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Detached macroalgae: Its importance to inshore sandy beach fauna

Kyla K. Orr [a,*], Thomas A. Wilding [a], Lena Horstmeyer [b], Simon Weigl [b], Johanna J. Heymans [a]

[a] Scottish Association for Marine Science, Scottish Marine Institute, Oban, Argyll PA371QA, UK
[b] Universität Konstanz, 78457 Konstanz, Germany

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A B S T R A C T

Kelp forests shed a large proportion of their biomass through storm-mediated defoliation, senescence of kelp blades, and constant erosion of particulate organic matter from the kelp fronds. Much of this detached macroalgae drifts in the water column and is deposited on intertidal zones of beaches. Detached macroalgae may provide inshore sandy beach fauna with refuge and food subsidies in an exposed and bare environment, with limited *in situ* primary production. We evaluated the relationship between detached macroalgae and the density of inshore fauna, where 'inshore' was the body of water extending from low water seawards for approximately 50 m. Inshore fauna were sampled using a push-net (1 mm mesh) on 11 beaches, and using a beam-trawl (4 mm mesh) on a subset of 8 beaches. On each beach, the density of detached macroalgae in the water column was quantified, together with a suite of physico-chemical beach characteristics. Push-net samples principally comprised omnivorous and detritivorous crustaceans such as gammarid amphipods, mysids and valviferan isopods, which have limited swimming abilities and reside inshore year-round. Beam-trawl fauna were mainly carnivorous decapods and fish, which undergo seasonal inshore-offshore migrations to utilize sandy beaches as nursery habitats. Linear models predicted increases of 11% (95% CI: 3.5–19%) and 2.4% (95% CI: 0.7–4.2%) in the density of push-net and beam-trawl fauna, respectively, with a 1 ℓ100 m^{-3} increase in detached macroalgae. This suggests that detached macroalgae is more important in the provision of food and shelter to small, weak-swimming detritivores/omnivores than to larger and more mobile predators. The densities of large predators were mostly explained by physical beach characteristics, which overshadowed the role of macroalgae. Maximum abundances of decapods and fish were found on wide, flat beaches with low wave heights. Large accumulations of macroalgae may inhibit the foraging efficiencies of predatory fauna such as decapods and fish, and restrict their abundance.

1. Introduction

Sandy beaches dominate much of the world's coastline (Schlacher et al., 2007) and support diverse faunal assemblages and provide valuable ecosystem services, such as the recycling of nutrients (Cockcroft et al., 1988; Soares et al., 1997), and sustaining commercial and recreational fisheries by serving as fish nursery grounds (Defeo, 2003; McLachlan and Brown, 2006; McLachlan et al., 2013). However, beaches provide limited shelter to macrofauna (>1 mm) because of their bare substrate, strong water currents and fluctuating physical conditions (Robertson and Lenanton, 1984; McLachlan and Brown, 2006). In addition, many beaches are characterized by low *in situ* primary production and limited food availability (McLachlan and Brown, 2006). Therefore, beach fauna often rely on the import of food in the form of detached macroalgae (Colombini and Chelazzi, 2003; Dugan et al., 2003; Crawley et al., 2009), which also provides shelter (Lenanton et al., 1982; Colombini and Chelazzi, 2003).

Kelp forests occur along temperate coastlines and are among the most productive ecosystems on earth (Kain, 1979; Steneck et al., 2002; Graham et al., 2007). A large percentage (>25%) of the subtidal kelp canopy is detached during storms, when rough seas physically break whole kelp (including the stipe) from the rocks (Walker and Richardson, 1955; Filbee-Dexter and Scheibling, 2012). Kelp fronds also senesce as part of the kelp's life cycle (Walker and Richardson, 1955; Rodriguez et al., 2013). In addition, kelp detritus (organic matter originating from kelp) is generated through the constant erosion of the kelp blades (Krumhansl and Scheibling, 2011, Krumhansl and Scheibling, 2012). This detached macroalgae

* Corresponding author.
E-mail addresses: kylaorr@gmail.com (K.K. Orr), tom.wilding@sams.ac.uk (T. A. Wilding), lena.horstmeyer@uni-konstanz.de (L. Horstmeyer), simon-weigl@gmx.net (S. Weigl), sheila.heymans@sams.ac.uk (J.J. Heymans).

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and fragments of detritus is washed onto beaches (e.g. see Colombini and Chelazzi, 2003; for a review), floats in the open ocean (Vetter, 1998; Filbee-Dexter and Scheibling, 2012; Rothäusler et al., 2012), or sinks to the seabed (Bedford and Moore, 1984; Wilding, 2006).

Detached macroalgae attracts fauna through the provision of food and/or habitat (Rothäusler et al., 2012), and may enhance secondary production (Field et al., 1977; Duggins et al., 1989; Dugan et al., 2003). The positive association between detached macroalgae and fauna has been documented in a variety of habitats, such as the intertidal zone of beaches (Colombini and Chelazzi, 2003), beach surf-zones (Robertson and Lenanton, 1984; Lavery et al., 1999; Crawley et al., 2006; Crawley et al., 2009), subtidal environments (Bedford and Moore, 1984; Duggins et al., 1989; Wilding, 2006), deep sea canyons (Vetter, 1998), and the open ocean (Thiel and Gutow, 2005; Rothäusler et al., 2012). By contrast, large accumulations of decaying macroalgae affects biogeochemical processes in the marine environment (Coupland et al., 2007) and ultimately leads to oxygen depletion and the build-up of sulphides, which are toxic to all fauna except a few specialist species (McGwynne et al., 1988; Neira and Rackemann, 1996; Malm et al., 2004; Wilding, 2006). Dense mats of detached macroalgae may also disrupting the burrowing and feeding activities of invertebrates (Soares et al., 1996), and restricting the foraging efficiency of fish (Florin et al., 2009).

In many ecosystems, the positive effect of increased food availability, e.g. macroalgae subsidies, cascades up through the food web from primary consumers to higher trophic level fauna (Polis and Strong, 1996; Polis et al., 1997), i.e. a bottom-up forcing. However, in sandy beach ecosystems, environmental conditions rather than food availability are considered to be the main mechanisms that control biological communities (McLachlan, 1990; McLachlan and Brown, 2006). This is especially true of ocean-exposed beaches where fauna are subjected to high physical energy, and biological communities are constantly perturbed by the changing environment. On less exposed, flatter beaches, the strength of physical factors (e.g. wave height, sediment transport) are reduced and food availability begins to play a more prominent role in structuring biological communities (Defeo and McLachlan, 2005). In addition, the paradigm that environmental control is the main mechanism controlling sandy beach fauna on exposed beaches is mainly applicable to large macrofauna (Schlacher and Hartwig, 2013). Resent research has found that increased nutrient concentrations and food availability can have a positive effect on the abundance of relatively small invertebrates, such as benthic meiofauna (nematodes and ostracods), even on very ocean-exposed beaches (Schlacher and Hartwig, 2013).

The ecological role of detached macroalgae that is deposited in the intertidal zone has been extensively studied, for examples see review by Colombini and Chelazzi (2003). Comparatively little research has focused on the importance of detached macroalgae to inshore fauna, which occur in the water column immediately adjacent to the beach (between low water and 50 m offshore). The inshore zone of beaches is an important marine habitat because it serves as a nursery area for fish (Gibson and Yoshiyama, 1999; McLachlan and Brown, 2006), and is utilized by invertebrates, such as decapods, amphipods, isopods and mysids (Beyst et al., 2001a, b; Beyst et al., 2002; Dominguez-Granda et al., 2004). Inshore invertebrates are a key food resource for fish (Crawley et al., 2006), and facilitate the recycling of nutrients (Cockcroft et al., 1988).

Inshore studies to date have found that on selected beaches, detached macroalgae floating in the water column attracts grazing invertebrates (Crawley et al., 2009), which are then preyed on by larger predators such as fish (Robertson and Lenanton, 1984). Fish visiting inshore waters may also hide amongst the detached macroalgae to seek shelter from larger predators (Robertson and Lenanton, 1984). However, the abundance of inshore fish on exposed beaches is mainly controlled by physical factors such as wave height, and this environmental control contrasts with the positive effects of detached macroalgae (Clark et al., 1996). There have been no attempts to model the complex relationship between the abundance of small (1–4 mm) inshore invertebrates and detached macroalgae on beaches with different physical conditions. In addition, there have been no attempts to determine how the mobility and diet of inshore fauna may influence their utilization of detached macroalgae as a source of food and shelter.

The main objective of this study was to assess how the quantity of detached macroalgae explains the distribution of: 1) small, weak-swimming primary consumers (1–4 mm), and; 2) larger, more motile, predatory fauna (>4 mm), utilizing the inshore zone of beaches. An additional aim of the study was to evaluate the role of detached macroalgae *versus* physical beach characteristics in structuring inshore beach communities. We hypothesize that detached macroalgae will have a positive affect on the density of inshore fauna, but that physical factors will have an overarching affect on relatively more exposed beaches, especially for larger, predatory fauna. A field-based observational approach was taken in which a number of beaches with different physical characteristics and quantities of detached macroalgae were sampled.

2. Material and methods

2.1. Study area

The study area comprised 11 beaches situated on the west coast of the Uists islands, Scotland (Fig. 1). Many of the beaches on the Uists are characterized by large inputs of detached macroalgae (principally kelp, *Laminaria* sp.) as a result of the storm-mediated defoliation of kelp, especially during winter (November–January)(SSRA, 1947; Walker and Richardson, 1955). Some of this detached kelp remains suspended in the inshore and nearshore waters, where it decays and fragments to fine particles.

Across the study area, the tides ranged between 3.8 m on spring tides to 2.9 m on neap tides (Ritchie, 1967). Mean sea surface temperatures range from 7 °C (February) to 13 °C (August) (Norton and Powell, 1979). The beaches studied present a gradient of morphodynamic types, from wide, flat beaches with small sand grains to short, steeper beaches with coarse grain sizes. A more detailed physical characterization is given in the results. All the beaches are of the 'intermediate' dissipative type, with small waves (<1 m) and would be classified as 'sheltered' in a global context (McLachlan and Brown, 2006). The beaches are low-energy due to the protection offered by nearshore rocky reefs that run parallel to the coast (Norton and Powell, 1979). Kelp beds populating these reefs attenuate wave energy (Chapman, 1948; Mollison, 1983), and as a result there is little wave action inshore except during large storms (Wolf and Woolf, 2005). Most beaches lack a distinct surf-zone.

2.2. Sampling design for inshore fauna

Samples were collected during daylight hours between 13 and 19th April 2011, 2 h either side of low water. The fauna of 11 beaches were sampled using a hand-held push-net, and a subset of 8 beaches were sampled for fauna using a beam-trawl (Gibson et al., 2002). The locations of beaches that were sampled with each gear type are shown in Fig. 1. Large waves, due to a storm, prevented us from using the beam-trawl on three beaches (BW, BOR and PB, Fig. 1). The push-net was used to obtain samples of small macrofauna (1–4 mm) living in the water column above the