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# Spatial patterns of littoral zooplankton assemblages along a salinity gradient in a brackish sea: A functional diversity perspective

Laura K. Helenius [a, b, *], Elina Leskinen [a], Hannu Lehtonen [a], Leena Nurminen [a]

[a] Department of Environmental Sciences, University of Helsinki, P.O. Box 65, 00014 Helsinki, Finland
[b] Tvärminne Zoological Station, University of Helsinki, J. A. Palménin tie 260, 10900 Hanko, Finland

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ABSTRACT

The distribution patterns and diversity of littoral zooplankton are both key baseline information for understanding the functioning of coastal ecosystems, and for identifying the mechanisms by which the impacts of recently increased eutrophication are transferred through littoral food webs. In this study, zooplankton community structure and diversity along a shallow coastal area of the northern Baltic Sea were determined in terms of horizontal environmental gradients. Spatial heterogeneity of the zooplankton community was examined along the gradient. Altogether 31 sites in shallow sandy bays on the coast of southwest Finland were sampled in the summer periods of 2009 and 2010 for zooplankton and environmental variables (surface water temperature, salinity, turbidity, wave exposure, macrophyte coverage, chlorophyll *a* and nutrients). Zooplankton diversity was measured as both taxonomic as well as functional diversity, using trait-based classification of planktonic crustaceans. Salinity, and to a lesser extent turbidity and temperature, were found to be the main predictors of the spatial patterns and functional diversity of the zooplankton community. Occurrence of cyclopoid copepods, as well as abundances of the calanoid copepod genus *Acartia* and the rotifer genus *Keratella* were found to be key factors in differentiating sites along the gradient. As far as we know, this is the first extensive study of functional diversity in Baltic Sea coastal zooplankton communities.



## 1. Introduction

Species tolerance to environmental conditions generally determines distribution limits, and within these limits, species abundances peak under optimal conditions. Large-scale biotic distribution patterns, on a scale of kilometers, are believed to result primarily from the responses of organisms to their physical environment, which acts as a physiological sieve and plays a vital role in the structuring of a community (Remmert, 1983). Biotic interactions, such as competition and predation, then refine species distribution patterns within the overall structure set up by abiotic factors (Sanders, 1968; Menge and Olson, 1990). In effect, it is thought that biotic interactions are more important as structuring mechanisms in habitats with low disturbance and more balanced abiotic conditions (Sousa, 1979; Menge and Sutherland, 1987).

In terms of abiotic variables, salinity, wave exposure and temperature shape the assemblages of organisms in marine and brackish coastal areas (Magill and Sayer, 2002; Bonsdorff et al., 2003; Boström et al., 2006). However, it has been suggested that salinity is not a fundamental determinant, but rather a descriptor, of species distribution in paralic ecosystems, and that biological communities are in fact organized according to distance from or connectivity to the open sea (Guélorget and Perthuisot, 1983). This concept of species distribution according to 'confinement' has been explored in salt marshes, lagoons, gulfs and coastal seas (e.g. Guélorget et al., 1983, 1990; Badosa et al., 2006; Snickars et al., 2009).

In aquatic environments characterized by steep horizontal gradients, the distribution and dynamics of communities are generally considered to be controlled by the interplay of abiotic physicochemical factors, river flow and mixing, and biological characteristics, creating spatially and temporally heterogeneous conditions (Li et al., 2000; Froneman, 2001, 2004). Such horizontal gradients of salinity, nutrients and plankton are evident in estuaries, marshes and coastal areas of brackish seas (Telesh, 2004; Veiga et al., 2006; Muylaert et al., 2009). This high environmental variability traditionally translates to low overall biodiversity, but high abundances

* Corresponding author. Department of Environmental Sciences, University of Helsinki, P.O. Box 65, 00014 Helsinki, Finland.
*E-mail address:* laura.helenius@alumni.helsinki.fi (L.K. Helenius).

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of adapted organisms capable of tolerating the variable conditions (Laprise and Dodson, 1994; McLusky and Elliott, 2004, 2007).

Shallow and sheltered coastal zones are an important source of refuge for zooplanktivorous fish, which are essential links coupling littoral and pelagic food webs (Rajasilta et al., 1999). Coasts are also nursery areas for fish with larvae that migrate to shallow depths to benefit from the warm surface water temperature and large zooplankton reserves (Urho and Hildén, 1990). The availability of zooplankton to match the timing of hatching fish larvae is crucial (Cushing, 1990), since zooplankton generally make up the bulk of the diet of larval and juvenile fish (e.g. Applegate and Mullan, 1967; Wong and Ward, 1972; Mehner and Thiel, 1999; Voss et al., 2003; Kallasvuo et al., 2010). Not only the quantity but also the quality (i.e. species composition and size) of zooplankton determines growth and recruitment success of juvenile fish (e.g. van der Meeren et al., 2008). Moreover, grazing zooplankton can heavily control coastal phytoplankton growth and protozoa, and again, community composition determines relative grazing pressure and subsequent effects (Sautour et al., 2000; Sutton et al., 2001; Calbet, 2001). Hence an understanding of zooplankton diversity is crucial when examining coastal food web processes.

Biodiversity may play an important role in controlling ecological processes related to the sustainability and productivity of ecosystems (Hooper et al., 2012; Reich et al., 2012). Zooplankton species diversity in estuarine environments varies spatially along gradients of abiotic and biotic parameters, and can be rather high below a 'critical' salinity level, even with substantial variability in the surrounding environment (Telesh, 2004). What ultimately determines spatial distributions of zooplankton along gradients is the way different species traits or combinations of traits are favored in different environmental conditions (Barton et al., 2013). Therefore, it may be the species functions and the diversity of functional traits, rather than taxonomic identity or species richness, that are relevant when examining ecosystem processes (e.g. Hooper and Vitousek, 1997). Consequently, there has been a recent call to begin examining zooplankton assemblages from a functional, rather than taxonomic, perspective and trait-based approaches are becoming increasingly important in understanding patterns in zooplankton diversity and distribution (Barnett et al., 2007; Barton et al., 2013; Litchman et al., 2013).

Despite the significance of zooplankton as a trophic link in coastal food webs, relatively little is known about the composition and diversity of littoral zooplankton communities of shallow brackish coasts. Large-scale monitoring of coastal plankton is generally conducted in areas with vertical depths of over 20 m due to restrictions in sampling methods. For example, many of the existing studies characterizing zooplankton distribution and ecology in Baltic Sea archipelagos have been conducted in deeper coastal water or further pelagic areas where the structure of zooplankton communities is fundamentally shaped by salinity, and euryhaline species of both freshwater and marine origin exist (e.g. Viitasalo, 1994; Uitto et al., 1997; Koski et al., 1999; Diaz-Gil et al., 2014). The communities inhabiting the 1–5 m depths of the immediate shore areas, however, have been predominantly ignored. Only recently, Scheinin and Mattila (2010) examined the structure and successional dynamics of zooplankton in shallow bays and related them to habitat trophic state; however, the spatial salinity gradient, which is a characteristic of brackish coasts, was not included.

This study provides a unique view of zooplankton assemblage structure and diversity along a shallow coastal area of the Baltic Sea in terms of horizontal environmental gradients. The aim of this study was to survey littoral archipelago habitats and provide a description of the spatial heterogeneity in the summer component of the zooplankton community structure over a subtle salinity gradient, including the protozoan ciliates and other microzooplankton elements, which are often overlooked. Our goal was to determine which locally variable environmental factors are the most important predictors of the spatial patterns and diversity of the zooplankton community, the extent to which spatial patterns differ interannually, and whether a traditional brackish sea archipelago zonation classification applies to littoral zooplankton communities. We investigated how functional diversity, based on traits related to feeding, changed from more saline sites with generally high wave exposure in the outer archipelago to the less exposed, nearly freshwater sites in the inner archipelago. We expected to find specific taxa that are characteristic to these areas in the summer community, and relate their occurrence directly to measured environmental variables, with interannual differences in species composition. We hypothesized that the diversity of feeding traits of crustacean zooplankton would vary along the salinity gradient according to phytoplankton availability. This baseline study will contribute to assessing the impacts of eutrophication and temperature rise on plankton communities in brackish coastal areas and similar ecosystems.

## 2. Methods

### 2.1. Study area and sampling

The Gulf of Finland is a eutrophic, highly seasonal sub-estuary of the Baltic Sea. Sampling took place at the northern side of the mouth of the Gulf at 31 shallow coastal bays along a 40 km salinity and exposure gradient in the fragmented Tvärminne Archipelago in Hanko, Finland. The sampling area stretched from the outer archipelago to immediately outside the semi-enclosed fjord-like Pojo Bay in the north, and the salinity gradient ranged from 6 to 2.55 from the outer archipelago to the mainland zone, respectively (Fig. 1). The Pojo Bay is separated from the outer archipelago by a shallow sill of 7 m, and the renewal of deep water in the bay is largely dependent on the periodic movement of saline archipelagic water over the sill (Niemi, 1978). There is a high inflow of freshwater from the Mustionjoki River at the north end of the bay. Primary production in the archipelago and the open sea areas is mainly limited by the availability of nitrogen (Kivi et al., 1993), and in the Pojo Bay area by that of phosphorus (Lignell et al., 1992). Similar to other shores of the northern Baltic Proper, the coast is divided into five zones based on hydrographical, morphological and biological features: a Pojo Bay zone, a mainland zone, inner and outer archipelago zones and an open-sea zone (Halme, 1944; Niemi, 1973; Munsterhjelm, 2005), representing an estuarine salinity surface water gradient of 2–7 on the Practical Salinity Scale. According to these traditional zonation classes of the Tvärminne Archipelago, the sampling sites belonged to either the outer archipelago zone (hereafter referred to as OZ, sites 1–18), the inner archipelago zone (IZ, sites 19–25) or the mainland zone (MZ, sites 26–31).

Each site was sampled in June/July 2009 and in August in 2010 during the high zooplankton abundance peaks. The emphasis on sampling was to obtain detailed species data on a relatively large regional scale, to be able to compare sites in terms of spatial differences in species composition. Sampling was conducted close to the shoreline at a depth of 0.8–1.2 m, with the exception of site 15, a sandy beach that had a maximum depth of 0.3 m in the littoral zone. Sites were chosen to represent shallow beaches with a fine, sandy bottom substrate and nonexistent to low macrophyte coverage when possible (of the genera *Chara*, *Potamogeton*, *Myriophyllum*, *Cheratophyllum* and *Fucus*). Zooplankton samples were collected with two 1 m horizontal hauls using a modified plankton net with a buoy, with a mesh size of 25 μm and mouth diameter of