Journal of Sea Research 85 (2014) 343–348

Contents lists available at ScienceDirect

Journal of Sea Research

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

Spatial and temporal patterns of subtidal and intertidal crabs excursions

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ARTICLE INFO

Article history:
Received 22 November 2012
Received in revised form 19 April 2013
Accepted 27 June 2013
Available online 5 July 2013

Keywords:
Intertidal
Subtidal
Mark-recapture
Crabs
Tidal height and Phase
Prey

ABSTRACT

Highly mobile predators such as fish and crabs are known to migrate from the subtidal zone to forage in the intertidal zone at high-tide. The extent and variation of these habitat linking movements along the vertical shore gradient have not been examined before for several species simultaneously, hence not accounting for species interactions. Here, the foraging excursions of *Carcinus maenas* (L.), *Necora puber* (Linnaeus, 1767) and *Cancer pagurus* (Linnaeus, 1758) were assessed in a one-year mark-recapture study on two replicated rocky shores in southwest U.K. A comparison between the abundance of individuals present on the shore at high-tide with those present in refuges exposed at low-tide indicated considerable intertidal migration by all species, showing strong linkage between subtidal and intertidal habitats. Estimates of population size based on recapture of marked individuals indicated that an average of ~4000 individuals combined for the three crab species, can be present on the shore during one tidal cycle. There was also a high fidelity of individuals and species to particular shore levels. Underlying mechanisms for these spatial patterns such as prey availability and agonistic interactions are discussed. Survival rates were estimated using the Cormack-Jolly-Seber model from multi-recapture analysis and found to be considerably high with a minimum of 30% for all species. Growth rates were found to vary intraspecifically with size and between seasons. Understanding the temporal and spatial variations in predation pressure by crabs on rocky shores is dependent on knowing who, when and how many of these commercially important crab species depend on intertidal foraging. Previous studies have shown that the diet of these species is strongly based on intertidal prey including key species such as limpets; hence intertidal crab migration could be associated with considerable impacts on intertidal assemblages.

1. Introduction

Animal movements can occur on various temporal and spatial scales. Small-scale (metres) migrations associated with circadian and circatidal rhythms are typical of many crab species (Gibson, 2003). For example, intertidal migration has been extensively studied for the common shore crab *Carcinus maenas*, and the majority of studies attribute this behaviour to foraging (e.g. Burrows et al., 1999; Crothers, 1968; Edwards, 1958; Hunter and Naylor, 1993; Mascaró and Seed, 2001; Naylor, 1958, 1962; Reid and Naylor, 1989; Warman and Nailor, 1995). Large-scale movements (kilometres) are also known to be an integral part of the life history of many migrating crabs and these can be related to ontogenic shifts in resource use (e.g. Mosknes, 2002), reproductive events (e.g. Aguilar et al., 2005) and to avoidance of harsh environmental conditions (e.g. Allen, 1966).

In the southwest U.K., *Necora puber*, *Cancer pagurus* and *C. maenas* are abundant crabs (Silva et al., 2010a), and generally considered to be commercially important species in Europe. The first two are primarily considered to be subtidal species and although they regularly feed in the intertidal (Silva et al., 2010a), little is known about how their subtidal–intertidal and within intertidal movement patterns. These subtidal and intertidal crabs have been shown to be key intertidal predators in southwest U.K. (Silva et al., 2008, 2010b). Hence, it is important for our understanding of the importance of rocky shores as a feeding habitat and for the management of these species, to study their population dynamics in the context of habitat linkages. There is currently limited knowledge on: i) how many of each crab species undertake daily intertidal foraging excursions, ii) what is their movement range and at what spatial scales it varies and, iii) which ontogenic stages are associated with these excursions.

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http://dx.doi.org/10.1016/j.seares.2013.06.006

Spatio-temporal patterns of movement, dispersal and habitat use are key information on population dynamics and community ecology (Turchin, 1991), and in the case of important predators that control prey populations (e.g. limpets) such as the crabs studied here (Silva et al., 2008, 2010a,b), can help predicting their impact on prey populations. Population dynamics are strongly related to growth patterns, which are meaningful for many size-dependent ecological processes such as diet. Frequently, small individuals are subject to higher predation mortality and the faster they grow the more rapidly this mortality decreases (Jennings et al., 2001). In crabs, growth rate is strongly influenced by temperature, with larger increments occurring in warmer months (Hartnoll, 1982). Equally, it is paramount to estimate survival rates, in order to understand population dynamics including density-dependent processes such as intra-specific and interspecific competition (Miller and Smith, 2003).

Mark-recapture methods are commonly used to address hypotheses on population dynamics in crustaceans (Hartnoll, 2001). In subtidal habitats, the mark-recapture technique has been applied to large scale (kilometres) migration patterns of lobsters and crayfish (e.g. Bell et al., 2003; Dunnington et al., 2005), but has seldom been used to analyse small scale migration between the subtidal and intertidal habitats (but see Edwards, 1958; Holsman et al., 2006). More importantly, no study has assessed subtidal–intertidal and within intertidal level movements of multiple species simultaneously, when potential interspecific agonistic and synergistic interactions are likely to occur between predators consuming temporally limited intertidal resources, and potentially influencing their intertidal usage pattern.

The present study aims to identify if there is a subtidal–intertidal linkage established by foraging crabs and to examine patterns of spatial and temporal partioning in the use of the intertidal. Two main questions where posed: what is the extent of subtidal–intertidal migration, and what is the fidelity of crabs to specific shore heights for each tidal phase? We accomplished this by examining the extent of movements of *C. maenas*, *N. puber* and *C. pagurus*. The spatial and temporal individual movement patterns and, growth and survival rates were assessed using a long-term (one year) mark-recapture experiment at two shores in southwest U.K. We also investigated differences in growth rate between summer and winter, to better understand temperature constraints. A novel aspect of this study was that several species were studied simultaneously together with information on tidal position, hence allowing an interspecific comparison of distribution patterns and examination of overlapping resource usage between species. For each species, the following specific questions were asked: (1) are individuals present in the intertidal at the low-tide different from those present at high-tide, (2) what is the spatial fidelity of individuals to tidal heights, i.e. are individuals associated with particular shore heights, (3) what are the annual survival and seasonal (winter and summer) growth rates and, (4) what are the population sizes?

2. Methods

2.1. Sampling sites and techniques

Two rocky shores were sampled (Mount Batten — 50°21′N, 4°07′W & Jennycliff — 50°21′N, 4°07′W) in southwest U.K, during 2006–2007. The shores are ~1 km apart but physical separated by an artificial pontoon and natural rock outcrop that extend far into the sublittoral area, hence greatly impeding any crab movement between shores. Two shore levels were defined: upper shore approximately 4 m above Chart Datum (CD), and the lower shore approximately 1 m above CD. On both shores, there was at least a 50 m gap between shore levels which were defined according to the biological zonation pattern. The upper corresponded to the barnacle dominated zone and the lower shore to the red algae zone. Sampling was made at high-tide and low-tide for both shore levels. Sampling at high-tide used standard commercial crab traps (55 cm long × 40 cm wide × 30 cm high, 1 cm mesh size), moulded in heavy duty plastic with two entrances of 8 cm diameter and a bait tube (Coastal Fishing Supplies U.K.). These were fixed to the rock platform via anchoring points. Traps are an efficient method to catch crabs and have previously been shown to be efficient in capturing the species considered in this study (Miller, 1990; Silva et al., 2010a). On each sampling date, three traps were positioned at least 40 m apart within a 1000 m^2 area at each shore level on each shore. This separation was considered sufficient to ensure independence of the areas fished (see Miller, 1990). Traps were baited with ~300 g fresh cut *Trachurus trachurus* L. as this bait had been proven successfully in preliminary trials, and left for a single nocturnal high-tide when crab activity is known to be greatest (Dare and Edwards, 1981; Hunter and Naylor, 1993). In addition to using traps during high-tide, low-tide observations were made during the day to establish the extent to which predators captured at high-tide were intertidal or subtidal populations. Surveys were made by performing 1 h searches amongst boulders/crevices at each shore level on both shores. The study was run over a one year period (September 2006–2007) and both high and low-tide sampling (tagging at low-tide and recapture at low and high-tides) were undertaken for two days each spring tide, approximately every 2–4 weeks, adding up to 24 recapture visits in one year.

2.2. Tagging

A key assumption of mark-recapture studies is that tag retention and visibility are reliable throughout the duration of the study. A particular difficulty in crustacean tagging is the ability to identify individuals for long periods because of loss of external tags through ecdysis. The Visible Implant Elastomer (VIE) consists of a non-toxic biocompatible fluorescent liquid injected into the tissue of the crab with a hypodermic needle where it cures into a pliable solid (Northwest Marine Technology™). It has been shown to be highly efficient for crustaceans such as prawns, crabs and lobsters, and to have an extremely high moult-retention rate (consistently above 90%) for periods of up to 18 months (Linnane and Mercer, 1998). It is also suitable for use on living organisms since it is non-toxic for crabs or if ingested by humans (Northwest Marine Technology™, USA). The elastomer does not alter behaviour, survival or potential for recapture and, there is a minimal mortality resulting from tagging procedure (Frisch and Hobbs, 2006).

For both trap and low tide searches and at time of first capture, *C. maenas*, *N. puber* and *C. pagurus* individuals were tagged and released during low-tide as close as possible to the collection area. Hence, trapped crabs were marked and released closely to each corresponding trap and hand-collected crabs were released along the search transect. All trap and hand collected search crabs were tagged in the same day of capture. In total, marking time lasted 30 days. Only individuals larger than 10 mm carapace width were tagged since tag retention and survival rates are potentially lower in smaller individuals (Linnane and Mercer, 1998). Tags were implanted ventrally by inserting the Visible Implant Elastomer (Northwest Marine Technology, Washington, USA) with a hypodermic syringe intramuscularly, from the edge of the sternite to the basis segment of the pereopods. Care was taken to end the flow of elastomer before the needle was drawn back to prevent the elastomer from trailing out of the injection hole and curing exteriorly. The volume of injected material was adjusted according to the size of the crab. Tags were clearly readable with the naked eye, but visibility was enhanced by illumination with ultraviolet light. Crabs were handled ~1–3 min depending on how many colours had to be injected in the legs. A combination of 5 elastomer colours and tag locations (i.e., left or right side in any of the pereopods) allowed individual markings for hundreds of individuals per shore. High-tide individuals were distinguished from those at low-tide individuals with an individual code, as were different tidal levels at the time of first capture. Tagging occurred every day that tidal conditions allowed accessing the lower shore lasting in total ~3 months. The longest period between tagging and recapture was approximately 11 months, and the shortest 2 weeks. At each marking event, the