Journal of Experimental Marine Biology and Ecology 335 (2006) 277–291
Journal of EXPERIMENTAL MARINE BIOLOGY AND ECOLOGY
www.elsevier.com/locate/jembe

Changes in growth and reproduction of green sea urchins, *Strongylocentrotus droebachiensis* (Müller), during repopulation of the shallow subtidal zone after mass mortality

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Received 15 December 2005; received in revised form 26 February 2006; accepted 30 March 2006

Abstract

Following a disease outbreak that caused mass mortality of green sea urchins, *Strongylocentrotus droebachiensis*, along the Atlantic coast of Nova Scotia in September 1999, changes in growth and reproduction were monitored over 3.75 years as surviving individuals migrated from deep water to repopulate the shallow subtidal zone at a wave-exposed site. Urchins were sampled at 4 depth strata: at 24 m on a boulder field where the population was unaffected by the disease, at 12 and 16 m on a steeply sloping bedrock ramp, and at 8–10 m along the lower margin of a kelp bed (*Laminaria digitata*) where urchins formed a grazing front by January 2002. Urchins migrating shoreward from the deep-water refuge responded rapidly to increased algal productivity in the shallows through increased growth and reproduction. Measures of annual increments of skeletal elements (rotules) from urchins across the depth gradient indicated that the fastest growing individuals from the source population formed the grazing front. Urchins in the front reached a larger asymptotic size and produced larger gonads than urchins lower on the ramp. The annual cycle in gonad index showed a pronounced spring spawning period across all depths; a secondary fall spawning was evident at the front and 12 m. The presence of mature, fertilizable ova and short response time to spawning induction in both spring and fall supported the occurrence of two spawning periods.

Keywords: Green sea urchin; *Strongylocentrotus droebachiensis*; Growth; Reproduction; Spawning; Mass mortality

1. Introduction

Many species of marine benthic invertebrates are capable of extensive movement during the adult stage. Dispersal occurs through the accumulation of small-scale movements such as foraging (Scheibling, 1981), and by large-scale migrations associated with seasonal environmental changes or breeding patterns (Pittman and MacAlpine, 2001). Movement at various scales enables animals to locate improved feeding conditions and enhance fitness through increased rates of growth and reproduction. Movement also promotes persistence of populations in heterogeneous environments, and provides a mechanism for recolonization of habitats following mass mortality (Turchin, 1998).

Herbivorous sea urchins are highly mobile and can readily locate patches of high quality food on the seabed (Sloan and Campbell, 1982). Urchins that encounter

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0022-0981/$ - see front matter
doi:10.1016/j.jembe.2006.03.016

energy-rich food resources, such as kelp beds or accumulations of detrital matter, exhibit a rapid response to enhanced nutritional conditions, as evidenced by accelerated rates of gonadal production and growth (Lawrence and Sammarco, 1982). Urchins are known to migrate over large areas while foraging (Propp, 1977). As they encounter stands of macrophytes, they form dense feeding aggregations (or fronts) that migrate across the seabed and denude it of all but grazing-resistant coralline algae (Lawrence, 1975).

The green sea urchin, *Strongylocentrotus droebachiensis* (Müller), commonly occurs on rocky substrates between 0 and 50 m depth throughout its circumpolar range (Scheibling and Hatcher, 2001). Population density generally declines with depth and concomitant decreases in the abundances of kelps and other fleshy seaweeds, which are the urchin's preferred food (Moore and Miller, 1983; Himmelman, 1986; Sivertsen and Hopkins, 1995). On the Atlantic coast of Nova Scotia, however, this trend is periodically reversed when *S. droebachiensis* is eliminated in the shallow subtidal zone by disease. The pathogenic agent, *Paramoeba invadens* (Jones and Scheibling, 1985), is infectious during peak sea temperatures causing mass mortality of urchins at depths down to ~25 m (Scheibling and Stephenson, 1984). With the removal of urchin grazing pressure, fleshy macroalgae rapidly recolonize the shallow zone, leading to the establishment of luxuriant kelp beds (Miller, 1985; Scheibling, 1986). As urchins repopulate these areas through migration from deeper water (Brady and Scheibling, 2005) and recruitment of planktonic larvae (Hart and Scheibling, 1988), they form grazing fronts that once again devour kelps and associated seaweeds, creating coralline algal-dominated barrens in their wake (Scheibling et al., 1999; Lauzon-Guay and Scheibling, in press).

Urchins in deeper water (below 20 m) have a temperature refuge from disease (Scheibling and Stephenson, 1984; Brady and Scheibling, 2005). However, they occupy food-limited environments where little more than the basic nutritional requirements for survival are met. Previous field studies have shown that gonad production of urchins from deep water is consistently low (Wahle and Peckham, 1999), and laboratory studies have shown that urchins limited to a diet of coralline algae (the predominant algal form in deep water) showed delayed maturation, reduced gonad production and negligible growth (Meidel and Scheibling, 1999). In contrast, urchins inhabiting shallow kelp beds, particularly along grazing fronts, show high rates of growth and reproduction (Vadas, 1977; Keats et al., 1984) due to the abundance of high quality food (Meidel and Scheibling, 1998a,b). As the nutritional condition of urchins increases following migration to shallower water, allocation of resources to reproduction and growth are predicted to increase.

In September 1999, a widespread mass mortality eliminated *S. droebachiensis* in the shallow subtidal zone over 100 s of kilometers along the Atlantic coast of Nova Scotia (Miller and Nolan, 2000; Scheibling and Hatcher, 2001). Urchins in deeper, colder water were unaffected (Brady and Scheibling, 2005). Following this catastrophic mortality, we monitored the repopulation of a disease-affected site for over 3 years (Brady and Scheibling, 2005). We selected a site where the rocky bottom sloped steeply and a deep-water population of urchins was relatively close to shore. This 'natural experiment' presented a rare opportunity to investigate changes in growth and reproduction of sea urchins as they migrated shoreward and eventually formed a grazing front along the lower margin of a kelp bed. Our study, which is the first to track these changes immediately following a mortality event, expands our understanding of the resilience of urchin populations to periodic catastrophic disturbance, and has important implications for management of the sea urchin fishery along this coast and elsewhere.

2. Materials and methods

2.1. The study site and sampling design

The study site at Chebucto Head is located on the western headland at the mouth of Halifax Harbour (44°30′ N, 63°31′ W). The study area is a steeply sloping bedrock ramp that extends from a boulder field at 24 m depth (below Chart Datum) to a rock ledge at 8 m. The eastward facing ramp is relatively featureless and spans ~40 m (linear along-bottom distance) with an average slope of 44%. The rocky substratum is completely encrusted with coralline red algae. A persistent kelp bed [*Laminaria digitata* (Huds.) J.V. Lamour],protected from urchin grazing by heavy wave surge, occurred along the ledge at ~10 m depth.

The die-off of *S. droebachiensis* at Chebucto Head occurred in late September 1999, and was associated with unusually warm sea temperatures in the upper 20 m (Brady and Scheibling, 2005). By mid-October, there were no surviving urchins above 20 m; urchins between 20 and 24 m exhibited symptoms of disease, but the population on the boulder field below 24 m appeared healthy. By November, the ramp was covered with a film of filamentous algae, and live urchins were dispersed along the base near the boulder field. By February 2000, urchins had migrated up the ramp to 12 m depth, and a front had formed along the kelp margin at 10 m by January 2002. Over the next 16 months, the front