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Original Research Article

Effect of spatial scale on the network properties of estuarine food webs

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ABSTRACT

Determining the spatial scale is a crucial stage in any ecological study. However, knowledge on the effect of spatial scale on food web network properties is still lacking in published literature. In this work, the effect of spatial scale on the network properties was determined for the Tagus estuary ecosystem. The food web of the Tagus estuary was assembled at three spatial scales, in terms of grain (resolution) and extent. In terms of grain, the three scales defined were: small grain (30 sites), medium grain (15 sites) and large grain (6 sites). In terms of extent, the three scales defined were: extended estuary (30 sites), strictly estuarine (20 sites), nursery area (6 sites). The lists of species for each site were merged and used to construct one major food web containing all species observed, at each of the spatial scales under analysis. It was concluded that the spatial extent of the sampling highly influenced food web networks properties, more than grain, and should thus be carefully chosen when conducting food web studies in estuaries, as well as in other ecosystems that exhibit strong environmental gradients. Studies that aim to characterize estuarine food webs should encompass the full extent of the salinity gradient.

1. Introduction

The role of spatial scale has long been acknowledged as of utmost importance when planning sampling operations (Turner et al., 1989; Wiens, 1989; Rahbek, 2005). This is particularly important in ecological studies (Wiens, 1989; Levin, 1992), as biological communities exhibit various patterns of spatial occupation that should be taken into account for an effective description of the community composition.

The spatial scale of ecological data encompasses both grain and extent. Grain refers to the resolution of the data, while extent refers to the overall size of the study area. Parameters that are important at one scale often are not important at another scale, moreover information is often lost at larger grains of resolution (Henderson-Sellers et al., 1985; Meentemeyer and Box, 1987).

Predators are often more sensitive to habitat extent than prey species (Holt and Hoopes, 2005; Ryall and Fahrig, 2006), because predators typically need larger areas to maintain viable populations. This means that increasing the sampling extent increases the probability of sampling top predators. Prey species, especially sessile animals in aquatic habitats, often present an aggregated spatial pattern, concentrating where environmental conditions are more beneficial for settlement and/or survival (Snelgrove, 1994; Armonies and Reise, 2003). This is particularly common in heterogeneous habitats that present different substrates offering variable conditions in terms of structure and food resources (Armonies and Reise, 2003; Vinagre et al., 2006). This way, a large grain sampling scale may not reveal the heterogeneity of prey abundance.

One of the problems that have arisen when comparing food web networks is the arbitrariness in the choice of spatial scale (Pahl-Wostl, 1993). The study of food web networks constitutes a holistic approach to the description of ecological communities. It does not focus on the details of biotic interactions; instead it concentrates on general properties of the community as a whole, investigating the topological properties of the network. Such properties have the potential to be used as macro-descriptors for the comparison of communities and ecosystems. However, defining the appropriate scale in ecological studies presents considerable difficulties given that all food webs are spatially open-ended and the in-depth knowledge of the biological communities needed to define sampling scale may not be available. The location and amount of sampling points within the study area is also not always comparable among studies. However, the determination of spatial scale is considered crucial given that it will influence the structure of the resultant web. Few detailed food web studies have determined spatial variation in food web structure (Schoenly and Cohen, 1991) and the effect of sampling scale on the food web

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network properties remains poorly studied (e.g. Warren, 1989; Jordán and Osváth, 2009).

Some of the most spatially diverse ecosystems on Earth are estuaries. Because they are located where freshwater meets marine water, these ecosystems are highly heterogeneous in terms of salinity, temperature, depth and substrate, variables that are crucial for the distribution of organisms (McLusky, 1981; Winemiller, 1990; Winemiller and Leslie, 1992; McLusky and Elliott, 2004, 2007). They provide nursery habitats, spawning grounds, refuge from predators and migratory routes for many species (McLusky, 1981; Able, 2005; Elliott and Hemingway, 2002).

The present work analysed a highly resolved estuarine food web, the Tagus estuary food web (Portugal, NE Atlantic, 38°N, 8°W, Fig. 1). This estuary is one of the largest of Western Europe and several works reported its importance as a nursery area for several fish (Cabral et al., 2007; Vinagre et al., 2010). The aim of this work is to investigate the impact of different scales of sampling on the perceived network structure of this estuarine food web.

2. Methods

2.1. The Tagus estuary food web

The Tagus estuary (Fig. 1) is a partially mixed estuary with an area of 325 km^2 and a tidal range of circa 4 m. About 40% of its area is composed of intertidal mudflats fringed by extensive areas of salt marshes (Cabral and Costa, 1999). Mean depth is less than 10 m and its bottom is composed of a heterogeneous assortment of substrates. The prevalent sediment is muddy sand in the upper and middle estuary and sand in the lower estuary and adjacent coastal area (Cabral and Costa, 1999). Mean river flow is 400 $m^3 s^{-1}$, though it is highly variable both seasonally and inter-annually (data obtained from the Portuguese Water Institute—INAG). Salinity in the estuary varies from 0‰, 50 km upstream from the mouth, to 35‰ at the mouth of the estuary (Cabral et al., 2001). Water temperature ranges from 8 °C to 28 °C (Cabral et al., 2001).

Sampling surveys were conducted during two years (2001–2002), on a bi-monthly basis, at 30 sites. Site was defined by the area sampled by a 2-m wide otter-trawl travelling a mean distance of 1400 m. At each site, 3 samples of sediment were collected with a VanVeen grab for the identification of macrobenthic species.

Humans were included in the food webs of the Tagus estuary as top predators of commercial species of fish, crustaceans, cephalopods, bivalves and polychaeta (as bait). Many of the food webs published to date do not include humans however, in the case of the Tagus estuary, humans are a very important predator because this has been an important fishing ground for thousands of years (Baeta et al., 2005). It must be pointed out, however, that the predator-prey relation between humans and their estuarine prey is generally quite different from that of other species. Humans were not originally top-predators in these systems, they became top predators through their use of accessory technology that helps the capture of prey that would otherwise be able to escape.

Sources of published information were used to complete the food web: Sousa-Dias and Melo (2008) for the macroalgae, Marques et al. (2006) for the zooplankton, Moreira (1997, 1999) for the birds and Carvalho-Varela et al. (1985) and Durieux et al. (2007) for the fish parasites. The complex food web structural networks for each site and references for prey-predator links have been previously published (Vinagre and Costa, 2014).

The food web of the Tagus estuary was assembled at three spatial scales, in terms of grain and extent. In terms of grain, the three scales defined were: small grain (30 sites), medium grain (15 sites) and large grain (6 sites) (Fig. 2). In terms of extent, the three scales defined were: extended estuary (30 sites), strictly estuarine (20 sites), nursery area (6 sites) (Fig. 1). The grain used for the various extent scales was always the small grain (Fig. 2). The lists of species for each site were merged and used to construct one major food web containing all species observed, at each of the spatial scales under analysis.

Most food web structural networks found in literature were built following the same approach used in the present study. Other authors also merged species lists from all sampling points coming

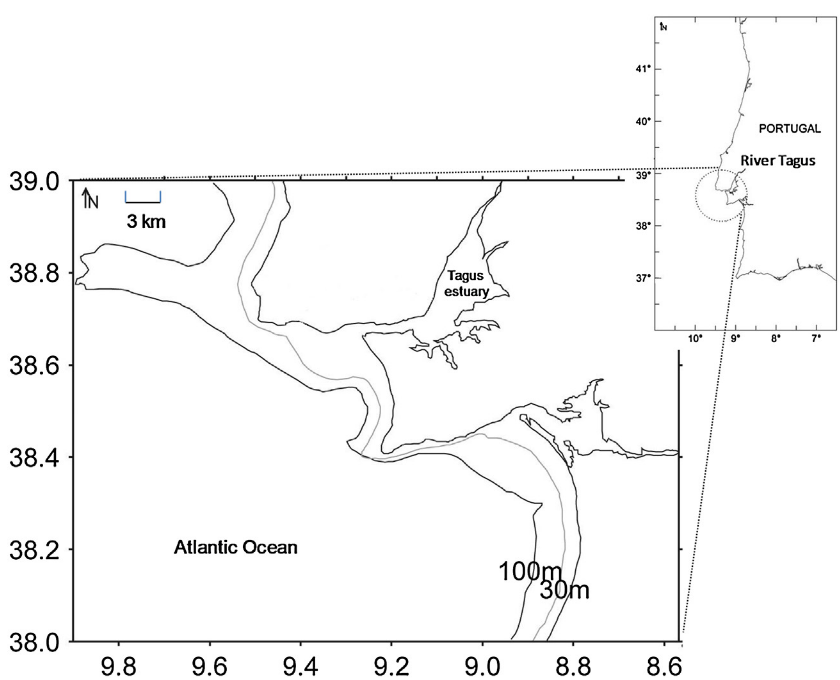

Fig 1. Location of the Tagus estuary, where food web network properties were investigated.