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Population dynamics of the green-lipped mussel, *Perna canaliculus*, at various spatial and temporal scales in northern New Zealand

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Abstract

Ecological processes that differentiate and maintain intertidal populations of mussels, *Perna canaliculus*, were studied within three sites at Ninety Mile Beach, northern New Zealand. At these three sites (Scott Point, The Bluff and Tonatona Beach), the dynamics of larval availability, primary and secondary settlement, recruitment and mortality rates were investigated at various spatial and temporal scales. (1) Mussel concentrations in seawater were variable with respect to study site and time of year, with highest abundances at the northernmost population (Scott Point) and lowest concentrations at the middle population (The Bluff). In seawater at all three sites, small mussels (<0.25 mm in shell length) were more abundant in August 2000, while larger mussels (>0.5 mm in shell length) were more abundant in March 2001. (2) Primary and secondary settlement patterns were investigated during short-term (daily) and long-term (monthly) settlement experiments, within quadrats that were cleared of all mussels in both the mussel bed and in adjacent algal band habitats. At all sites, primary settlement (<0.5 mm in shell length) was high within the algal band habitat in August 1999, 2000 and 2001. Conversely, secondary settlement (>2.0 mm in shell length) was high within cleared areas in the mussel beds in November–March 1999–2000 and 2000–2001. Abundance of mussels settling on artificial substrates placed in the intertidal did not differ greatly from comparable areas of natural substrates (bare rock or algae within cleared quadrats). (3) Recruitment and mortality rates were recorded during monthly surveys of the adult populations. Within three mussel size classes (<24, 25–74 and >75 mm in shell length), peak recruitment coincided with high mortality in August of the 2 years studied. However, the most dramatic turnover of the population was observed at Scott Point in both years, following a spawning event. In adjacent waters at Scott Point, large accumulations of drift algae covered (up to 100% cover) with juvenile mussels may deplete food supplies usually delivered to intertidal adult mussels, causing their demise. Mats of adult mussels were observed "peeling-off" from the rocky shore at this time of the year, making space available to the new recruits. Where nearshore algal accumulations were moderate to low, only moderate to low mussel turnovers were observed (e.g. Tonatona Beach and The Bluff).

Keywords: Drift algae; Mortality; Mussels; *Perna canaliculus*; Population dynamics; Recruitment; Settlement patterns; Spatial scales; Temporal scales

1. Introduction

Most intertidal invertebrates depend on the successful settlement and recruitment of dispersing larvae to maintain populations. Successful recruitment to the

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adult population may be highly variable in space and time, reflecting the demographic diversity of a population (Hughes, 1990; Doherty and Fowler, 1994; Hunt and Scheibling, 1997; Reusch and Chapman, 1997; Enderlein and Wahl, 2004). Numerous studies have focused on the physical and biological processes that influence settlement patterns of planktonic larvae on morphologically and chemically distinct substrates (Butman, 1987; Schneider and Mann, 1991a,b; Butman and Grassle, 1992; Grassle et al., 1992; Pawlik, 1992; Bourget and Harvey, 1998; Alfaro and Jeffs, 2002; Alfaro et al., 2004). However, many marine invertebrates, such as mussels, may re-settle several times on different substrates during their post-larval and juvenile stages (Armonies, 1992; Buchanan and Babcock, 1997; Hunt and Scheibling, 1998; Alfaro and Jeffs, 2002; Alfaro et al., 2004; Alfaro, 2005). Re-settlement may take place through passive waterborne dispersal, mucous-drifting and crawling behavior (Bayne, 1964; Kennedy, 1984; Lane et al., 1985; Martel, 1993; Buchanan and Babcock, 1997; Alfaro, 2005). Bayne (1964) first recognized the importance of filamentous algae as the primary settlement substrate of larvae (<0.5 mm) for the mussel *Mytilus edulis*, which later move to the adult mussel beds as secondary settlers (1–2 mm) through a bysso-pelagic phase. Juvenile mussels in the primary and secondary settlement phases actively explore and choose settlement substrates by a crawling behavior that involves foot movements and anchoring with mucous threads and filaments (Sigurdsson, 1976; Board, 1983; Kennedy, 1984). Further studies on settlement patterns of mussel larvae and juveniles on filamentous substrates have revealed size-specific selectivity to morphologically distinct algae and hydroid species from subtidal to intertidal areas (King et al., 1990; Hunt and Scheibling, 1996; Buchanan and Babcock, 1997; Alfaro and Jeffs, 2002, 2003; Alfaro et al., 2004). Thus, algal substrates, especially those found near adult mussel beds, may provide an important transition stage for primary mussel settlers to attain a large enough size before transferring to the adult mussel bed. By entering the adult mussel bed as larger juveniles, these mussels may reduce the risks of ingestion by adult conspecifics and increase their ability to compete for space. Indeed, Alfaro (2006) demonstrated that cannibalism on larvae and juveniles constituted a large portion of adult mussel (*Perna canaliculus*) diets, especially around spawning periods.

While the mussel settlement process is dynamic and may involve various settlement substrates and transitions to new substrates, recruitment involves the successful establishment of individuals in the adult mussel bed. Variations in recruitment rates among populations reflect differences in larval and post-larval availability and/or early mortality of post-settlers (Connell, 1985; Hunt and Scheibling, 1997; Jenkins et al., 1997; Helson and Gardner, 2004). The balance between initial settlement on the mussel bed and early mortality is regulated by biological processes, such as larval production, competition and predation, and physical processes, such as water motion, temperature, salinity and desiccation, of a particular geographical area.

Due to the unique oceanographic conditions at Ninety Mile Beach, northern New Zealand, large quantities (>170 tonnes/year) of drift algae with associated mussel juveniles, or spat, accumulate nearshore. The drift algae serve as primary settlement sites for 0.25 mm to 5 mm sized spat and can transport spat along shore for several kilometers before being washed ashore onto the beach (Alfaro et al., 2004). These wash-ups or spatfall events are unique in New Zealand and are harvested to supply about 80% of the national mussel industry seed requirements (Jeffs et al., 2000). Such pulses of floating algae and mussel spat are likely to have a major effect on the structuring of adult mussel populations of the area. The populations themselves also may be regulated by biological and physical factors that affect adult mussels, such as competition, predation, hydrodynamic forces, temperature and salinity. The sum total of these biological and physical factors is likely to be reflected in the growth and mortality rates of mussels within various populations. Therefore, comparisons among mussel populations must take into account a combination of interacting factors that affect mussels at various life-history stages. Hence, this study addresses the spatial and temporal variability in abundance and size-specific settlement patterns, recruitment and mortality rates that affect the population dynamics of the major intertidal mussel populations at Ninety Mile Beach, northern New Zealand. This comprehensive approach allows for the direct evaluation of the relative importance of major structuring forces in the mussel populations of this region.

2. Materials and methods

2.1. Study site

Settlement experiments were conducted at three intertidal sites along Ninety Mile Beach, northern New Zealand (Fig. 1). Rocky intertidal areas at Scott Point, The Bluff and Tonatona Beach support the only intertidal mussel populations along the 90-kilometer stretch of sandy coast (Fig. 1). The coast at Ninety Mile