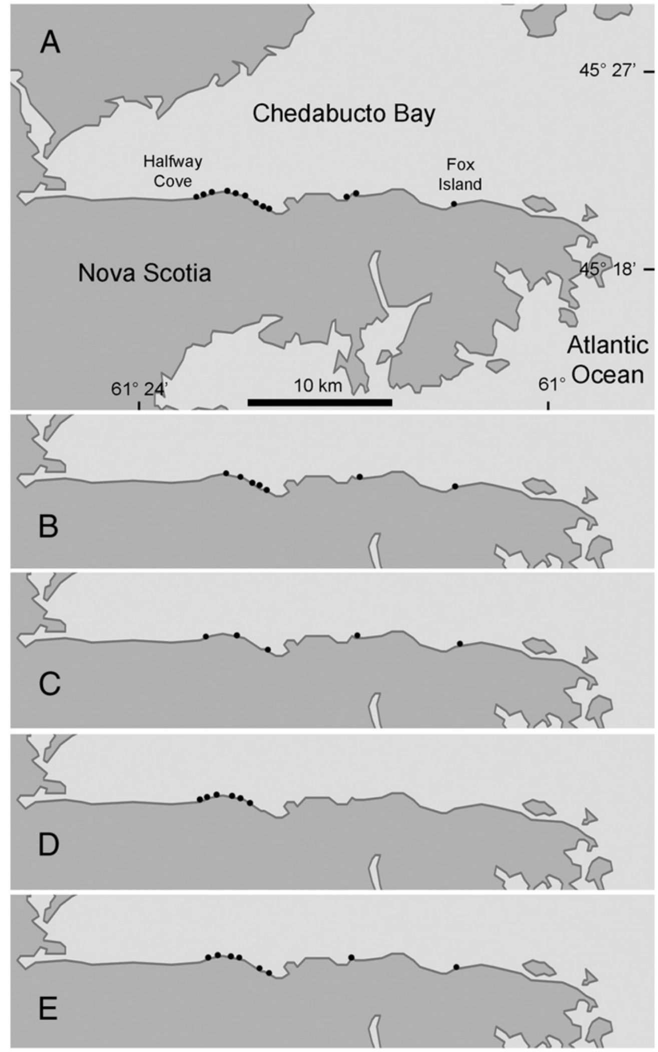

Fig. 1. Map of Chedabucto Bay (Nova Scotia, Canada) indicating the location of the experimental blocks used to evaluate (A) the effects of seaweed canopies and adult barnacles on barnacle recruitment, (B) canopy whiplash effects, (C) canopy effects on understory temperature, (D) canopy effects on substrate moisture, and (E) cage effects on water motion.

2.2. Effects of seaweed canopies and adult barnacles on barnacle recruitment

We did a field experiment based on a randomized complete block design with replicated treatments within blocks (Gotelli and Ellison, 2004). We created all treatments in the field between 3 and 16 April 2012, before barnacle larvae started to settle on the shore, as indicated by periodic observations with a magnifying glass. The experimental units where we measured recruitment (recruit density) were