Journal of Experimental Marine Biology and Ecology 478 (2016) 34–44

Contents lists available at ScienceDirect

Journal of Experimental Marine Biology and Ecology

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

Human impacts on biogenic habitats: Effects of experimental trampling on *Sabellaria alveolata* (Linnaeus, 1767) reefs

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ARTICLE INFO

Article history:
Received 8 July 2015
Received in revised form 28 January 2016
Accepted 2 February 2016
Available online 15 February 2016

Keywords:
Biodiversity
Biogenic reefs
Sabellaria alveolata
Anthropogenic disturbance
Trampling
Rocky intertidal

ABSTRACT

Human trampling is one of the main anthropogenic threats to coastal communities, especially in rocky intertidal habitats. The adverse effects of human trampling have recently received increasing attention from conservation biologists, especially when concerning species playing key functional roles. These include biogenic reefs providing extremely productive and diverse habitats due to their structural heterogeneity and three-dimensional complexity. The degradation of such habitats could not only adversely affect the whole coastal biota, but it could also have strong socio-economic implications. This study investigated the potential impact of human trampling on biogenic reefs built by the honeycomb worm *Sabellaria alveolata* in north-western Portugal. Three increasing intensities of human trampling were manipulated to test for their direct effects on *S. alveolata* bio-constructions and indirect effects on associated benthic infauna. Experimental trampling, even at low intensity, negatively affected reefs by reducing the percentage cover of intact *S. alveolata* concretions over a period of two months, but it did not alter the structure of whole assemblages compared to the unmanipulated condition. Idiosyncratic responses were shown by the most conspicuous taxa, ranging from no significant effects on *S. alveolata* and Amphipoda to spatially and temporally variable effects on the Syllidae and Sabellidae polychaetes, the Mytilidae bivalves and the Rissoidae gastropods. When present, however, differences were always in the direction of larger abundances under the highest intensity of trampling than in the less disturbed treatments and the unmanipulated control. This study provides one of the first experimental evidence linking the intensity of human trampling to the physical damage of *S. alveolata* reefs. Direct implications of present findings as tools to promote a sustainable use of these systems at a local scale and to stimulate protection and management initiatives at other locations are discussed.

1. Introduction

Human activities are causing major impacts on natural environments both at local and global scales, producing changes in the number, identity and relative density of species in assemblages (Vitousek et al., 1997). It has been estimated that humans have severely modified or exploited to complete loss more than 70% of natural habitats in the habitable portion of the planet, causing the extinction of 5–20% of species in many groups of organisms (Hannah et al., 1994). This is particularly true for coastal areas, where human impacts are often concentrated (Halpern et al., 2008).

Human trampling is one of the main anthropogenic disturbances adversely affecting coastal communities from rocky intertidal habitats (e.g. Araújo et al., 2009; Casu et al., 2006a). Trampling is directly associated with commercial and recreational activities that are common on rocky shores, such as the simple reconnaissance of the area, hunting for baits and collecting living and dead shells (Addessi, 1994; Brosnan and Crumrine, 1994; Casu et al., 2006b; Keough and Quinn, 1998). After being relatively overlooked for a long time, the effects of human trampling have recently received increasing interest from conservation biologists. It was widely reported that trampling might affect the biodiversity of rocky shores by modifying patterns of distribution, abundance and diversity of populations and assemblages at local scale (Keough and Quinn, 1998; Sousa, 1984). Structural damage of the habitat, mortality or dislodgement of sessile organisms, escape of vagile fauna or lowering of algal holdfast are among the documented direct effects of trampling (Casu et al., 2006a). Indirectly, trampling can make intertidal assemblages more vulnerable to other biotic and/or abiotic disturbances (Brosnan and Crumrine, 1994; Brown and Taylor, 1999). Previous studies have mainly focused on the effects of trampling on the algal coverage

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http://dx.doi.org/10.1016/j.jembe.2016.02.001
0022-0981/

and the abundance of sessile fauna (Brosnan and Crumrine, 1994; Keough and Quinn, 1998; Povey and Keough, 1991; Santos et al., 2015). For example, trampling can be associated with a reduced cover of canopy-forming macroalgae (Brosnan and Crumrine, 1994; Milazzo et al., 2002; Povey and Keough, 1991) and to lower abundances of their hosted herbivores (Casu et al., 2006c). On the Portuguese coasts, it was reported that high experimental intensities of trampling could drastically reduce the abundance of the brown alga *Ascophyllum nodosum*, of the co-occurring fucoid *Fucus vesiculosus* and of several under-storey species (Araújo et al., 2009). Most previous studies, however, targeted individual algal species, largely overlooking the mobile fauna associated with trampled vegetation (Brown and Taylor, 1999; Keough and Quinn, 1998) as well as the effects of trampling on the structure of whole assemblages (but see Casu et al., 2006a, 2006c).

The honeycomb worm *Sabellaria alveolata* (L.) is the most widely distributed species belonging to the Sabellariidae family, commonly found along the European Atlantic coast, from West Scotland to the south of Morocco (Anadon, 1981; Cunningham et al., 1984; Dubois et al., 2002). Its reefs usually develop in the intertidal or in the shallow subtidal habitat, normally growing parallel to the coastline and to the direction of main tidal currents (Dubois et al., 2006). Under suitable environmental conditions (i.e. moderate hydrodynamics, not too low salinity, availability of hard substrates), they can spread over hundreds of hectares (Holt et al., 1998). In general, they can develop as encrusting "ball-shaped" colonies adhering to rocks, or, more rarely, as large "platform" banks, with each structural type characterized by a specific infaunal assemblage (Desroy et al., 2011; Dubois et al., 2002, 2006). The ecological importance of these biogenic reefs is recognised worldwide. In fact, they represent local hotspots of biodiversity, by adding micro--scale topographic complexity to the environment and so providing shelters for a large number of marine species. However, they constitute a highly dynamic habitat subject to numerous natural perturbations (e.g. cold winters or storms) and are increasingly threatened by direct and indirect anthropogenic disturbances (Dubois et al., 2002, 2006, 2007). Besides the engineer species itself, associated species could also be negatively affected by the degradation of the reef. Previous research on *S. alveolata* reefs have mainly focused on fitness traits, namely reproduction, fecundity, larval stages and development strategies (Wilson, 1968, 1970), while little information is available regarding the responses of such systems to trampling. By means of a small-scale experiment, however, Cunningham et al. (1984) indicated that even low intensities of trampling could damage *S. alveolata* colonies by removing a fair chunk of them and by creating large holes between the tubes. In the Bay of Mont-Saint-Michel, which hosts the largest European *Sabellaria* formations, Dubois et al. (2002, 2003, 2006) have emphasized that anthropogenic threats, such as oyster farming and fishing, are able to cause significant damages to the structure of mature reefs and a reduction in density of new recruits. Nevertheless, no manipulative studies suitable to unambiguously examine effects of human trampling on *S. alveolata* reefs were ever conducted. The present study aimed at contributing to fill this gap by experimentally investigating direct and indirect effects of human trampling on both *S. alveolata* reefs and associated infaunal assemblage. A manipulative multi-factorial experiment was performed involving unmanipulated controls and three increasing intensities of pulse human trampling in order to test hypotheses on the vulnerability of *Sabellaria* reefs occurring at multiple locations in north Portugal. In detail, the goals of the present study were to assess the direct impact (i.e. physical damage of the biogenic habitat) on the reef structure and the indirect impact on the associated organisms. Specifically, the direct impact was measured in terms of variation in the percentage cover of intact *S. alveolata*, whereas the indirect impact was estimated as changes in the structure of whole assemblages and in the abundance and richness of benthic infaunal taxa. Two independent experimental trials, based on the same protocol, were performed at each of two study sites to test for the consistency of responses over a temporal scale of one month and a spatial scale of tens of kilometres. Under the logistic impossibility to test for a priori hypotheses on differences due to specific drivers, such temporal and spatial replication was included to capture the scale of variation of a number of uncontrolled factors and processes that could play a role in the responses of the *S. alveolata* reef system to trampling disturbance. This could include, for instance, local hydrodynamics (e.g. Raimondi, 1990) affecting pelagic larval transport, which is a key process affecting dispersal, establishment, persistence and recovery of populations of benthic invertebrates, in general and *S. alveolata* in particular (Dubois et al., 2007; Cowen and Sponaugle, 2009; Ayata et al., 2011). The broader goal of the present study was to provide a scientifically and experimentally based support to management and conservation actions of the Portuguese, and potentially analogous other, *S. alveolata* reefs as both physical traits of the coastline and habitat-formers, with the ultimate objective of guaranteeing a sustainable use of such ecologically important, but vulnerable, systems.

2. Materials and methods

2.1. Study system

The study was carried out on two sites located about 100 km apart along the NW Portugal (NE Atlantic) coast: Belinho and Praia da Aguda (Fig. 1). Each site was characterized by a rocky shore hundreds of metres long, interspersed within an almost continuous sandy beach. The two sites were comparable in terms of a number of environmental and physical traits (i.e. orientation of the coastline, exposure to prevailing north-western winds and waves, typically granitic horizontal or gently sloping substratum, tidal range) and use by humans (i.e. same accessibility and lack of obvious differences in terms of year-round frequentation for commercial and recreational activities, including harvesting of intertidal organisms and fishing). At both sites, *S. alveolata* formed well-developed tri-dimensional and complex reefs.

2.2. Sampling design and collection of data

The study was performed between July 2012 and October 2012 in the low intertidal habitat (between 0 m and 0.5 m above Chart Datum). At each study site, eight areas (2.5 m × 2.5 m, some metres apart) were randomly selected in July 2012 (first experimental trial: ET1) and marked at corners with screws and plastic tags for subsequent relocation. Two areas chosen at random out of the total eight were left unmanipulated as control (C) and two were assigned to each of three levels of intensity of experimental trampling: low (LI), medium (MI) and high (HI). Trampling was performed at the same time by two persons (average weight 70 kg) wearing gumboots and walking through the whole of the area one, two or three times (LI, MI and HI, respectively) in a row. A second independent experimental trial (ET2) was set-up in August 2012, using the same protocol with a new set of independent areas at each site. For each experimental trial, response variables were sampled in control and manipulated area one and two months after the experimental trampling event, each time choosing new replicate plots, in order to investigate the short-term recovery ability of the community towards the undisturbed (unmanipulated) condition. Although the full recovery of heavily damaged reefs could take a much longer time, which is logistically impossible to take into account, such observation period was considered appropriate to capture the reported ability of *S. alveolata* to repair reef areas of limited damage within weeks through its tube-building activity (Cunningham et al., 1984; Vorberg, 2000). A schematic of the experimental design is provided in Appendix A.

The cover of intact *S. alveolata* bio-constructions was visually estimated in each of two plots (20 × 20 cm, tens of centimetres apart) randomly placed in each area, by superimposing a frame divided into 25 sub-quadrates. A score ranging from 0 to 4 was given to the cover in each sub-quadrate, the 25 estimates were added up and the final value was expressed as percentage (Dethier et al., 1993).