Journal of Experimental Marine Biology and Ecology 390 (2010) 106–117

Contents lists available at ScienceDirect

Journal of Experimental Marine Biology and Ecology

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

# Invertebrate dispersal and habitat heterogeneity: Expression of biological traits in a seagrass landscape

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ARTICLE INFO

*Article history:*
Received 1 October 2009
Received in revised form 6 May 2010
Accepted 14 May 2010

*Keywords:*
Biological traits
Dispersal
Patch size
Physical disturbance
Post-settlement
Recruitment
Seagrass landscape

ABSTRACT

Seagrass meadows harbour diverse faunal assemblages, but the relative importance of landscapes attributes, settlement processes and biological traits of individual species for recruitment patterns is poorly understood. To quantify the influence of habitat heterogeneity on larval, juvenile and adult post-larval dispersal, invertebrates (>125 µm) were collected in benthic settlement traps at five occasions (June–August) in three habitats; continuous seagrass, seagrass patches and bare sand. The study was carried out by SCUBA diving in a subtidal (2.5 m depth) seagrass landscape dominated by *Zostera marina* L. in the Baltic Sea. Traps collected totally >30 taxa, with non-significant effects of habitat on species richness and total abundance. Total number of invertebrates exhibited strong temporal variability, probably driven by wind-induced bedload and water column transport. Surprisingly, traps located in small (<12 $m^2$) patches contained on average almost twice as many individuals as traps located in the continuous vegetation. Dominating taxa such as nematodes, copepods, and oligochaetes were found in similar densities across the landscape. In contrast, location within the landscape had strong effects on bivalve settlement and redistribution patterns, resulting in significantly lower densities in continuous vegetation compared to patches and bare sand. A biological trait analysis indicated that semi-mobile taxa with annual protracted direct development, and short-distance dispersal are probably of higher importance for the community assembly process in this environment than long-distance larval dispersal. Results suggest that seagrass landscapes are highly dynamic environments, characterized by time and species-specific effects of landscape attributes on animal dispersal and recruitment. A conceptual model illustrating interactions between settling larvae and landscape heterogeneity is presented.



## 1. Introduction

Organism–environment relationships are usually studied at the fine-scale in relatively homogenous environments, preventing predictions of patterns and processes operating over broad spatial scales in heterogeneous landscapes. To consider broad-scale spatial habitat patterns is important and distinguishes the seascape approach from traditional marine ecological studies. Consequently, seascape ecology has developed as a valuable tool to encompass the complex heterogeneity that influences species–environment relationships in shallow water benthic ecosystems (Boström et al., 2006; Hinchey et al., 2008; Zajac, 2008). On shallow soft bottoms, scale, variability and spatial patterns have been acknowledged (Bergström et al., 2002; Hewitt et al., 2008), and broad-scale processes recognised in larval recruitment (Todd, 1998). However, studies extending the understanding of these processes beyond single-species populations, to whole assemblages and communities are rare (Menge and Sutherland, 1987; Kinlan and Gaines, 2003).

On soft substrates, dispersal patterns of marine invertebrates are known to be highly variable in space and time (Commito and Tita, 2002; Munroe and McKinley, 2007, Bowen and Hunt, 2009; Valanko et al., 2010). The variability in density of larvae, newly settled and redistributing individuals is caused by complex interactions between hydrodynamics, habitat structure, habitat configuration, predation and species-specific traits (Armonies, 1994; Hunt and Scheibling, 1997; Bologna and Heck, 2000; Commito and Tita, 2002). Soft sediment benthic systems are in this perspective impeded by difficulties in both logistic and practical sampling problems as well as quantification of settlement compared to hard substrate systems, but methods to tackle these issues are emerging (e.g. Hewitt et al., 2007; Valanko et al., 2010).

Settlement, i.e. change in larval activity to a benthic life stage, on soft sediments differs from hard substrata in that the attachment to the substrate is not permanent (Commito and Tita, 2002), and ongoing redistribution is a common feature, especially in tidal environments (Bowen and Hunt, 2009). The term recruitment generally refers to settled individuals that survive an arbitrary time-period to adulthood

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doi:10.1016/j.jembe.2010.05.008

and contribute to the assemblage (Connell, 1985). In this context, life-history and functional traits such as reproductive type, feeding habits and larval type have been identified as important factors influencing dispersal, settlement and community development (Tamaki, 1987; Armonies, 1994; Commito and Tita, 2002; Bremner et al., 2003a, b).

Seagrass meadows sustain important ecological services in coastal waters but show increasing loss rates due to human activities (Waycott et al., 2009). Due to human impact, and also due to natural processes such as physical disturbance and grazing, continuous meadows are fragmented into heterogeneous landscape-mosaics consisting of smaller, isolated patches (Boström et al., 2006). How such continuous changes in habitat structure influence invertebrate dispersal and community assembly is poorly understood. In particular, the relative contribution of habitat characteristics *vs.* species traits (Bremner et al., 2003a, b) for the structure of benthic communities has not been contrasted with recruitment studies.

Both plant and landscape attributes influence settlement patterns. Thus, structurally complex plant assemblages may trap organisms more efficiently than structurally simple leaf canopies (Hovel and Fonseca, 2005; Boström and Bonsdorff, 2000). In contrast, according to the "settle and stay"-hypothesis (Bell and Westoby, 1986), settling larvae are distributed patchily, and do not discriminate among seagrass patches of differing complexity, suggesting that the physical location of the patch in relation to the larval source pool is critical, and more important than complexity itself (Sogard, 1989). Some studies further suggest that due to increased perimeter:area (P:A) ratios in small vegetation patches, the probability of encounter rates of passively dispersing fauna should be higher in patchy landscapes (Bologna and Heck, 2000).

The effects of habitat complexity on flow dynamics have been experimentally demonstrated in flumes (Butman et al., 1988), and responses of single species to seagrass landscape structure (Bologna and Heck, 2000) and other biogenic structures (Eggleston et al., 1999; Commito et al., 2005) have been studied extensively. However, there is a scarcity of community level studies focusing on how seagrass landscape attributes influence dispersal and diversity of the whole macrofaunal assemblage. In particular, it is unclear how habitat heterogeneity interacts with temporally variable dispersal and recruitment patterns of infauna.

To quantify the influence of habitat heterogeneity on larval, juvenile and adult post-larval dispersal, we established permanent settlement traps in three parts of a high-energy seagrass landscape; on bare sand, in small isolated seagrass patches and in continuous vegetation, and sampled the traps at five occasions during the summer season. Based on previous studies on physical (Gambi et al., 1990) and biological, i.e. settlement (Orth, 1992; Bologna and Heck, 2000) processes in seagrass ecosystems, and unstructured soft-sediment environments (Valanko et al., 2010), we hypothesized that accumulation of individuals would be greatest in patches and lowest in bare sand, while the meadow should exhibit intermediate densities. While species traits such as feeding mode and mobility have been acknowledged as an important driver of local scale succession dynamics (Zajac et al., 1998), these issues have not been specifically addressed within an experimental framework in heterogeneous seascapes, but see Hewitt et al. (2008) for a descriptive approach. Due to the obvious physical differences between these habitats in seagrass–sand mosaics, we further hypothesized that the invertebrate assemblages in these habitats would be characterized by highly different biological traits in terms of e.g. mobility, reproduction and feeding habit.

The following specific questions were posed:

(1) To what extent are larval and post-larval abundance, diversity and dispersal patterns influenced by seagrass landscape attributes?
(2) What biological traits characterize the faunal assemblages and are traits expressed differently across the landscape?

## 2. Material and methods

### 2.1. Study area and site characteristics

The study site is located at the Hanko Peninsula at the entrance of the Gulf of Finland, in the northern Baltic Sea (Fig. 1). This area is characterized by extensive (10–20 ha) seagrass meadows dominated by *Zostera marina* interspersed with *Potamogeton pectinatus* (Boström et al., 2002). The study was conducted in a subtidal (2–3 m depth) seagrass landscape (Ryssholmen: 59°60′N, 23°05′E) exposed to southerly winds (90–180°), which prevail during the summer months (June–August). Data on daily wind speed and direction during the study period was obtained from a nearby (<10 km, Russarö) weather station operated by the Finnish Meteorological Institute. The studied seagrass landscape consists of a ~7 ha *Zostera* meadow characterized by elongated bare sand areas in the interior parts, and more continuous vegetation towards the edges, while isolated seagrass patches are found in the more exposed areas south of the meadow edge (Fig. 1). The patches are highly variable in terms of size (5–200 $m^2$) and shape, and form a mosaic landscape consisting of both circular and elongated seagrass patches (perimeter:area ratios 0.5–2.7).

### 2.2. Invertebrate traps and field sampling

To investigate potential spatial and temporal differences in larval and post-larval abundance, diversity and dispersal patterns across the seagrass landscape, we established clusters of three permanent traps in three distinct microhabitats in the seagrass landscape: in bare sand (hereafter "Sand"), in small isolated patches (hereafter "Patch"), and in the continuous meadow (hereafter "Meadow"). This design was replicated ($n = 2$) spatially (Fig. 1), and the traps clustered in each habitat were treated as subsamples and averaged in the statistical analysis (see below). To avoid confounding effects of varying depths, the bare sand traps were located 20 m from the patches towards the open sea. As it was impossible to locate patches of exactly the same size and shape with similar degree of isolation (i.e. minimum of 3 m from the nearest neighbouring patch), traps were established in two different sized patches, namely 4 and 11 $m^2$, but with similar perimeter to area ratios, 0.62 and 0.56, respectively. These patch sizes represent the smallest at the study site. The patches were located in the outermost zone of the patchy area about 60 m from the edge of the continuous meadow (Fig. 1). As the most interior parts of the meadow were deeper and contained bare sand areas with occasionally dense accumulations of drifting algal mats, and as the goal with the design was not to compare the intensity of edge effects in different sized patches, traps in the meadow were positioned in continuous vegetation at least 10 m from the southern meadow edge, and considered to represent core area of continuous vegetation (Bologna and Heck, 2000), while the other vegetation traps were placed in the centre of the isolated patches 1–1.5 m from the patch edge.

A trap was constructed of a pvc tube (diameter 10 cm, length 50 cm) equipped with a 350 ml removable glass jar (aspect ratio of 2.2:1). The opening of the jar was kept at the same level as the upper end of the tube by means of a bolt below the jar. To avoid trapping and clogging of drift algae, but allow trapping of invertebrates, traps were covered with a 10 mm mesh. This was a trade-off, as the mesh probably reduced trap efficiency. To ensure survival of organisms, the jar contained 1 dl of sieved (<500 µm) azoic sand. The tubes containing the traps were pushed into the sediment to a depth of about 20 cm, leaving the opening of the trap at the same height (30 cm) as the upper parts of the leaf canopy. Traps in bare sand were positioned at the same height as the vegetation traps. Protruding traps generally capture less benthic invertebrates compared to bottom traps (Smith and Brumsickle, 1989; Valanko et al., 2010). However, due to the high exposure, mobile sandy sediment and long deployment times, bedload traps flush with the sediment surface