

Estuarine-coastal gradient in food web network structure and properties

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ABSTRACT: Longitudinal changes in the structure and properties of food webs are known to occur in river systems from mountains to lowland areas. However, it is still unknown how food web structure and properties change along the estuarine-coastal gradient. Highly resolved estuarine food webs were assembled for 30 sites in the Tagus estuary and adjacent coastal waters to investigate changes in food web structure and properties along 4 sections: upper estuary, middle estuary, channel and coast. This work confirmed the highly variable nature of estuarine systems, not only in terms of physicochemical and biological communities, but also in food web structure and network properties. The upper estuary stood out for having the highest variability for many food web properties. Overall, more significant differences were detected within this estuarine-coastal gradient than previously reported for river systems, and over a much smaller spatial scale.

KEY WORDS: Transition ecosystems · Tagus estuary · Niche model · Network analysis · Topology · Structural complexity

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INTRODUCTION

By definition, estuaries are located where freshwater meets marine water. Within these ecosystems there is significant habitat heterogeneity in terms of salinity, temperature, depth and substrate; variables that are crucial for the distribution of organisms (McLusky 1981, McLusky & Elliott 2004, 2007). Gradual alterations in physicochemical and biotic variables, such as community composition and photosynthetic sources, are characteristic of estuarine systems (Vannote et al. 1980, Minshall et al. 1983, Muylaert et al. 2000). Despite the daily variations in abiotic variables that make them stressful environments, estuaries provide nursery habitats, spawning grounds, refuge from predators and migratory routes for many species (McLusky 1981, Elliott & Hemingway 2002, Able 2005).

The relationship between environmental factors and the distribution of organisms within estuaries has been the focus of much attention, especially from fish

ecologists aiming to understand the compositional patterns of fish assemblages (e.g. Winemiller & Leslie 1992, Elliott & Dewailly 1995, Ley et al. 1999, Martino & Able 2003, Able 2005). It is believed that large-scale (km) patterns in the structure of estuarine fish assemblages are a result of species' responses to environmental gradients, whereas biotic interactions such as predation, competition or predator avoidance define species distribution patterns at smaller scales (<1 km) (e.g. Menge & Olson 1990, Elliott & Dewailly 1995, Allen & Baltz 1997, Martino & Able 2003, Vinagre et al. 2006, 2009).

Estuarine food webs generally rely on a high level of primary production (e.g. from salt marshes, mangroves, seagrasses, etc.), which is associated with a detritus food chain that often supports complex trophic webs (Simenstad & Wissmar 1985, Deegan & Garritt 1997, Vinagre et al. 2008a, 2011). A considerable amount of research has been conducted on estuarine food web dynamics (Michener & Schnell 1994, Peterson 1999, Hadwen & Arthington 2007, Carlier et

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al. 2008, Choy et al. 2008), as well as on the influence of river input into estuarine and coastal food webs and fisheries (Deegan et al. 1986, Nixon 1997, Sklar & Browder 1998, Loneragan & Bunn 1999, Darnaude et al. 2004, Vinagre et al. 2011, 2012a).

Historically, the study of food webs has been based on 2 different basic approaches. The energetic view, proposed by Lindeman (1942), depicting food webs as networks of pathways of energy flow; and a different approach, initiated by May (1973) and developed by Pimm (1982) and others, focusing on the dynamic constraints that arise from species interactions. This second approach led to many comparative topological studies on the structure of food webs (e.g. Briand & Cohen 1984, Hall & Raffaelli 1991). A considerable amount of recent work on food web structure has focused on food web network theory—a field of research that falls at the intersection of food webs and complex networks (e.g. Williams & Martinez 2000, Dunne et al. 2002, 2004, Williams & Martinez 2004). In these studies, species are represented by vertices (nodes), and feeding links are represented by edges (links) between vertices. As with any other network, the structure of these food web networks can be quantified, analyzed and modelled. This approach has allowed the comparison of food web topology among habitats and other types of networks, as well as the search for universal topological characteristics and research into what network characteristics promote food web stability (e.g. Solé & Montoya 2001, Montoya et al. 2006, Bascompte 2009).

Food web network theory has been applied to the study of longitudinal patterns in food web structure and properties along river systems, and has revealed that fish species richness, network connectance and the proportion of herbivores and cannibals consistently change from mountain to lowlands (Romanuk et al. 2006). Estuaries are a particularly distinctive part of the river system, as contact with sea water and tidal action make gradients in abiotic and biotic variables more pronounced here than in any other part of the river system (McLusky 1981). However, information is still lacking regarding the mechanics of variation in food web network structure and properties in the estuarine system.

To determine how the network structure and properties of food webs change along an estuarine-coastal gradient, a highly resolved estuarine food web was assembled for 30 sites in the Tagus estuary and adjacent coastal waters (Portugal, NE Atlantic, 38°N, 8°W; Fig. 1). This estuary is one of the largest in Western Europe, and several studies have documented its importance as a nursery area for various fish species (Costa & Bruxelles 1989, Cabral et al. 2007, Vinagre et al. 2010).

MATERIALS & METHODS

The Tagus estuary food web

The Tagus estuary (Fig. 1), with an area of 325 km², is a partially mixed estuary with a tidal range of ap-

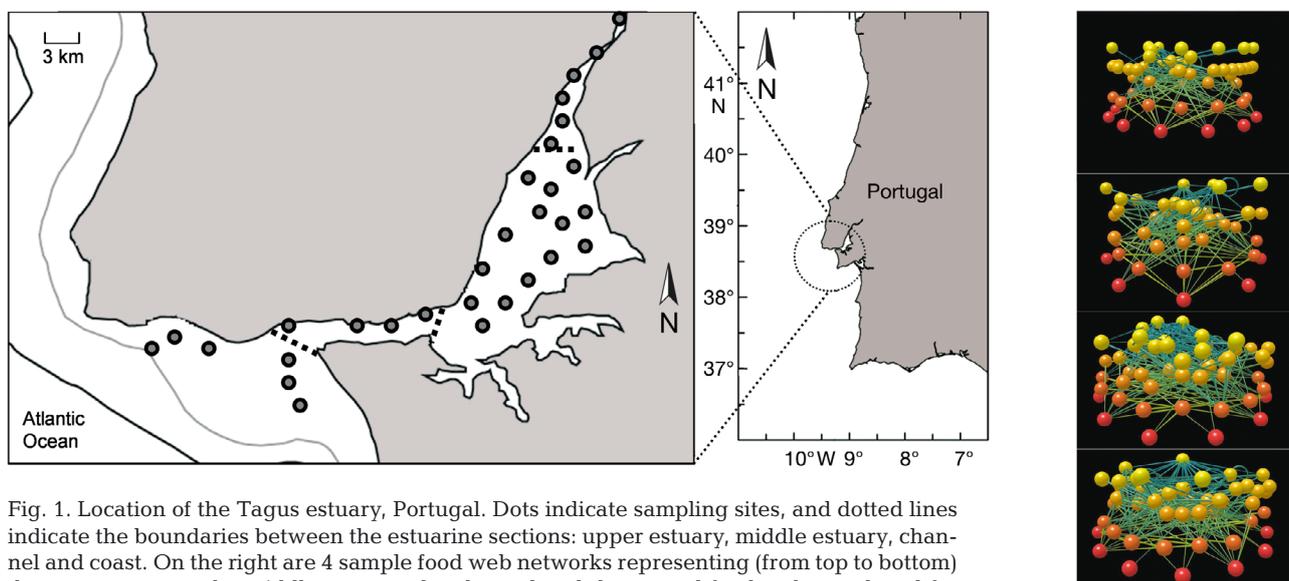


Fig. 1. Location of the Tagus estuary, Portugal. Dots indicate sampling sites, and dotted lines indicate the boundaries between the estuarine sections: upper estuary, middle estuary, channel and coast. On the right are 4 sample food web networks representing (from top to bottom) the upper estuary, the middle estuary, the channel and the coastal food webs produced for this investigation

proximately 4 m. Mean depth is less than 10 m, and about 40% of the estuarine area is composed of intertidal mudflats fringed by extensive areas of salt marshes (Cabral & Costa 1999). Although its bottom is composed of a heterogeneous assortment of substrates, the sediment most prevalent in the upper and middle estuary is muddy sand, while sand is common in the low estuary and adjoining coastal area (Cabral & Costa 1999). Mean flow of the Tagus river is $400 \text{ m}^3 \text{ s}^{-1}$, though it is highly variable both seasonally and inter-annually (data obtained from the Portuguese Water Institute — INAG). Salinity in the estuary varies from zero, 50 km upstream from the mouth, to 35 at the mouth of the estuary (Cabral & Costa 1999). Water temperature ranges from 8 to 28°C , and mean residence time is 25 d (Cabral & Costa 2001).

Sampling surveys were conducted over a 2 yr period (2001 and 2002), every 2 mo. The food web network of the Tagus estuary was assembled for 30 sites (Fig. 1), each defined by the area sampled with a 2 m wide otter-trawl travelling a mean distance of 1400 m. The mesh size used was 18 mm, with 10 mm mesh size at the cod-end. Otter-trawls capture mostly nektonic species (including fish, crustaceans and mollusks) that occur in the water column or near the bottom. At each site, 3 samples of sediment were collected with a VanVeen grab for the identification of macrobenthic species. All 30 sites were sampled during each sampling session. These data have been previously described by Prista et al. (2003), Vinagre et al. (2006), Costa et al. (2007) and Gutiérrez-Estrada et al. (2008), and are part of the Centro de Oceanografia database on the Tagus estuary. Species accumulation curves have been published by Neves et al. (2008) for a subset of these data.

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). Sources of published information used to complete the food web include Sousa-Dias & Melo (2008) for the macroalgae, Marques et al. (2006) for the zooplankton, Moreira (1997, 1999) for the birds, and Carvalho-Varela et al. (1981) and Durieux et al. (2007) for the fish parasites. The method employed to assign feeding links between species was through published works on species' diets; a list of the references used, as well as a list of the trophic species used to assemble the food network, is provided in Tables S1

& S2 in the Supplement at www.int-res.com/articles/suppl/m503p011_supp.pdf.

The food web networks studied were trophic species versions. Trophic species are groups of taxa whose members share the same set of predators and prey (Briand & Cohen 1984). The use of trophic species is a convention in structural food-web studies which can reduce methodological biases of uneven resolution among food webs (Briand & Cohen 1984, Williams & Martinez 2000). The food webs assembled are binary networks describing who eats whom. We contended that 2 species that share all their resources and all consumers are trophically similar, and thus were aggregated in the same node.

For each food web, 11 common properties of estuarine trophic species food webs were calculated (Table 1). The most basic of these (S) was the number of trophic species in the food web. In addition, two standard measures of food-web trophic interaction richness were included: links per species (L/S), which equals the mean number of species' predators plus prey (also referred to as link density); and connectance (C), where $C = L/S^2$. Eight other properties, each providing a percentage of the types of species in the food web, included top (T; taxa lacking any predators or parasites), intermediate (I), and basal species (B; taxa lacking any prey items); cannibals (Can); omnivores (Omn; taxa with food chains of different lengths, where a food chain is a linked path from a non-basal to a basal species); herbivores plus detritivores (H), and Resource count and Consumer count — the count of all species that serve as a resource or a consumer in the food web. These 11 properties are commonly calculated in food web network analyses (e.g. Williams & Martinez 2000, Dunne et al. 2004).

Seven overall properties of estuarine trophic webs structure were also quantified: mean shortweighted trophic level (TL), a trophic level measure which gives the most accurate estimate of trophic level based on binary link information (Williams & Martinez 2004); chain length (Chain), the mean number of links in every possible food chain or sequence of links connecting top species to basal species; characteristic path length (Path), the mean shortest path length between species pairs; standard deviation of mean generality (GenSD), the number of prey items a species has; vulnerability (VulSD), the number of predators a species has; normalized standard deviation of links (LinkSD), which estimates links per taxon; and clustering coefficient (Clust), the mean fraction of species pairs connected to the same species that are also connected to each other (Camacho et al. 2002, Dunne et al. 2002, Montoya & Solé 2002, Williams et al. 2002).

Table 1. Definition of the food web properties calculated

Food web property	Definition
S	Number of trophic species
L/S	Links per species: mean number of species' predators + prey
C	Connectance: $C = L/S^2$
T	Top species: taxa lacking any predators or parasites
I	Intermediate species
B	Basal species: taxa lacking any prey items
Can	Cannibals
Omn	Omnivores: taxa with food chains of different lengths, where a food chain is a linked path from a non-basal to a basal species
H	Herbivores + detritivores
Resource count	Count of all species that serve as resources in the food web
Consumer count	Count of all species that serve as consumers in the food web
TL	Mean shortweighted trophic level
Chain	Mean number of links in every possible food chain or sequence of links connecting top species to basal species
Path	Mean shortest path length between species pairs
GenSD	Standard deviation of mean generality: how many prey items a species has
VulSD	Standard deviation of mean vulnerability: how many predators a species has
LinkSD	Normalized standard deviation of links: an estimate of links per taxon
Clust	Clustering coefficient, the mean fraction of species pairs connected to the same species that are connected to each other

Mean values of food web properties were estimated for sections of the estuarine-coastal gradient. These sections were upper estuary (encompassing the first 6 sites), middle estuary (including 14 sites), channel (including 4 sites at the river mouth) and coast (including 6 sites in the adjacent coastal waters) (Fig. 1). Analyses of variance (ANOVA) were conducted for all food web properties, abiotic variables and the percentage of niche model errors (see Tables 2, 3 & 4). Tukey post hoc tests were carried out whenever the null hypothesis was rejected. A significance level of 0.05 was used in all test procedures. All statistics were performed using the software SYSTAT13 (Cranes Software International).

The niche model

The ability of the niche model (Williams & Martinez 2000) to predict food web properties was compared for the various sections. The niche model has 2 input parameters: S and C. In this model, each species is assigned a randomly drawn 'niche value' (n_i) from the interval (1, 0). Each species is then constrained to consume all prey species within a range of values (r_i) whose randomly chosen center (c_i) is less than the consumer's niche value. The niche model allows up to half a consumer's range to include species with higher niche values than the consumer, thus allowing looping and cannibalism. Also, the consumer must feed on all species that fall within its feeding range.

For each estuarine food web, we used Monte Carlo simulations to generate 1000 niche model webs with the same S and C as the empirical web, allowing the calculation of a model mean and standard deviation for each of the network properties. If the normalized error (raw error divided by model SD) between the empirical property and the mean model value for that property falls within ± 1 model SD, the model is considered to be a good fit to the empirical data (Williams & Martinez 2000). The software Network 3D (Yoon et al. 2004, Williams 2010) was used for all calculations.

RESULTS

The abiotic parameters varied along the estuarine-coastal gradient. Salinity increased from the upper estuary to the coastal zone, showing a very pronounced variability in the upper section (Fig. 2a, Table 2). Depth also increased towards the coast

Table 2. ANOVA results for the abiotic variables along the estuarine-coastal gradient sections (significant values are in **bold**)

	SS	df	MS	F	p
Salinity	95.43	3	31.81	29.28	<0.01
Depth	323.18	3	107.73	8.92	<0.01
Temperature	10.64	3	3.55	12.80	<0.01

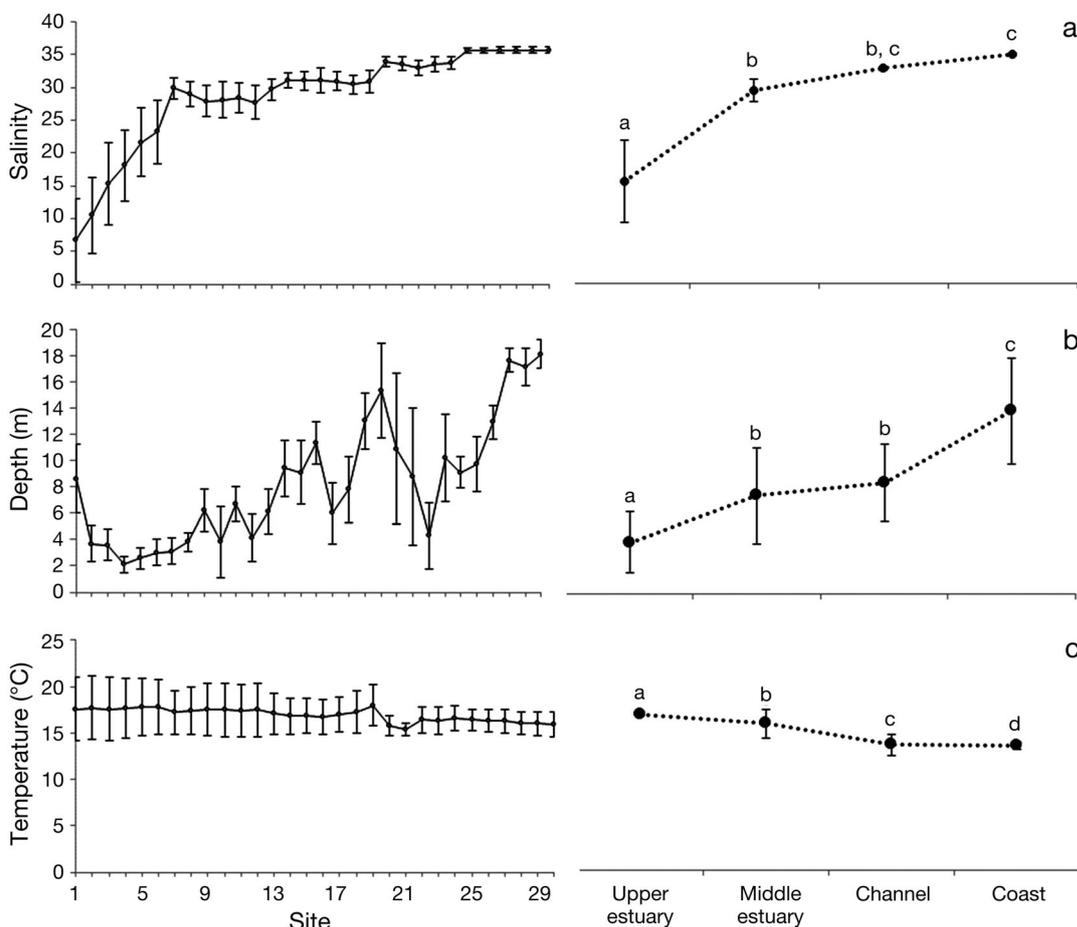


Fig. 2. Variation of the main abiotic variables along the estuarine-coastal gradient: (a) salinity, (b) depth and (c) temperature. Letters indicate significantly different pairs of values; bars indicate standard deviation

(Fig. 2b, Table 2), while temperature decreased (Fig. 2c, Table 2).

Significant differences were detected among sections for the basic and overall food web network properties, yet general continuous trends from the upper estuary to the coast were not identified. S, C, Can, Consumer count, Path, GenSD, VulSD, LinkSD and Clust did not vary among the sections. L/S and T were lower in the upper estuary, showing higher variability than in the remaining sections; I was highest in the upper estuary showing higher variability than in the remaining sections; B was highest in the coastal section; Omn was lowest in the upper estuary; H was higher in the upper estuary than in coastal waters and Resource count was lower in the upper estuary than in coastal waters (Fig. 3, Table 3). TL was highest in the middle section and lowest in the upper estuary and coastal section; whereas Chain was highest in the middle estuary and lowest in coastal waters (Fig. 4, Table 4).

The percentage of niche model errors varied between 18 and 29%, and was different among sections (Fig. 5, Table 4), being highest in the middle estuary and lowest in the coast.

Table 3. ANOVA results for the basic properties of the food web networks along the estuarine-coastal gradient sections (significant values are in **bold**).

	SS	df	MS	F	p
S	121.87	3	40.62	0.54	0.66
L/S	5.89	3	1.96	3.84	0.02
C	0.00	3	0.00	1.09	0.37
T	0.08	3	0.03	4.45	0.01
I	0.08	3	0.03	3.74	0.02
B	0.01	3	0.00	5.59	<0.01
H	0.01	3	0.00	3.59	0.03
Omn	0.03	3	0.01	3.12	0.04
Can	0.01	3	0.00	1.45	0.25
Resource count	601.45	3	200.48	4.81	0.01
Consumer count	74.57	3	24.86	0.31	0.82

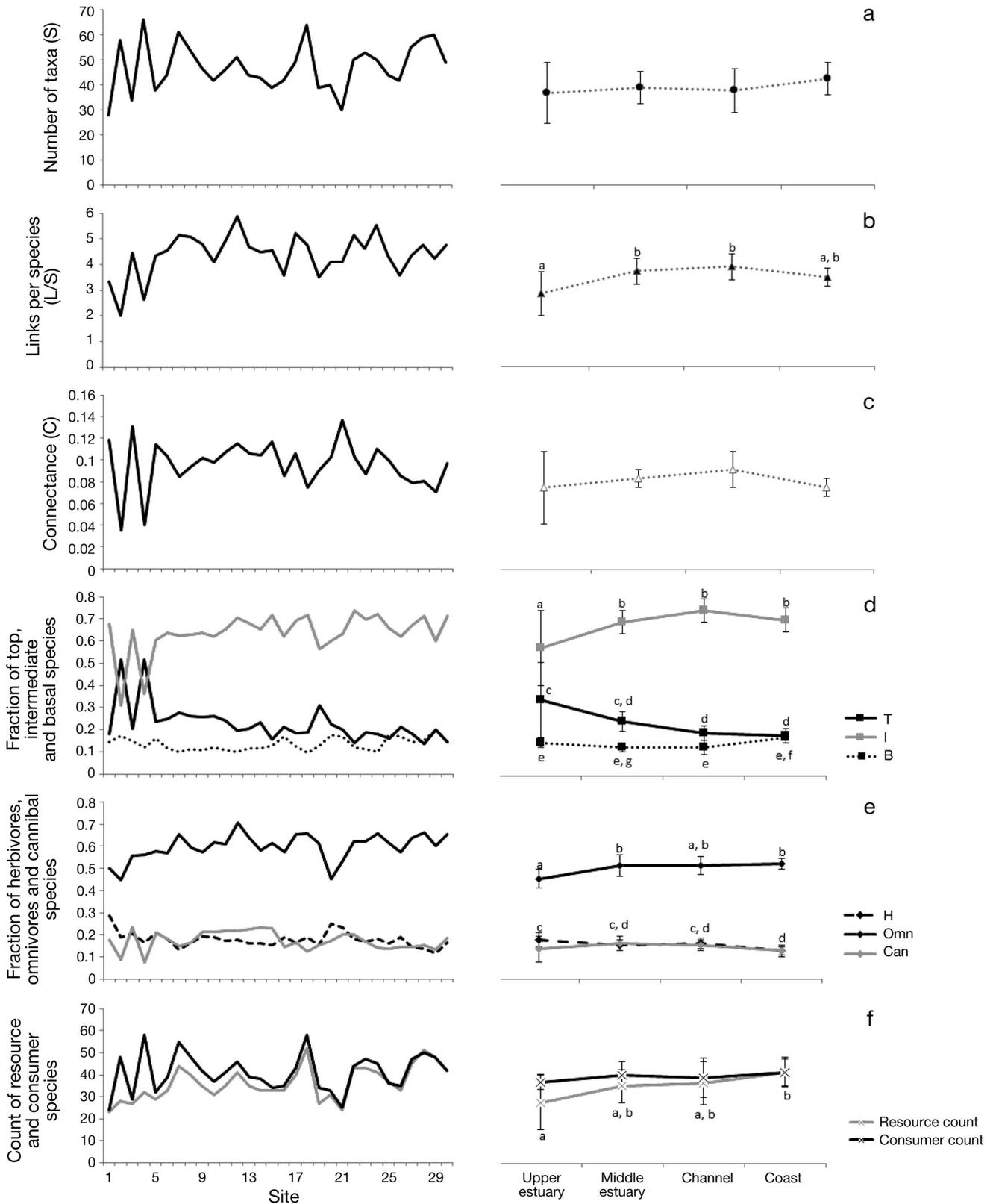


Fig. 3. Variation in the basic properties of the food web networks along the estuarine-coastal gradient: (a) number of taxa, S; (b) links per species, L/S; (c) connectance, C; (d) fraction of top species, T, intermediate species, I, and basal species, B; (e) fraction of herbivores, H, omnivores, Omn, and cannibals, Can; (f) Resource and Consumer counts. Letters indicate significantly different pairs of values; bars indicate standard deviation

Table 4. ANOVA results for the overall properties of the food web networks and percentage of niche model errors, along the estuarine-coastal gradient sections (significant values are in **bold**)

	SS	df	MS	F	p
TL	0.14	3	0.05	4.50	0.01
Chain	0.07	3	0.02	3.03	0.04
Path	0.20	3	0.07	1.94	0.15
GenSD	0.01	3	0.00	0.87	0.47
VulSD	0.04	3	0.01	0.49	0.69
LinkSD	0.01	3	0.00	0.48	0.70
Clust	0.01	3	0.00	1.10	0.37
% Niche model errors	634.55	3	211.52	3.26	0.04

DISCUSSION

This work confirms the highly variable nature of estuarine systems, not only in terms of physico-chemical and biological communities, but also with respect to food web network structure and properties. Overall, although clear longitudinal trends were not detected in the estuarine-coastal gradient we analyzed, more significant differences were detected within this gradient than had been previously reported for other river systems Romanuk et al. (2006). Clear longitudinal trends had previously been reported in other estuarine systems, in terms of fish and phytoplankton assemblages (e.g. Winemiller 1990, Winemiller & Leslie 1992, Ley et al. 1999, Muylaert et al. 2000, 2009).

In the South Saskatchewan River Basin, Canada, 4 out of 17 food web network properties were found to differ over a longitudinal gradient from the mountain to the lowlands, ranging between 450 and 700 km (Romanuk et al. 2006). In the present study of the Tagus estuary, 9 out of 18 food web network properties were found to be different within the estuarine-coastal gradient, within a span of only 60 km. Clues to this high variability of estuarine food web structure had already been reported for the Tagus estuary in a study using stable isotopes, which reported fluctuating trophic levels both temporally and spatially (Vinagre et al. 2012b).

The salinity gradient that is present in estuaries and absent from river systems is probably the main reason for these differences, given that river systems also have high variation in most of the other physico-chemical variables that affect estuaries. Most of the biota present in estuaries include marine organisms that can withstand brackish waters to a certain extent (an ability which is species-specific and often life-

stage-specific), while the vast majority of river organisms do not tolerate even low levels of salinity (Wu & Woo 1983, Dunson et al. 1993, Elliott & Dewailly 1995, Martino & Able 2003). This means that along the estuarine-coastal gradient, the successive food webs are composed of organisms with a decreasing salinity tolerance—and those tolerant species may have different predators and prey as the salinity changes.

Intermediate species in the middle estuary may be top species in the upper estuary if they tolerate very low salinities but their predators do not; this seems to be the case in the present study, where the percentage of top species decreases and the percentage of intermediate species increases from the upper estuary to the coast. This is well known for early life-stages of fish, such as the soles *Solea solea* and *S. senegalensis*, the flounder *Platichthys flesus*, and the seabass *Dicentrarchus labrax*, whose 0-group juveniles use the upper estuarine zone as a refuge from predation (Cabral & Costa 1999, 2001, Vinagre et al. 2005, 2008b, 2011). Because other species cannot live in such low salinities, these juveniles also benefit from reduced interspecific competition for food resources. When these species finally migrate out of the upper estuary, they will have attained a size that excludes them from being preyed upon by most predators in the estuary and coastal zone.

The upper estuary is, in fact, the section that stands out most often in the present study as being different in terms of food web network properties. This is also where variability was highest for many food web properties, even when no significant difference was found among sections. The high variability in food web structure seems to reflect the highly variable conditions that make the upper estuary the harshest of all estuarine environments for many marine species. Our data shows that salinity is the most variable abiotic parameter in the upper estuary; thus, it is probably the main factor driving the high variability found in the food webs. Other studies concerning the biological communities of estuaries have consistently found that salinity and geographical distance to the sea were the most important factors determining trends in species composition (e.g. Winemiller & Leslie 1992, Ley et al. 1999, Martino & Able 2003).

No longitudinal trends were detected for S in our estuary (as they have been in rivers); however, S was much higher in the coastal-estuarine system than those reported for other river systems (Romanuk et al. 2006). This is probably due to the method used to assemble the species list; while Romanuk et al. (2006)

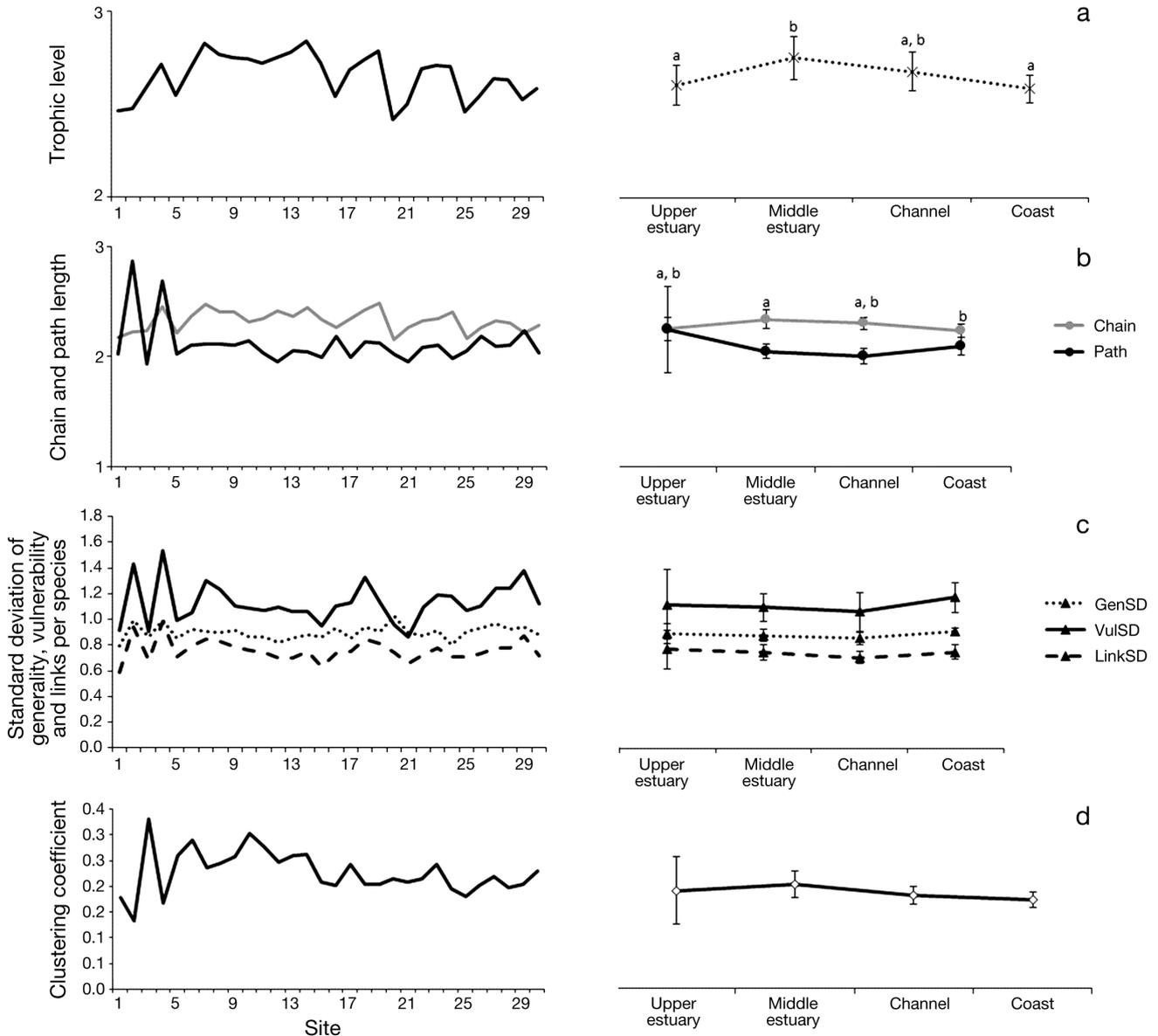


Fig. 4. Variation of the overall properties of the food web networks along the estuarine-coastal gradient: (a) mean short-weighted trophic level; (b) chain length, Chain, and characteristic path length, Path; (c) standard deviations of mean generality, GenSD, mean vulnerability, VulSD, and links, LinkSD; and (d) clustering coefficient. Letters indicate significantly different pairs of values; bars indicate standard deviation

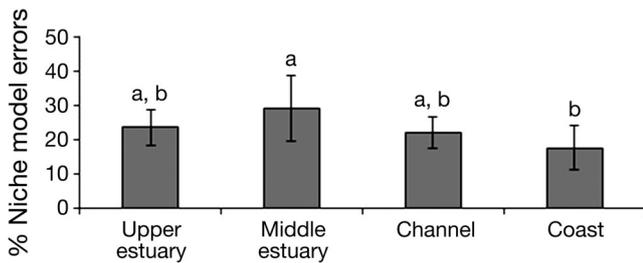


Fig. 5. Percentage of niche model errors for 18 network structure properties that were greater than 111, for the food webs analyzed. Letters indicate significantly different pairs of values; bars indicate standard deviation

used data from the literature alone and focused on fish, our food web was based on data collected directly from the field. Also, although fish are among the better resolved groups in this study, a high level of resolution was also accomplished for other groups, such as crustaceans, mollusks and birds.

L/S, C, T, I and H were much more variable here than in the river system studied by Romanuk et al. (2006). Variables that differed among river sections in that study were C, I, H and Can, while in our estuarine-coastal study, differences were found for I and H, but not for C and Can. Differences were also

found for L/S, T, Omn, TL and Chain, while they were not detected in the river system. Additionally, we found differences in Resource count (although this parameter was not analyzed in the river study of Romanuk et al. 2006).

We found that H was much higher (12 to 29%) in the estuary compared to that found in the river system (6 to 12%), although this may be an effect of a latitudinal trend in fish herbivory, given that the study of Romanuk et al. (2006) was conducted at higher latitudes than our study, and herbivory in fishes tends to increase towards the equator (Horn 1989, Floeter et al. 2005). In the river system, H was highest in mountain sections, while in the estuary it was highest in the upper estuary and lowest in the coastal waters—possibly the continuation of the trend described by Romanuk et al. (2006). Values of B, Omn, and Can were similar to those reported for the river system (Romanuk et al. 2006), while TL and Chain were lower. Winemiller & Leslie (1992) also reported a trend of decreasing herbivory from the river to the ocean in tropical coastal lagoons. These authors reported H values of 9% in lagoons, lower than we found in the Tagus estuary in the present study. They also reported 9% of omnivores, a much lower value than that found in our study, which varied between 45 and 71%. These differences may be due to the different types of ecosystems analyzed (i.e. estuaries vs. coastal lagoons), to the different latitudes and/or to the different methodologies used for data analysis.

The niche model fit to the Tagus estuary food webs was similar to that found in other ecosystems. The percentage of errors in our study was 18 to 29%, which gives a predictive success of 71 to 82%. Dunne et al. (2004) and Williams & Martinez (2000) reported niche model predictive success values of 87% and 79% for 3 highly resolved marine food webs, and for 7 non-marine food webs, respectively.

Comparison with other estuarine food web networks shows that our values of S, C, Omn and TL were within the range of those previously reported, while L/S was lower and T, B and Can were higher (Huxham et al. 1996, Lafferty et al. 2006, Dieter Zander et al. 2011, Hechinger et al. 2011, Mouritsen et al. 2011, Thielges et al. 2011). Upper estuary-coastal linkages and the longitudinal nature of processes forcing the biota require more thorough investigations on the variation of food web network structures in estuarine-coastal gradients. Assembling additional food web networks for other estuaries is crucial for the clarification of the consistency of the patterns revealed in this study.

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