



Short food chains, highly diverse and complex food web networks in coastal lagoons

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ABSTRACT

Shallow semi-enclosed coastal lagoons are recognized as important biodiversity hotspots and nursery areas for many organisms. However, the topology of the complex food web networks therein has never been studied. Highly defined food web networks were assembled for Ria de Aveiro, Ria de Alvor and Ria Formosa. Their structural network properties were analysed and compared to those of large open estuaries, small intermittent estuaries, as well as other marine ecosystems. The main conclusion was that these coastal lagoons are dominated by intermediate species like other estuarine systems, however they present more complex trophic networks (higher connectance) than large open estuaries, even though having shorter food chains. They also have lower mean path length between pairs of species. Shorter chain length means that disturbance is more likely to travel from basal to top species and likewise from the top to the bottom of the food web, while low path between species pairs implies a higher likelihood that disruption of one species affects any other species. These fragilities may be somewhat counterbalanced by the high connectance of these networks. The most connected species (with the highest degree = highest number of links at node) in the networks are crab and shrimp species. The non-indigenous blue crab appears as the most connected species in Ria de Alvor and among the top 5 most connected species in Ria Formosa. Highly commercial Sparid fishes play particularly important roles in the network as both highly connected and generalist predators. Top species are mostly birds. The top 10 species with more predators are all amphipods in Ria de Aveiro, while in Ria de Alvor they encompass insects, crabs, and gastropods, and in Ria Formosa they are all gastropods, with the exception of a non-indigenous polychaete. The particular network topology and inherent potential fragility of coastal lagoon food webs should be taken into account when designing environmental management plans.

1. Introduction

Coastal lagoons are semi-enclosed coastal systems, separated from the ocean by sand barriers and connected to the sea by restricted openings (Kjerfve, 1994; Newton et al., 2014). The river freshwater input has a reduced inflow in these systems compared to large open estuaries (Chapman, 2012). These transition zones hold a high ecological value, acting as nursery grounds for many fish species (Antunes et al., 1988; Abecasis et al., 2009; Chícharo et al., 2012) and supporting human communities which benefit from their natural resources (Pérez-Ruzafa et al., 2011; Chapman, 2012; Lillebø et al., 2019). Due to nutrient accumulation and their high primary productivity, they support remarkable biodiversity (Brito et al., 2009; Garrido et al., 2011; Clara et al., 2018; Bellino et al., 2019), while being also stop-spots for many

migratory birds (Ayache et al., 2009; Morgado et al., 2009; Cruz et al., 2011; Bueno-Pardo et al., 2018).

Complex, highly resolved, food web networks have been described for various marine ecosystems, including large open estuaries, like the Ythan and the Tagus estuary (Huxham et al., 1996; Lafferty et al., 2006; Vinagre and Costa, 2014), and small intermittent estuaries (Mendonça and Vinagre, 2018). However, to the best of our knowledge, the present study is the first description of coastal lagoons' complex food web networks from a topological perspective.

The word *Ria* in Portugal stands for relatively large coastal lagoons, it does not apply to small intermittent estuaries (Mendonça and Vinagre, 2018) and differs from its use in Galicia, where it corresponds to narrow river-valleys, funnel shaped, wider at the ocean end and narrowing as it approaches the river mouth (Newton et al., 2014). The Portuguese *Rias*

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are among the best studied coastal lagoons in the world in terms of biodiversity and were, thus, chosen as models for the description of coastal lagoons' complex food web networks. Knowing the complex network topology that structures feeding relations in coastal lagoons is a fundamental step to understand how these ecosystems function and how they may respond to disturbance (e.g. Dunne et al., 2002, 2004; Vinagre et al., 2019).

The modelling approach used in the present study uses binary predator-prey matrices to investigate food web network structure and properties, merging food web ecology and complex network analysis, as set by May (1973) and Pimm (1982) and further developed by many other authors in the search for trophic networks' organization patterns, potential response to disturbance, as well as universal features ruling all food webs (e.g. Williams and Martinez, 2000, 2004; Sole and Montoya, 2001; Bascompte and Stouffer, 2009; Dunne et al., 2002, 2004; Mendonça and Vinagre, 2018). In this kind of analysis, species are represented by nodes and predator-prey relations by lines that unite those nodes.

We hypothesize that the network properties of coastal lagoons fall in between those previously published for larger open estuaries and small intermittent estuaries, considering that their size is intermediate between these two types of systems and that they share characteristics with both. Complex networks of predator-prey relations were assembled for three coastal lagoons, Ria de Aveiro, Ria de Alvor and Ria Formosa, and their network properties compared to previously published networks from larger open estuaries, small intermittent estuaries and other marine and non-marine food webs. The coastal lagoons' networks were analysed to find which species have particularly important trophic roles in each system.

2. Materials and methods

2.1. Study areas

Ria de Aveiro ($40^{\circ} 39' N$, $8^{\circ} 41' W$) is located in the north of the Portuguese coast and Ria de Alvor ($37^{\circ} 07' N$, $8^{\circ} 37' W$) and Ria Formosa ($36^{\circ} 59' N$, $7^{\circ} 53' W$), in the south (Fig.1). Ria de Aveiro is a shallow coastal lagoon separated from the sea by a sand barrier, which receives freshwater inputs from two rivers: Vouga and Antuã. It encompasses several channels, being the most important the Mira channel, which receives water from a small system of ponds and rivers (Dias et al., 1999). It is connected to the Atlantic Ocean by an artificially stabilized channel (Dias et al., 1999). Ria de Alvor is a shallow lagoon with a U-shape due to the position of their two major fluvial inputs: Rio de Arão and Ribeira de Odiáxere. It is separated from Lagos Bay by two sand barriers and the entrance of water has also been artificially stabilized (Mateus et al., 2016; Ventura, 2019; Picado et al., 2020). Ria Formosa is the most important wetland of Portugal. It is separated from the ocean by a set of sandy islands along around 50 km of coast and is connected to the sea through six inlets (Falcão et al., 2003; Newton and Mudge, 2003; Duarte et al., 2007).

All three ecosystems are shallow water masses with large intertidal zones, multiple sand/mud banks and encompass diverse habitats like seagrass meadows, saltmarshes, and sand/mud flats (Dias et al., 1999, 2000; Falcão et al., 2003; Newton and Mudge, 2003; Lillebø et al., 2011; Mateus et al., 2016; Picado et al., 2020; Monteiro et al., 2022). All have been recognized as Natura 2000 and Ramsar sites. Ria Formosa is the largest of the three systems, both in total area and catchment area, while Ria de Alvor is the smallest (Table 1). They encompass adjacent fishing

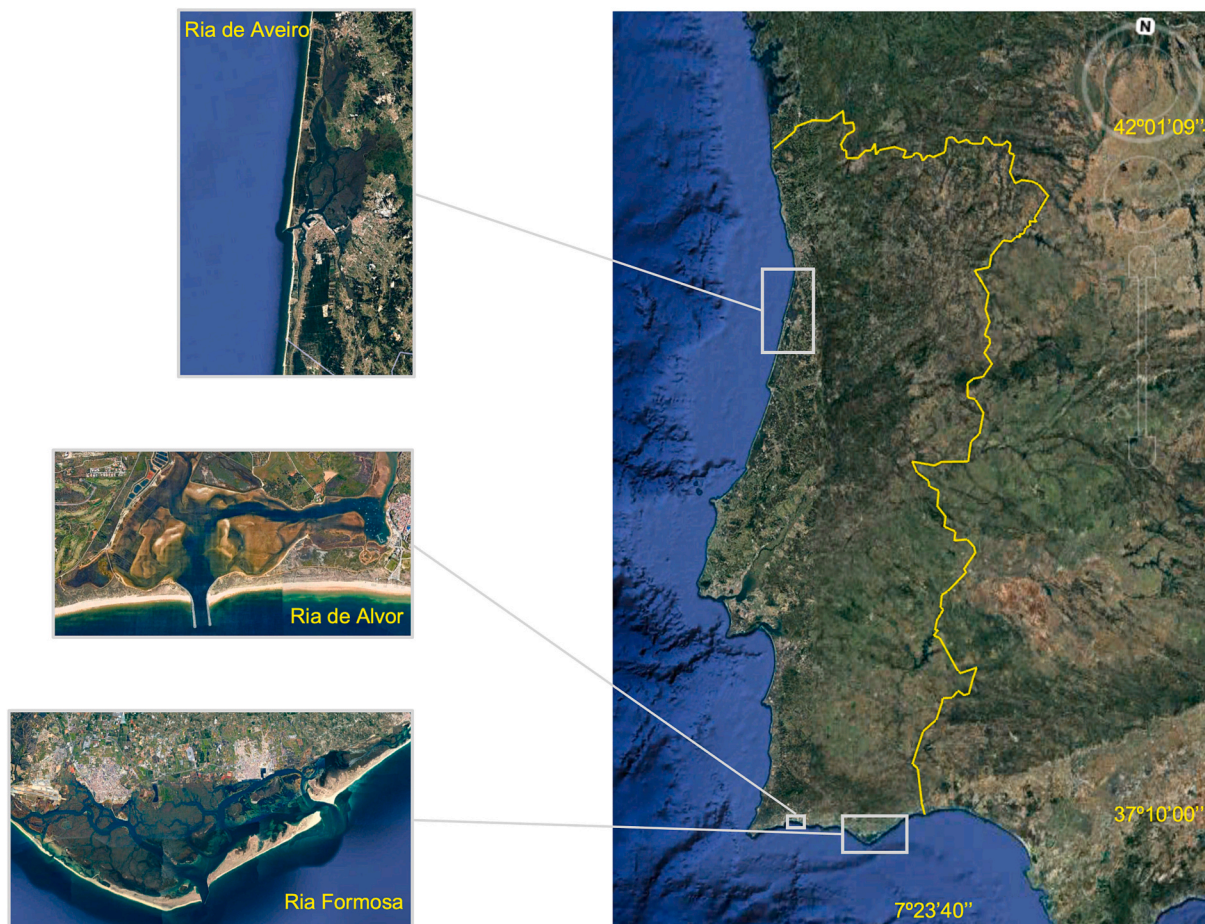


Fig. 1. Location of of Ria de Aveiro, Ria de Alvor and Ria Formosa, in Portugal. Images adapted from Google Maps.

Table 1

General description of the study sites.

Study site	Catchment area (km ²)	Surface area (km ²)	Average depth (m)	Salinity range (‰)	Temperature (°C) (range of means)
Ria de Aveiro	83	66	1	0–36	9–25
Ria de Alvor	15	3	2	0–37	14–25
Ria Formosa	864	180	2	0–36.5	12–27

communities that benefit from their natural resources and are engaged in tourism activities, specially marked during summer, making these lagoons important for the economy of the country (Vaz et al., 2005; Duarte et al., 2007; Mateus et al., 2016).

2.2. Food web modelling

Lists of species for each of the three ecosystems were assembled based on a review of published literature, between 1980 and 2021. The most important articles used for Ria de Aveiro were: Cunha et al. (1999), Morgado et al. (2003), Nunes et al. (2008), Rodrigues et al. (2011) for invertebrates; Arruda et al. (1988), Rebelo (1992) and Pombo and Rebelo (2002) for fish; Schricke and Triplet (1987), Morgado et al. (2009), Cruz et al. (2011) for birds. For Ria de Alvor, it was: Rodrigues and Dauvin (1987) and Rolo (2007) for invertebrates; Antunes et al. (1988) for fish; Rethore (2014) for birds. For Ria Formosa: Cruz et al. (2003), Gamito (2008), Gamito et al. (2012) and Parreira (2018) for invertebrates Ribeiro et al. (2008) and Gamito et al. (2003) for fish; Fonseca et al. (2004) and Amaral and Fonseca (2010) for birds. The lists of species were completed with information from the Natura 2000 data forms. Only species classified as having good data quality in Natura 2000 lists were used. The complete list of species of the three Rias and the references used for their creation can be found in Supplement 1 and 2, respectively.

Detritus, fungi, bryozoans, entoproct, rotifers and tunicates were included as agglomerated nodes (the agglomeration method was agglomeration by taxonomy, as described by Gauzens et al., 2013). This is a standard procedure in complex food web network structure analysis (e.g. Dunne et al., 2004; Vinagre et al., 2019). Only the intertidal plants that have trophic relations with aquatic organisms were included. Fish were included only if juveniles or adults were found in the Rias. Birds and mammals (adults and juveniles) were included only if they had a trophic link with marine species. Amphibians and reptiles (adults and juveniles) were only considered if they tolerate brackish waters. Humans were considered in all systems as predators of all commercial species and also of species collected as bait.

Binary predator-prey matrices were created for the three Rias depicting trophic interactions, including predator-prey links found in literature from any part of the world, based on stomach content analysis or feeding behaviour observations (Supplement 3, 4, 5). Network3D (Yoon et al., 2004; Williams, 2010) was used to build the food web networks and investigate their network properties. This software merges all the species that have the same predators and prey into a unique node, called trophic species (Briand and Cohen, 1984), which reduces biases of uneven resolution among different food webs (Williams and Martinez, 2000).

2.3. Comparison of network properties

For each food web network analysed by Network3D, an output of 18 network properties was used to characterize the food webs (Tables 2, 3), including the number of trophic species (S), links per species (L/S) and Connectance (C), which is calculated as $C = L/S^2$. Also including the percentage of Top predators (T), Intermediate species (I) and Basal species (B) indicates the prevalence of species with different trophic positions, and the percentage of omnivores (Omn), herbivores and detritivores (H) and Cannibalism (Can), that show the prevalence of different feeding strategies used by the species present in the ecosystem.

Table 2

Definition of the food web properties calculated.

Food-web properties		Description
Number of trophic species	S	Species or groups of species used to build the food web networks
Links per species	L/S	Mean number of predator/prey links per species
Connectance	C	Proportion of actual trophic links to all possible links (L/S^2)
Top species (%)	T (%)	Fraction of species with prey and not predators or parasites
Intermediate species (%)	I (%)	Fraction of species with both predators and prey
Basal species (%)	B (%)	Fraction of species with predators and no prey
Herbivores plus detritivores (%)	H (%)	Fraction of species who prey on primary producers
Cannibals (%)	Can (%)	Fraction of species which prey on their own species
Omnivores (%)	Omn (%)	Fraction of species with food chains of different lengths, where a food chain is a linked path from a nonbasal to a basal species
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
Trophic level	SWTL	Short-weighted trophic level or the average of prey trophic level
Mean food chain length	Chain	Mean number of links in every possible sequence of links connecting top to basal species
Mean shortest path length	Path	The mean shortest set of links between species pairs
Generality standard deviation	GenSD	Standard deviation of the number of resources per taxon
Vulnerability standard deviation	VulSD	Standard deviation of the number of consumers per taxon
Normalized standard deviation of links	LinkSD	Standard deviation of the number of links per taxon
Clustering coefficient	Clust	The mean shortest set of links between species pairs

Resource and consumer count were also included as they indicate the number of species that serve as resources/consumers in the food web. Seven structure properties were calculated: the mean short-weighted trophic level (SWTL), the mean number of links in every possible food chain connecting top species to.

basal species (Chain), the mean shortest number of links between species pairs (Path), the mean clustering coefficient, which is the mean fraction of species pairs connected to the same species that are connected to each other (Clust) and the standard deviations of normalized total links (LinkSD), standard deviation of mean generality (generality = how many prey items a species has) (GenSD) and standard deviation of mean vulnerability (vulnerability = how many predators a species has (VulSD)).

Species in the Top 10 positions in terms connectivity (degree, number of links at node), vulnerability, generality and trophic level (SWTL) were selected to describe each system in terms of the species with the most important trophic roles. This will allow a better understanding of the food webs.

The range of the properties of the three food web networks were compared to that of other previously published food web networks (that

Table 3

Properties of the food web networks of Ria de Aveiro, Ria de Alvor and Ria Formosa. Number of trophic species (S); links per species (L/S); connectance (C); T, I and B (percentages of top, intermediate and basal species, respectively); Can (percentage of cannibals); Omn (percentage of omnivores); H (percentage of herbivores and detritivores); Resource count; Consumer count; SWTL (mean short weighted trophic level); Chain; Path (characteristic path length); GenSD (standard deviation of mean generality); VulSD (standard deviation of vulnerability); LinkSD (normalized standard deviation of links); and Clust (clustering coefficient).

Properties	Trophic web network Ria de Aveiro	Trophic web network Ria de Alvor	Trophic web network Ria Formosa
S	306	186	382
L/S	63.67	33.36	82.60
C	0.21	0.18	0.22
T (%)	14	27	3
I (%)	79	66	92
B (%)	7	7	5
Can (%)	29	22	29
Omn (%)	81	85	84
H (%)	12	7	12
Resource count	264	136	371
Consumer count	284	172	361
SWTL	2.9	3.0	2.9
Chain	2.2	2.3	2.0
Path	1.7	1.7	1.7
GenSD	1	0.88	0.99
VulSD	0.74	1.02	0.74
LinkSD	0.64	0.71	0.62
Clust	0.35	0.33	0.36

followed the same modelling method) from larger open estuaries, small intermittent estuaries, and other marine and terrestrial ecosystems.

3. Results

The total number of species found was highest at Ria Formosa and lowest at Ria de Alvor (Table 3). Some of the species found in the three ecosystems belong to non-indigenous species.

Most of the network properties did not differ among the Rias (Table 3). Ria Formosa stands out for having higher species diversity (S), links per species and complexity (C) (Table 3). It is also the only system with more resource than consumer taxa (Table 3). Ria de Alvor is less diverse (S) and less complex (C) (Table 3). The proportion of top species (T) is different among systems, with highest values in Ria de Alvor, lowest at Ria Formosa and intermediate in Ria de Aveiro. Percentage of intermediate species (I) is higher at Ria Formosa and lower at Ria de Alvor (Table 3). Herbivory (H) and cannibalism (C) are lower at Alvor

Table 4

Top 10 taxa with the highest vulnerability (Vul) for the food webs of Ria de Aveiro, Ria de Alvor and Ria Formosa. *Tritia spp* (*) corresponds to the species *Tritia corniculum*, *Tritia pygmaea*, *Tritia reticulata*, *Tritia pfeifferi*, *Tritia unifasciata* and *Tritia varicosa*. Non-indigenous species in bold.

Rank	Ria de Aveiro	Vul	Ria de Alvor	Vul	Ria Formosa	Vul
1	<i>Caprella equilibra</i> (Amphipod)	1.84	<i>Insecta</i>	2.70	<i>Hexaplex trunculus</i> (Gastropod)	1.88
2	<i>Ampithoe ferox</i> (Amphipod)	1.84	<i>Callinectes sapidus</i> (Crab)	2.64	<i>Bolinus brandaris</i> (Gastropod)	1.88
3	<i>Caprella penantis</i> (Amphipod)	1.84	<i>Carcinus maenas</i> (Crab)	2.64	<i>Elysia viridis</i> (Gastropod)	1.88
4	<i>Gammarella sp</i> (Amphipod)	1.84	<i>Pachygrapsus marmoratus</i> (Crab)	2.64	<i>Tritia spp</i> (Gastropod)	1.86
5	<i>Pontocrates altamarinus</i> (Amphipod)	1.84	<i>Afruca tangeri</i> (Crab)	2.64	<i>Tritia incrassata</i> (Gastropod)	1.86
6	<i>Apolochus neapolitanus</i> (Amphipod)	1.84	<i>Clibanarius erythropus</i> (Crab)	2.61	<i>Ficopomatus enigmaticus</i> (Polychaeta)	1.86
7	<i>Pontocrates arenarius</i> (Amphipod)	1.84	<i>Afropinnotheres monodi</i> (Crab)	2.61	<i>Ocenebra erinaceus</i> (Gastropod)	1.86
8	<i>Aora gracilis</i> (Amphipod)	1.84	<i>Cerithium sp</i> (Gastropod)	2.46	<i>Gracilipurpura rostrata</i> (Gastropod)	1.86
9	<i>Caprella acanthifera</i> (Amphipod)	1.84	<i>Cymbium olla</i> (Gastropod)	2.46	<i>Conus ventricosus</i> (Gastropod)	1.86
10	<i>Gammarus insensibilis</i> & <i>G. locustra</i> (Amphipod)	1.84	<i>Hexaplex trunculus</i> (Gastropod)	2.46	<i>Crepidula fornicata</i> (Gastropod)	1.86

and similar at Ria de Aveiro and Ria Formosa (Table 3).

The top 10 species with higher vulnerability (with more predators) in the networks were all amphipods in Ria de Aveiro, while in Ria de Alvor they were insects, crabs, and gastropods, and in Ria Formosa they are all gastropods except for a non-indigenous polychaete (Table 4).

Among the top 10 most connected species (with the highest degree = highest number of links at node) in the networks are common crab (e.g. *Polybius henslowii* and *Carcinus maenas*) and shrimp species (e.g. *Crangon crangon*) (Table 5). Snails from the genus *Tritia* are also among the most connected species in Ria de Aveiro and Ria Formosa (Table 5). The non-indigenous blue crab, *Callinectes sapidus*, appears as the most connected species in Ria de Alvor and ranks as fifth most connected species in Ria Formosa (Table 5). Highly commercial Sparid fishes play particularly important roles in the network as both highly connected (Table 5) and highly generalist species (Table 6).

Top TL species are mostly birds (Table 7). The cormorant *Phalacrocorax carbo* is at the highest rank in Ria de Alvor, ranks fourth in Ria Formosa and fifth in Ria de Aveiro. The venomous fish *Lagocephalus lagocephalus* assumes the highest TL rank in Ria de Aveiro and ranks fifth in Ria de Alvor. Snakes of the genus *Natrix* rank as second and eighth highest TL in Ria Formosa, fourth in Ria de Aveiro and seventh in Ria de Alvor. Mammals also appear in the top 10 species.

of highest TL, the fox *Vulpes vulpes* in Ria de Aveiro and the ferret *Mustela putorius* in Ria Formosa (Table 7).

Table 8 compares the food web network properties of the three Rias with food web networks from other ecosystems.

4. Discussion

This study presents, for the first time, the complex food web networks of coastal lagoons. It shows that these systems share organizational similarities with larger open estuaries and smaller intermittent estuaries, however they have differences that set them apart from those two categories of coastal systems, thus meriting a separate analysis. They are dominated by intermediate species, like other estuarine systems (e.g. Vinagre and Costa, 2014; Mendonça and Vinagre, 2018), however they display higher diversity of species and higher complexity (given by connectance) than open estuaries. Their food chains are, however, smaller than those occurring in open estuaries, in fact they have an intermediate length between the ranges observed for open estuaries and small intermittent estuaries. Coastal lagoons also have lower mean path length between pairs of species than open estuaries.

Having short food chains and lower path length between species pairs, than open estuaries, may confer higher fragility to these food webs. Shorter food chains means that any disturbance can rapidly travel bottom-up or up-down the web, easily reaching top or basal species (Williams et al., 2002), while low path means that disruption to one

Table 5

Top 10 taxa with the highest connectivity (Conn) (degree, number of links at node) for the food webs of Ria de Aveiro, Ria de Alvor and Ria Formosa. *Tritia spp* (*) corresponds to the species *Tritia corniculum*, *Tritia pygmaea*, *Tritia reticulata*, *Tritia pfeifferi*, *Tritia unifasciata* and *Tritia varicosa*. Non-indigenous species in bold.

Rank	Ria de Aveiro	Conn	Ria de Alvor	Conn	Ria Formosa	Conn
1	<i>Polybius henslowii</i> (Crab)	2.40	<i>Callinectes sapidus</i> (Crab)	2.56	<i>Tritia spp</i> * (Gastropod)	2.40
2	<i>Crangon crangon</i> (Crab)	2.39	<i>Carcinus maenas</i> (Crab)	2.52	<i>Crangon crangon</i> (Crab)	2.32
3	<i>Tritia reticulata</i> (Gastropod)	2.38	<i>Pachygrapsus marmoratus</i> (Crab)	2.38	<i>Sicyonia carinata</i> (Shrimp)	2.31
4	<i>Palaemon serratus</i> (Crab)	2.37	<i>Diplodus vulgaris</i> (Fish)	2.37	<i>Palaemon serratus</i> (Crab)	2.29
5	<i>Spondyliosoma cantharus</i> (Fish)	2.33	<i>Diplodus sargus</i> (Fish)	2.37	<i>Callinectes sapidus</i> (Crab)	2.26
6	<i>Maja squinado</i> (Crab)	2.31	<i>Diplodus annularis</i> (Fish)	2.37	<i>Diplodus cervinus</i> (Fish)	2.25
7	<i>Diplodus annularis</i> (Fish)	2.31	<i>Diplodus cervinus</i> (Fish)	2.37	<i>Spondyliosoma cantharus</i> (Fish)	2.20
8	<i>Diplodus vulgaris</i> (Fish)	2.30	<i>Spondyliosoma cantharus</i> (Fish)	2.35	<i>Diplodus annularis</i> (Fish)	2.20
9	<i>Gobius paganellus</i> (Fish)	2.29	<i>Gobius paganellus</i> (Fish)	2.35	<i>Gobius paganellus</i> (Fish)	2.19
10	<i>Taurulus bubalis</i> (Fish)	2.26	<i>Salaria pavo</i> (Fish)	2.32	<i>Carcinus maenas</i> (Crab)	2.18

Table 6

Top 10 taxa with the highest generality (Gen) for the food webs of Ria de Aveiro, Ria de Alvor and Ria Formosa. *Tritia spp* (*) corresponds to the species *Tritia corniculum*, *Tritia pygmaea*, *Tritia reticulata*, *Tritia pfeifferi*, *Tritia unifasciata* and *Tritia varicosa*.

Rank	Ria de Aveiro	Gen	Ria de Alvor	Gen	Ria Formosa	Gen
1	<i>Spondyliosoma cantharus</i> (Fish)	3.15	<i>Diplodus vulgaris</i> (Fish)	2.61	<i>Diplodus cervinus</i> (Fish)	3.10
2	<i>Diplodus annularis</i> (Fish)	3.09	<i>Diplodus sargus</i> (Fish)	2.61	<i>Spondyliosoma cantharus</i> (Fish)	3.00
3	<i>Diplodus vulgaris</i> (Fish)	3.08	<i>Diplodus annularis</i> (Fish)	2.61	<i>Diplodus annularis</i> (Fish)	2.98
4	<i>Gobius paganellus</i> (Fish)	3.08	<i>Diplodus cervinus</i> (Fish)	2.61	<i>Gobius paganellus</i> (Fish)	2.98
5	<i>Polybius henslowii</i> (Crab)	3.05	<i>Gobius paganellus</i> (Fish)	2.61	<i>Diplodus vulgaris</i> (Fish)	2.95
6	<i>Crangon crangon</i> (Crab)	3.02	<i>Tringa totanus</i> (Bird)	2.61	<i>Serranus cabrilla</i> (Fish)	2.95
7	<i>Taurulus bubalis</i> (Fish)	3.02	<i>Spondyliosoma cantharus</i> (Fish)	2.58	<i>Sepia officinalis</i> (Cephalopod)	2.93
8	<i>Calliactis parasitica</i> (Anemone)	3.02	<i>Spherooides spengleri</i> (Fish)	2.55	<i>Tritia spp</i> * (Gastropod)	2.93
9	<i>Palaemon serratus</i> (Crab)	2.98	<i>Salaria pavo</i> (Fish)	2.52	<i>Pagellus bogaraveo</i> (Fish)	2.92
10	<i>Sepia officinalis</i> (Cephalopod)	2.98	<i>Sepia officinalis</i> (Cephalopod)	2.52	<i>Mullus barbatus</i> (Fish)	2.91

Table 7

Top 10 taxa with the highest trophic level (SWTL) for the food webs of Ria de Aveiro, Ria de Alvor and Ria Formosa. *H.caspia* corresponds to *Hydropogne caspia*, *M.basanus* to *Morus bassanus* and *P.carbo* to *Phalacrocorax carbo*.

Rank	Ria de Aveiro	SWTL	Ria de Alvor	SWTL	Ria Formosa	SWTL
1	<i>Lagocephalus lagocephalus</i> (Fish)	4.17	<i>H.caspia</i> , <i>M.basanus</i> , <i>P.carbo</i> (Birds)	4.08	<i>Alca torda</i> (Bird)	4.23
2	<i>Ardea purpurea</i> (Bird)	4.16	<i>Milvus migrans</i> (Bird)	4.06	<i>Natrix natrix</i> (Snake)	4.22
3	<i>Chlidonias leucopterus</i> (Bird)	4.16	<i>Ciconia nigra</i> (Bird)	4.05	<i>Mergus serrator</i> (Bird)	4.22
4	<i>Natrix natrix</i> (Snake)	4.16	<i>Ardeola ralloides</i> (Bird)	4.04	<i>Phalacrocorax carbo</i> (Bird)	4.22
5	<i>Phalacrocorax carbo</i> (Bird)	4.16	<i>Ardea purpurea</i> (Bird)	4.04	<i>Ixobrychus minutus</i> (Bird)	4.22
6	<i>Puffinus mauretanicus</i> (Bird)	4.15	<i>Lagocephalus lagocephalus</i> (Fish)	4.04	<i>Ardeola ralloides</i> (Bird)	4.21
7	<i>Ixobrychus minutus</i> (Bird)	4.15	<i>Natrix maura</i> (Snake)	4.04	<i>Mustela putorius</i> (Ferret)	4.21
8	<i>Vulpes vulpes</i> (Fox)	4.14	<i>Nycticorax nycticorax</i> (Bird)	4.03	<i>Natrix maura</i> (Snake)	4.20
9	<i>Luciobarbus bocagei</i> (Fish)	4.14	<i>Gelochelidon nilotica</i> (Bird)	4.01	<i>Circus cyaneus</i> (Bird)	4.20
10	<i>Milvus migrans</i> (Bird)	4.14	<i>Himantopus Himantopus</i> (Bird)	4.01	<i>Porphyrio porphyrio</i> (Bird)	4.10

species can rapidly impact any other species (Williams et al., 2002). Small intermittent estuaries also have short food chains, even shorter, and low path lengths, and, thus, share this fragility with coastal lagoons

(Mendonça and Vinagre, 2018). Like small intermittent estuaries, the coastal lagoons studied here, have higher network complexity (connectance) than larger open estuaries (Mendonça and Vinagre, 2018).

Table 8 Ranges of commonly reported values for food web properties for food web networks of different ecosystems. S = number of trophic species, C = Connectance, L/S = links per species, T = % top species, I = % intermediate species, B = % basal species, Can = % cannibal species, Omn = % omnivorous species, TL = mean trophic level, Chain = mean number of links in every possible food chain or sequence of links connecting top species to basal species, Path = characteristic path length. Ranges that do not totally overlap with those of open estuaries are presented in bold; ranges that do not totally overlap with any of those of other marine and/or non-marine ecosystems are underlined.

Ecosystem	N	S	C	L/S	T	I	B	Can	Omn	TL	Chain	Path	Source
Ria de Aveiro	1	306	0.21	<u>63.7</u>	14	79	7	29	81	2.9	2.2	1.7	Present work
Ria de Alvor	1	186	0.18	<u>33.4</u>	27	66	7	22	85	3	2.3	1.7	Present work
Ria Formosa	1	382	0.22	<u>82.6</u>	3	92	5	29	84	2.9	2.0	1.7	Present work
Large open estuaries	12	48-117	0.03-0.14	2.0-10.1	7-52	31-86	4-20	1-24	53-84	2.4-2.9	4.0-6.6	2.0-2.7	Huxham et al., 1996; Lafferty et al., 2006; Hechinger et al., 2011; Zander et al., 2011; Thielges et al., 2011; Mouritsen et al., 2011; Vinagre and Costa, 2014.
Small intermittent estuaries	23	26-59	0.16-0.29	6.9-11.4	8-27	64-83	5-12	22-37	83-92	2.4-2.7	1.9-2.0	1.5-1.7	Mendonça and Vinagre, 2018
Rock tide pools	116	7-52	0.11-0.39	1.6-7.0	0-46	14-88	7-43	14-60	43-84	1.68-2.5	1.6-2.5	1.3-2.0	Mendonça et al., 2018
Seagrass beds	16	53-68	0.17-0.23	11.4-12.9	13-18	58-65	21-26	13-19	70-75	1.8-2.0	1.9-2.0	2.0-2.3	Coll et al., 2011
Marine	6	29-513	0.04-0.24	7.0-33.19	0-19	47-98	2-14	4-42	67-87	2.1-3.2	6.4-15.3	1.6-1.9	Opitz, 1996; Yodzis, 1998; Link, 2002; Dunne et al., 2004, 2016; Gaichas and Francis, 2008; Jacob et al., 2011, Marina et al., 2018
Lake/pond	5	25-172	0.12-0.32	4.3-25.1	0-9	66-92	4-32	12-32	38-60	2-2.7	4.0-10.7	1.3-1.9	Warren, 1989; Martinez, 1991; Havens, 1992; Dunne et al., 2004
Stream	5	31-109	0.07-0.13	3.7-7.6	6-25	22-86	7-56	1-2	6-10	1.5-3.4	3.1-3.2	2.3-2.3	Townsend et al., 1998; Romanuk et al., 2006

Higher connectance has been shown to protect food web networks from species loss (Albert et al., 2000; Sole and Montoya, 2001; Dunne et al., 2002, 2004) and could, therefore somewhat counterbalance the network fragility brought by short food chains and low mean path.

Ria Formosa, with 641 species, which resulted in 382 trophic species after the analysis, was the most diverse system and, also, the most complex network (Fig. 2.). This is not surprising given that this system was the larger under study and it is considered the most important wetland of Portugal for its high biodiversity (Moura et al., 2019). This status also results in more biodiversity studies available. Ria Formosa is also the only of the three *Rias* where the number of Resource count is higher than Consumer count, which is possibly related to its important function as refuge and nursery area for fish (Abecasis et al., 2009; Vinagre et al., 2010) and stop-over spot for wintering and migrant birds (Neto 2003; Fonseca et al., 2004).

The food web networks of both Ria Formosa and Ria de Aveiro have a species diversity that is among the highest ever reported for any food

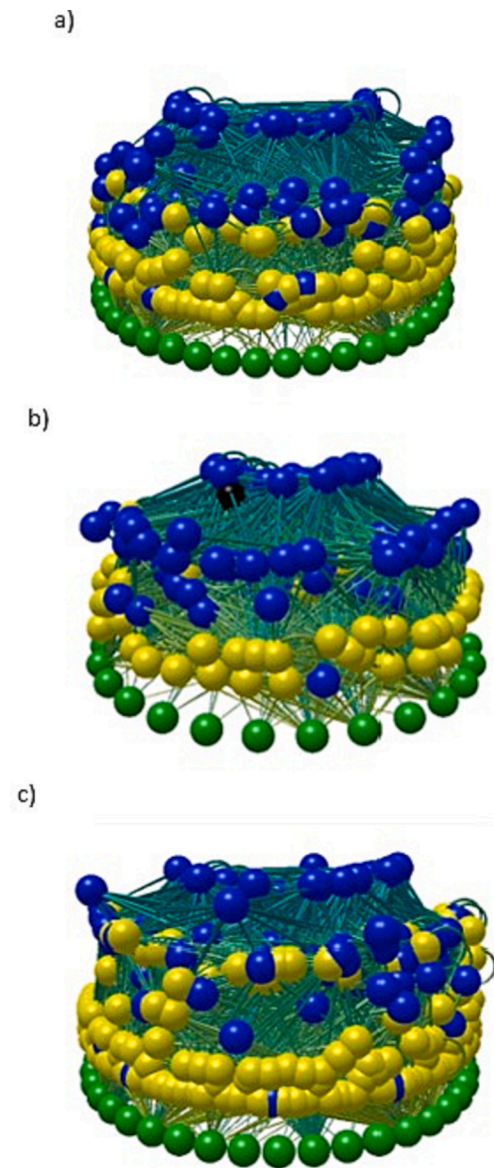


Fig. 2. Representation of the trophic web networks of Ria de Aveiro (a), Ria de Alvor (b) and Ria Formosa (c). Nodes correspond to trophic species. Green: basal taxa; yellow: invertebrates; blue: vertebrates; black: non-indigenous species. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

web network. Higher values of trophic species have only been reported for a few marine ecosystems analysed within the food web network theory framework (Gaichas and Francis, 2008; Jacob et al., 2011; Dunne et al., 2016). This is probably because Ria Formosa and Ria de Aveiro are well-studied systems lying at a mid-latitude that constitutes a transitional zone between temperate and subtropical waters, where cold-temperate, warm-temperate, and even tropical species can occur in sympatry (Briggs, 1974; Vinagre et al., 2011).

Ria de Alvor is the smallest of the *Rias* analysed and, as such, presents lower diversity and complexity. Nevertheless, most of the network properties did not differ among the *Rias*, despite their different size and species richness, revealing a similar web topology.

Interesting differences were found among the *Rias* in what concerns the top 10 species with higher vulnerability, that is with more predators, which constitute the food supply of the systems. These were all amphipods in Ria de Aveiro, while in Ria de Alvor a greater variety of groups was found, including insects, crabs and gastropods. In Ria Formosa the most vulnerable species were all gastropods, with the exception of a non-indigenous polychaete, the Australian tubeworm *Ficopomatus enigmaticus*. This tubeworm displays high tolerance to different conditions of salinity, eutrophication and pollution (Dittmann et al., 2009), and it has become a worldwide invader of brackish waters (Bianchi and Morri, 2001; Muniz et al., 2005; Costa et al., 2019). It is a suspension feeder and habitat engineer that can alter water flow, primary production and benthic communities (Vanni, 2002; Costa et al., 2019).

Among the top 3 most connected species (with the highest degree = highest number of links at node) are common crabs and shrimp, like the swimming crab *Polybius henslowii*, the green crab *Carcinus maenas*, and the brown shrimp, *Crangon crangon*. *C. maenas* was also among the most connected species in the food web networks of European small intermittent estuaries (Mendonça and Vinagre, 2018).

An impressive number of gastropod species of the genus *Tritia* are also among the top 3 most connected species, both in Ria de Aveiro and Ria Formosa. These mud snails are very numerous and visible over sand and mudflats in all three systems (personal observation) however little is known about their ecology.

Interestingly, the most connected species in Ria de Alvor was the non-indigenous Atlantic blue crab, *Callinectes sapidus*, which ranked fifth in Ria Formosa. This is a species that raises concern because it can become invasive, like it did in other regions of Europe and Asia (Zenetos et al., 2005; Mancinelli et al., 2021; Clavero et al., 2022). Originally from western Atlantic coasts, it plays a keystone species role in its native range (Mancinelli et al., 2017) and there are signs that it can rapidly become a keystone species in invaded estuaries, too (Clavero et al., 2022). It is a highly opportunistic generalist predator that can impact different trophic levels (Carrozzo et al., 2014; Mancinelli et al., 2016). The densities registered in both systems are still very low, and it was never detected in Ria de Aveiro, however if it becomes invasive it could be disruptive to local shellfish farms (Sousa et al., 2020) because it is well-known as an efficient predator of clams (Smith and Chin, 1951; Glude, 1955). There are also concerns that the blue crab will outcompete the green crab, *C. maenas* leading to its decline (Morais et al., 2019), like observed in the Ebro delta, in Italy (Clavero et al., 2022).

Highly commercial sparid fish do not occupy top 3 positions among the most connected species, however they dominate the top 10 positions in all systems. They also dominate the top 10 of highest generality, as flexible opportunistic predators (e.g. Horta et al., 2004). Among these sparids, there are various species of the genus *Diplodus*. These seabreams use coastal lagoons as refuge, feeding and nursery grounds (Abecasis and Erzini, 2008; Vinagre et al., 2010) and are part of the much-appreciated local gastronomy. The present work shows that they play important networks roles as both highly connected and high generalists.

A seabream of the genus *Diplodus*, namely *Diplodus vulgaris*, was also found among the top3 species with higher generality in the food web networks of the Tagus estuary, along with humans and rays, which were

both also included in the present work but did not occupy such top positions in the studied systems.

Top TL species are dominated by birds, some of them migrating or wintering birds, as is the case of the species with the highest TL in Ria de Alvor, the great cormorant *Phalacrocorax carbo* a very efficient fish predator (e.g. Boström et al., 2012; Veen et al., 2012; Catry et al., 2017), which elicits complaints from fish farmers all over Europe (Marzano et al., 2013). This species ranks fourth in TL in Ria Formosa and fifth in Ria de Aveiro, so it can be considered an important top predator in all the systems studied.

The balloon fish, *Lagocephalus lagocephalus*, is the top predator in Ria de Aveiro, and ranks sixth in TL in Ria de Alvor, certainly because its tetraodontidae venom grants it exclusion from predators (Pinto et al., 2019). Water snakes of the genus *Natrix* are also among the top10 TL in all systems. Mammals that feed directly on aquatic organisms (mostly on fish, crustaceans and amphibians) were also found in top10 TL ranks: the fox, *Vulpes vulpes*, in Ria de Aveiro and the ferret *Mustela putorius*, in Ria Formosa.

In the Tagus estuary (Portugal), a large open estuary, the cormorant *P. carbo* was also among the species with highest TL (Vinagre et al., 2019). Humans were also in the Top 10 TLs, in the Tagus estuary, which did not occur in the present study, even though humans were included in the webs. Mammals were not considered in the Tagus web (except for humans), while fish parasites were, and occupied most of the top TL positions, which did not occur in the present study because parasites were not included (due to lack of literature). Mendonça and Vinagre (2018) analysed food web networks from 23 small intermittent estuaries from around the world, including four systems from the Portuguese coast, and reported mostly fish at top TL positions, probably because the datasets used did not include birds, nor mammals.

It can be concluded that the complex networks of the food webs occurring in coastal lagoons present high diversity of species, organized in highly complex, yet short food chains, where disturbance can easily travel and affect many food web nodes due to low mean path length. They also differ from smaller intermittent estuaries, which are much less diverse, albeit similarly complex. The food chain length of coastal lagoon webs has intermediate size, smaller than that of large open estuaries but larger than that of small intermittent estuaries. These food web networks should thus be regarded as in a category of its own. More studies are needed to fully understand the networks particularities found here, however the present results should be taken into account when designing management plans for coastal lagoons.

CRedit authorship contribution statement

Catarina Vinagre: Conceptualization, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Writing – original draft, Writing – review & editing. **Cristina L. Gastón:** Data curation, Formal analysis, Investigation, Methodology, Validation, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.fooweb.2024.e00341>.

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