

Short food chains, high connectance and a high rate of cannibalism in food web networks of small intermittent estuaries

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ABSTRACT: Small intermittent estuaries are a common feature in some parts of the world. They are recognized as important refuge and nursery areas for several marine species. However, their biological dynamics are still poorly known. In fact, the network structure of their food webs remains undescribed. Highly resolved food webs were compiled for 23 small intermittent estuaries in the Northeast Atlantic, Mediterranean, Southwest Indian Ocean, and South Pacific. The structural network properties of these food webs were compared with those of larger open estuaries, lakes, and rivers, as well as marine and terrestrial ecosystems. The most important conclusion is that the network properties of these systems are different from those of larger open estuaries and more like other non-estuarine ecosystems. They also stand out from all other ecosystems, including larger open estuaries, in terms of omnivory, which was found to be remarkably high (83–92 %), probably due to the prevalence of opportunistic feeding. Nevertheless, all other properties were well within the ranges reported for other ecosystems; thus, the general organization rules of food web networks also apply to small intermittent estuaries. It was concluded that general rules applied to the management of estuaries should be looked at carefully when managing these smaller intermittent systems, since they have shorter chain lengths, higher connectance, and more cannibalism. Shorter chain length implies that disturbance is more likely to rapidly affect many food web components through predator–prey links, which may be counterbalanced by the effect of high connectance. These systems should, thus, not be looked at simply as smaller versions of larger open systems.

KEY WORDS: Estuarine ecosystems · Coastal lagoons · Niche model · Network theory

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INTRODUCTION

Small intermittent estuaries are common along microtidal to low mesotidal coastlines at mid-latitudes (McSweeney et al. 2017). Often, in these areas, during the dry season, the connections between the estuaries and the sea are closed, due to low freshwater input. Longshore beach sediment transport may also be an important factor leading to sand barrier formation at the mouths of small estuaries, restricting the marine influence for periods of time ranging from hours to years (Pollard 1994, Potter et

al. 2010). In such estuarine systems, freshwater inflows depend mostly on the rainfall regime and thus there are large fluctuations in their physical parameters (Riddin & Adams 2008).

Early definitions of estuaries excluded these water-bodies (Bell & Edwards 1980, Day 1980) because they encompassed only brackish waters with a permanent connection to the sea. However, the definition of estuary used by Potter et al. (2010) included, for the first time, also intermittent estuaries. Such small intermittent estuaries are very common and relatively well documented in Australia and South Africa

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(e.g. Cowley & Whitfield 2001, Froneman 2002, Teske & Wooldridge 2003, Dye & Barros 2005, Jones & West 2005, Gladstone et al. 2006, Haines & Thom 2007, James & Harrison 2010, Kennedy 2011, Scharler 2012, Edwards 2013), but they also occur in other parts of the world with similar climatic patterns (Barnes 1980, Dumay et al. 2004, Mouillot et al. 2007, Franco et al. 2008, Cardoso 2011). Globally, they represent 13% of the world's coastline (Barnes 1980).

Despite their small areas and highly variable physical conditions, intermittent estuaries are important ecological features in the coastal areas where they occur. Early stages of marine species that recruit to estuaries may enter these systems when they are open to the sea. The existence of a sand barrier makes the recruitment of larvae and juveniles from adjacent surf zones highly variable (Bell et al. 2001, Griffiths 2001a,b,c, Strydom 2003). The link between the fish populations occupying the surf zone and small intermittent estuaries has been documented in South Africa, where it was suggested that early life stages of fish concentrate in surf zones near small intermittent estuaries, entering the estuarine waters as soon as a connection to the sea is established (Whitfield 1989, Harris & Cyrus 1996, Cowley & Whitfield 2001, Strydom 2003, Kemp & Froneman 2004). Artificial openings to improve the water quality of these water bodies are conducted regularly throughout the world (Griffiths 1999, Jones & West 2005).

Small intermittent estuaries may encompass varied habitats, such as shallow open waters, seagrasses, macroalgae stands, sandy and muddy sediments, and shorelines fringed by mudflats, saltmarshes, or mangroves, which deems them important biodiversity spots (Pollard 1994, Gray et al. 1998). Despite important efforts to describe the biota of small intermittent estuaries, mostly concerning fish and macrozoobenthic communities (e.g. Teske & Wooldridge 2001, 2003, Dumay et al. 2004, Mouillot et al. 2005, 2007, James et al. 2007, James & Harrison 2010, Cardoso 2011, Edwards 2013), the food webs of these estuaries remain relatively understudied. These food webs probably have particularities linked to their small size and intermittent opening, such as high detritus processing, absence of organisms that do not tolerate environmental variability, reduced marine algal subsidy, etc.

May (1973) and Pimm (1982) proposed a topological approach to food webs that focused on the dynamic constraints that arise from species interactions. This gave way to many comparative works on the topology of food webs (e.g. Briand & Cohen 1984, Hall & Rafaelli 1991). Much recent work has centred

on food web network theory, a field of research that integrates food web ecology and complex networks (e.g. Williams & Martinez 2000, 2004, Dunne et al. 2002, 2004).

In complex network analyses, species are symbolized by nodes, and predator-prey links are depicted by links between such nodes. The structure of these food web networks can be assessed, analysed, modelled, and compared. This allows the comparison of food web topology at a high complexity level among vastly different ecosystems and the search for common universal organization characteristics of food webs (e.g. Solé & Montoya 2001, Montoya et al. 2006, Bascompte 2009). However, food web network properties are scale dependent, changing as diversity and complexity change (Martinez 1993, 1994) and thus direct comparisons can be misleading. The introduction of the niche model, proposed by Williams & Martinez (2000), was very important since it incorporated scale dependence, allowing the comparison of food webs encompassing different levels of diversity.

Comparative studies revealed that marine and terrestrial food webs share a fundamental network structure of prey-predator relations, supporting the idea that the food web complex networks are based on the same evolutionary and thermodynamic rules that set the universal organization for all natural systems (Dunne et al. 2004). However, Dunne et al. (2013) reported that estuarine food webs were consistently poorly fit by the niche model. The network structure of the food webs that occur in small intermittent estuaries is still unknown. Therefore, the present study assembled and analysed 23 highly resolved food webs based on data previously published for various parts of the world (Northeast Atlantic, Portugal, Mediterranean, France, Southwest Indian Ocean, South Africa, and South Pacific, Australia), to allow a good range of variation, and compared them with other recently published food webs from different types of ecosystems. The aim was to search for differences in the ranges of properties and niche model fit, and investigate whether the general organization rules of food web networks also apply to these highly variable ecosystems.

We hypothesized that the food web networks of small intermittent estuaries should be somewhat similar to those of larger open estuaries; however, due to the higher abiotic variability, a lower number of species is to be expected. A high rate of cannibalism should also occur in these systems, given that they are attractive feeding grounds for different life stages of the same species, exposing smaller individuals to predation by larger conspecifics. We also anticipated

that these networks should have a low fit by the niche model, similar to what has been repeatedly observed in larger open estuarine systems.

METHODS

Study areas

The literature was searched with the objective of finding areas with multiple small intermittent estuaries, where studies listing species from all biological compartments could be found. Portugal (Northeast Atlantic), France (Mediterranean), South Africa (Southwest Indian Ocean), and Australia (South Pacific) stood out as areas where these systems are frequent and where studies were available. Four study sites were selected from the NE Atlantic Portuguese coast (Aljezur, Bensafrim, Odeceixe, and Gilão), 5 from the Mediterranean French coast (Mauguio, Salses-Lecaute, Ingril, Thau, and Saint-nazaire), 7 from SW Indian Ocean South African coast (East Kleinemonde, Gqutywa, Kabeljous, Kasouga, Mpekweni, Mtati, and Van Stadens), and 7 from the South Pacific Australian coast (Avoca, Burril, Cockrone, Conjola, Illawarra, Terrigal, and Wamberal) (Fig. 1, general system features in Table 1). Some of the basic abiotic

data are missing for some of the systems. These small systems are very under-studied all over the world; their small size keeps them out of the focus of major abiotic and biotic studies. Many of these systems receive freshwater from various small inputs that have not been characterized from a hydrological perspective (or any other perspective). The use of more variables in a multivariate analysis to investigate how abiotic characteristics influence food web structure was initially planned; however, the scarcity of data rendered this task impossible.

For the NE Atlantic, the study by Cardoso (2011) was used to compile lists of species; for the Mediterranean, the studies by Dumay et al. (2004) and Mouillot et al. (2005, 2007) were used; for the SW Indian Ocean, the studies by Cowley & Whitfield (2001), Teske & Wooldridge (2001, 2003), Froneman (2004), James et al. (2007, 2008) and James & Harrison (2010) were used; and for the South Pacific, the studies by Dye & Barros (2005), Jones & West (2005), Gladstone et al. (2006), and Edwards (2013) were used.

Samples from all the estuaries included various sampling sites per system, encompassing the salinity gradient. All the studies used in the present study intended to characterize the systems from a biological perspective. Fish were captured using a beach seine in all systems. This is an active capture method



Fig. 1. Aerial photos of the study sites

Table 1. General description of the study sites

Area	Site	Coordinates	Catchment area (km ²)	Surface area (km ²)	Average depth (m)	Sal (%) average	Temp (°C) ave (range)
NE Atlantic	Aljezur ^a	37°21'02"N, 8°50'46"W	200	No data	Shallow	(0–37)	(12.2–28.9)
	Bensafrim ^b	37°06'37"N, 8°40'34"W	85	No data	1.95	No data	No data
	Gilão ^c	37°07'29"N, 7°38'72"W	221	No data	Shallow	No data	No data
	Odeceixe ^a	37°26'10"N, 8°47'08"W	250	No data	Shallow	(0–37)	(11.2–26.0)
Mediterranean	Mauguio ^d	43°34'28"N, 4°03'00"E	32	31.7	0.8	18.7 (4.7–29.3)	21.7 (16.9–25.7)
	Thau ^d	43°24'00"N, 3°36'00"E	75	70	4.0	37.8 (33.2–40.4)	20.9 (15.1–24.2)
	Salses-Leucate ^d	42°50'43"N, 2°59'43"E	54	65	2.0	33.0 (24.2–38.4)	20.6 (16.4–24.5)
	Ingril ^e	43°26'40"N, 3°47'12"E	No data	5.49	0.6	(24–32)	No data
	Saint-nazaire ^f	42°40'39"N, 3°00'24"E	260	7.8	<1.5	17.3 (8.20–37.70)	15.54 (12.80–16.80)
SW Indian Ocean	East Kleinemonde ^g	33°32'00"S, 27°03'00"E	46	17.5	1.3	16.93 (10.69–23.71)	21.06 (13.28–26.02)
	Gqutwyag ^g	33°21'59"S, 27°21'34"E	85	39.9	1.4	39.82 (35.66–43.19)	21.92 (15.11–28.01)
	Kabeljous ^g	34°00'00"S, 24°56'00"E	276	No data	1.0–1.5	32.76 (19.79–40.57)	20.16 (14.33–26.43)
	Kasouga ^h	33°39'00"S, 26°44'00"E	39	22	2.0	(0–40)	10–30
	Mpekwensi ⁱ	33°26'13"S, 27°13'57"E	65	57.9	1.1	(20–35)	(15.3–32.2)
	Mtati ⁱ	33°25'24"S, 27°15'34"E	130	37.9	1.6	(16.5–20.1)	(11–31)
	Van Stadens ^g	33°58'00"S, 25°13'00"E	271	No data	<2.0	13.02 (2.69–18.94)	20.10 (11.99–28.64)
South Pacific	Avoca ^j	33°28'00"S, 151°25'00"E	10.8	0.7	0.4	No data	No data
	Burrill ^k	35°24'00"S, 150°27'00"E	75	4.2	4.3	(25.0–37.5)	(11.4–26.0)
	Cockrone ^j	33°26'38"S, 151°25'44"E	6.9	0.3	0.6	No data	No data
	Conjola ^k	35°16'00"S, 150°30'00"E	145	4.3	1.0	(6.8–37.5)	(10.2–29.0)
	Illawarra ^k	34°33'00"S, 150°52'00"E	150	36	2.1	(22.2–38.1)	(10.5–28.4)
	Terrigal ^j	33°26'00"S, 151°26'00"E	8.9	0.3	0.5	No data	No data
	Wamberal ^j	33°26'00"S, 151°27'00"E	5.8	0.5	1.7	No data	No data

References: ^aMagalhães et al. (1987), ^bGomes (2010), ^cIsidoro et al. (2010), ^dIsnard et al. (2015), ^eMouillot et al. (2005), ^fMouillot et al. (2007), ^gStrydom & Neira (2006), ^hFroneman (2004), ⁱVorwerk et al. (2003), ^jGladstone et al. (2006), ^kJones & West (2005)

that covers the entire water column from the bottom to the surface, ensuring that both pelagic and benthic species are sampled. In the East Kleinemonde and Kasouga estuaries (SW Indian Ocean, South Africa), fish were captured by seine nets and gill nets (James et al. 2008, James & Harrison 2010). Invertebrates were collected with van veen grabs in the NE Atlantic (Portugal) (Cardoso 2011) and the SW Indian Ocean (South Africa) (Teske & Wooldridge 2001, 2003), Ekman-Birge grabs in the Mediterranean (France) (Mouillot et al. 2005), and hand corers in the South Pacific (Australia) (Dye & Barros 2005, Gladstone et al. 2006, Edwards 2013). Estuaries in the NE Atlantic (Portugal) and the Mediterranean (France) were sampled when open. The East Kleinemonde estuary, in South Africa, was sampled for 11 yr, encompassing both open and closed periods. We chose to work with the list of species captured when the system was open (James et al. 2008, James & Harrison 2010). For the Australian estuaries, there was available information on the species before and after barriers were open. For standardization purposes, we chose to work with the systems when open to the sea.

The lists of species published for these systems were used to build predator-prey matrices for each estuary, based on a literature search on their diets (see Table S1, in Supplement 1, and Supplement 2 for the species list and diet references, respectively; available at www.int-res.com/articles/suppl/m587p017_supp.pdf). Detritus was considered a food web node in all estuaries. The predator-prey matrices were developed from literature not restricted to small intermittent estuaries. This is general practice in the field of food web network structure analyses, the idea being that if a predator eats prey in one environment it cannot be ruled out that it could eat it if it finds it in another environment. There is no way of quantifying the error inherent to this method, given that literature on the diets of these organisms in small intermittent estuaries is non-existent for most of the species.

These matrices were used as input on the software Network3D (Yoon et al. 2004, Williams 2010) to assemble highly defined food webs, describing predator-prey relations. The networks assembled were based on trophic species. Trophic species are taxa

that share a similar set of prey and predators (Briand & Cohen 1984). The use of trophic species is a convention in structural network food webs. They reduce biases in the methodology associated with unbalanced resolution of different biological compartments between food webs (Williams & Martinez 2000).

Eighteen network properties were calculated (Table 2): number of trophic species (S), links per species (L/S), connectance (C), where $C = L/S^2$, T (percentage of top predators), I (percentage of intermediate species), B (percentage of basal species); Can (percentage of cannibals); Omn (percentage of omnivores), H (percentage of herbivores and detritivores), resource count, consumer count, TL (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). All calculations were carried out using the software Network3D (Yoon et al. 2004, Williams 2010).

The ranges of the food web network properties analysed were compared with those of highly defined food web networks published for other ecosystems (see Table 4). Significant differences among the network properties, and the percentage of niche model errors, for the various locations were in-

vestigated with an ANOVA. The ANOVA assumptions were previously investigated. Normality was investigated through a Shapiro-Wilk's test and homoscedasticity through a Levene's test. Each property was tested separately and a significance level of 0.05 was considered.

The factor 'location' was tested to ensure that we were describing similar entities with no important differences. At the starting point of this study, we knew that these systems vary widely but have some similarities (climate, size, intermittent nature) that might set their food web structure apart from that of larger open estuaries. If differences existed then small intermittent estuaries should not be dealt with using the same management strategies applied to larger open estuaries.

Comparison with other highly defined food web networks published is a common procedure in the field of food web structural network analysis. It intends to confirm or refute the important issue of whether there are general rules in the organization of food web networks possibly due to common evolutionary and thermodynamic mechanisms that shape the general complex structure of all food webs (Williams & Martinez 2000, Camacho et al. 2002, Dunne et al. 2004). General organization rules could, in the future, lead to some common management strategies.

Table 2. Description of the food web network properties estimated

Food web network property	Network property description
S	Number of trophic species
L/S	Links per species
C	Connectance, $C = L/S^2$
T	Top species (taxa that lack any predators or parasites)
I	Intermediate species
B	Basal species (taxa that lack 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 plus 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 short-weighted 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, which estimates links per taxon
Clust	Clustering coefficient, the mean fraction of species pairs connected to the same species that are connected to each other

The Niche model

The predictive success of the niche model in terms of food web properties was compared among the food web networks (Williams & Martinez 2000). The niche model uses solely 2 parameters: the number of trophic species (S) and connectance (C). It gives each species (i) a random 'niche value' (n_i) from the interval (1, 0), and each species is limited to feed on all prey species within a range of values (r_i) of which randomly chosen centre (c_i) is less than the consumer's niche value. This model allows up to half a consumer's range to include species with higher niche values than the consumer, this way allowing looping and cannibalism.

The predator is forced to consume all species within its feeding range. Monte Carlo simulations were used, for each food web, to create 1000 niche model webs with the same S and C as the original empirical web, allowing the estimation of a model mean and standard deviation for each of the network properties. Whenever the normalized error (raw error divided by model SD) between the empirical property and the mean model value for that property was within ± 1 model SD, the model was deemed to be a good fit to the empirical data (Dunne et al. 2004).

RESULTS

The data assembled for the food webs of the study sites resulted in lists ranging from 39 to 61 taxa in the NE Atlantic (Portugal), 36 to 54 taxa in the Mediterranean (France), 48 to 78 taxa in the SW Indian Ocean (South Africa), and 50 to 119 taxa in the South Pacific (Australia). These taxa corresponded to 26 to 36 trophic species in the NE Atlantic (Portugal), 28 to 34 trophic species in the Mediterranean (France), 35 to 43 trophic species in the SW Indian Ocean (South Africa), and 37 to 59 trophic species in the South Pacific (Australia) (Fig. 2).

As is common practice in food web networks, some biological compartments were aggregated due to low definition of predator's diet. This was particularly evident for phytoplankton, zooplankton, and some macrobenthic groups.

Some differences among countries were detected for some food web network properties. Number of taxa was lower in the NE Atlantic (Portugal) and the Mediterranean (France) than in the SW Indian Ocean (South Africa) and the South Pacific (Australia) (Fig. 2). This pattern was similar for L/S , resource count, and consumer count (Fig. 2). The Mediterranean (France) presented lower I but higher TL . The NE Atlantic (Portugal) presented lower T . No differences were found among countries for C , H , Omn , Can , chain, and path (Fig. 2).

Taxa most frequently among the top 3 highest TL were marine fish species in all countries, with only one exception, *Paragnathia formica*, an isopod, in the NE Atlantic study sites (Table 3). The taxa most frequently found in the top 3 in terms of connectivity varied within and among the countries analysed, with detritus present in 7 out of the 7 study sites in the SW Indian Ocean (South Africa), the fish *Pomatoschistus microps* in 4 out of 4 in the NE Atlantic study sites, Polychaeta in 4 out of 5 of the Mediterranean study sites, and Amphipoda in 5 out of 7 of the South Pacific study sites (Table 3).

The small intermittent estuaries analysed here presented a number of taxa in the lower range of what was previously reported for larger open estuaries, but well within the ranges reported for other marine and terrestrial ecosystems (Table 4). Connectance and cannibalism were higher than in larger open estuaries, but well within the ranges reported for other marine and terrestrial ecosystems (Table 4).

One of the food web network properties that stood out was chain length, which was remarkably lower than in larger open estuaries, and much lower than in all other ecosystems, marine and terrestrial, except for seagrass beds, whose chain lengths are also reported to range from 1.9 to 2.0 (Table 4). The omnivory values observed in these small intermittent estuaries stand out from those found in any other ecosystems, including larger open estuaries, because of their remarkably high values (Table 4).

Mean niche model percentage of errors varied between 34 and 38% for the Mediterranean, the SW Indian Ocean, and the South Pacific. The NE Atlantic presented a significantly lower percentage of errors with only 17% (Fig. 3). This means that the niche model predictive success varied between 62% (Mediterranean) and 83% (NE Atlantic). Fig. 4 shows a visual representation of the complex food web networks assembled.

DISCUSSION

The food web networks of the small intermittent estuaries analysed in the present work revealed that these systems are different from larger open estuaries. Yet, their food web network properties fall within the ranges reported for other non-estuarine ecosystems, both marine and terrestrial.

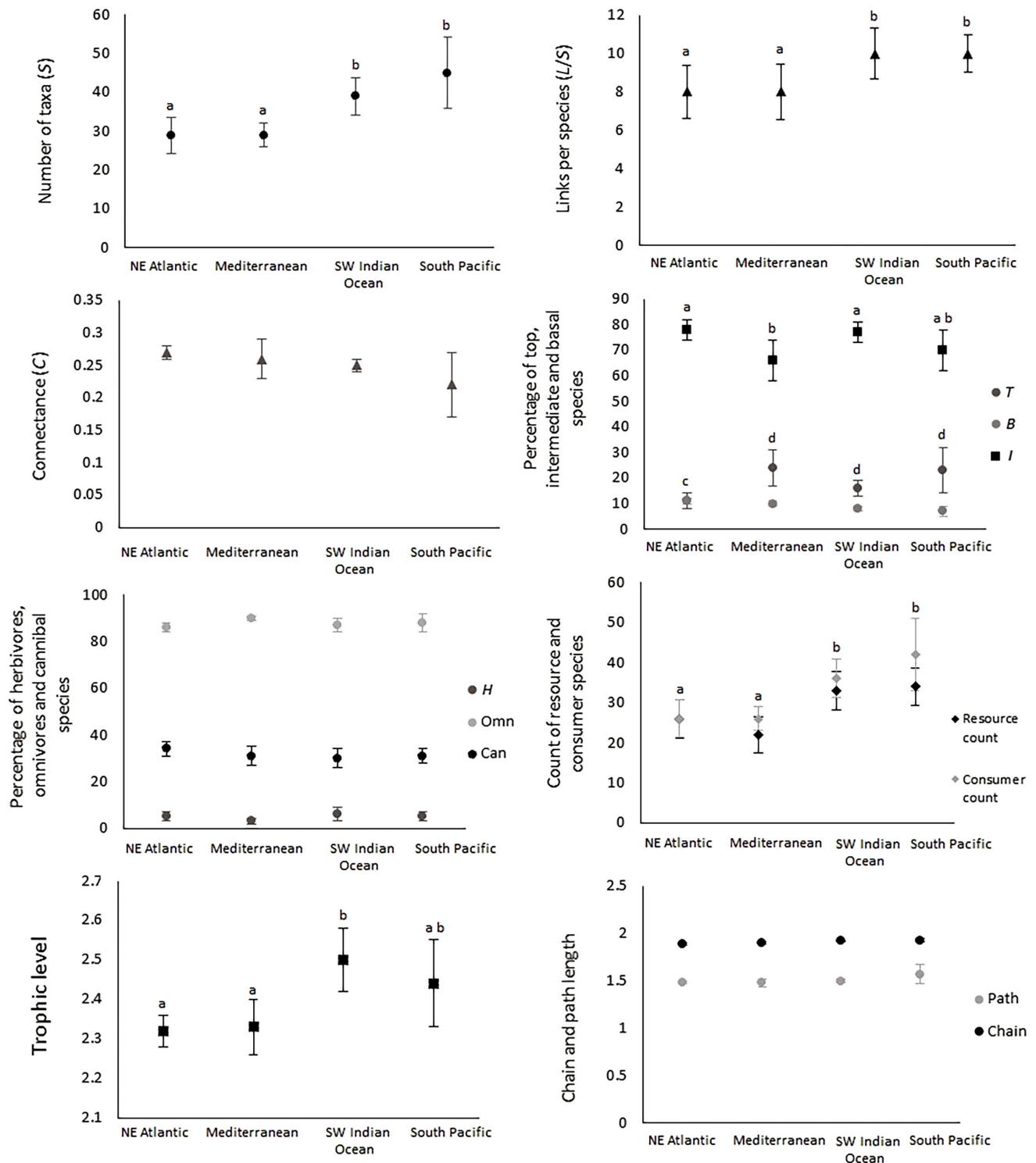


Fig. 2. Variation of the main food web properties (defined in Table 1) across the different locations (dots indicate mean values, bars indicate standard deviation, letters indicate significant differences)

The highest trophic levels in the small intermittent estuaries analysed were generally occupied by marine fish species. This highlights the important role of these systems as feeding areas for species of marine

fish that tolerate the large amplitudes in abiotic variables that occur in these systems, similar to what occurs in larger open estuaries, but requiring even higher levels of tolerance to abiotic variation

Table 3. Taxa most frequently in the top 3 of highest trophic level (short-weighted) and connectivity in the food webs analysed

	Taxa most frequently in the top 3 highest trophic level	Number of webs where the taxa were in the top 3 highest trophic level	Taxa most frequently in the top 3 highest connectivity	Number of webs where the taxa were in the top 3 highest connectivity	Total webs analysed
NE Atlantic	<i>Dicentrarchus labrax</i> (fish)	4	<i>Pomatoschistus microps</i> (fish)	4	4
	<i>Paragnathia formica</i> (isopod)	3	<i>Carcinus maenas</i> (crab)	2	
	<i>Pomatoschistus microps</i> (fish)	2	Zooplankton	2	
Mediterranean	<i>Echiichthys vipera</i> (fish)	5	Polychaeta	4	5
	<i>Solea solea</i> (fish)	4	<i>Gobius niger</i> (fish)	4	
	<i>Anguilla anguilla</i> (fish)	3	<i>Pomatoschistus microps</i> (fish)	3	
SW Indian Ocean	<i>Argyrosomus japonicus</i> (fish)	7	Detritus	7	7
	<i>Lichia amia</i> (fish)	6	Zooplankton	4	
	<i>Caranx sexfasciatus</i> (fish)	16	Polychaeta	3	
South Pacific	<i>Anguilla reinhardtii</i> (fish)	3	Amphipoda	5	7
	<i>Atherinosoma microstoma</i> (fish)	3	Polychaeta	4	
	<i>Atherinosoma elongata</i> (fish)	5	Detritus	4	

(McLusky 1981, Elliott & Hemingway 2002, Able 2005, Jones & West 2005). Previous studies in South Africa and Australia revealed that fish abundance and composition is associated with whether the estuary mouth was recently closed, and the timing and

duration of closure (Bennett 1985, 1989, Potter & Hyndes 1994, 1999, Young et al. 1997, Young & Potter 2002). When these systems remain closed for long periods of time, fish diversity and density declines (Loneragan & Potter 1990).

Table 4. Ranges of commonly reported structural food web properties for food webs from small intermittent estuaries and a variety of other ecosystem types. *S*: number of trophic species; *C*: connectance; *L/S²*: 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 estuarine ecosystems 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	<i>N</i>	<i>S</i>	<i>C</i>	<i>L/S</i>	<i>T</i>	<i>I</i>	<i>B</i>	<i>Can</i>	<i>Omn</i>	<i>TL</i>	<i>Chain</i>	<i>Path</i>
Small intermittent estuaries, (all) ^a	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
Small intermittent estuaries, NE Atlantic ^a	4	26–36	0.27–0.28	6.9–9.9	8–15	74–83	8–12	31–37	85–89	2.4–2.4	1.9–1.9	1.5–1.5
Small intermittent estuaries, Mediterranean ^a	5	28–34	0.25–0.27	7.5–8.3	21–25	64–70	9–11	27–32	89–91	2.4–2.4	1.9–1.9	1.5–1.5
Small intermittent estuaries, SW Indian Ocean ^a	7	35–43	0.23–0.27	8.2–11.4	10–19	72–83	7–9	22–33	83–89	2.4–2.6	1.9–1.9	1.5–1.6
Small intermittent estuaries, South Pacific ^a	7	37–59	0.16–0.29	8.4–10.6	16–27	67–76	5–8	28–35	86–92	2.5–2.7	1.9–2.0	1.5–1.7
Large open estuaries ^b	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
Seagrass beds ^c	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
Marine ^d	4	29–245	0.05–0.24	7.0–17.8	0–4	93–98	2–7	4–42	76–87	2.9–3.2	6.4–15.3	1.6–1.9
Lake/pond ^e	5	25–172	0.12–0.32	4.3–25.1	0–9	66–92	4–32	12–32	38–60	2.0–2.7	4.0–10.7	1.3–1.9
Stream ^f	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
Terrestrial ^g	4	29–155	0.03–0.31	1.6–9.0	0–31	56–90	13–18	0–66	21–76	2.4–3.0	3.2–8.4	1.4–3.7

References: ^aPresent study; ^bHuxham et al. (1996), Lafferty et al. (2006), Hechinger et al. (2011), Mouritsen et al. (2011), Thieltges et al. (2011), Zander et al. (2011), Vinagre & Costa (2014); ^cColl et al. (2011); ^dOpitz (1996), Yodzis (1998), Link (2002), Dunne et al. (2004); ^eWarren (1989), Martinez (1991), Havens (1992), Dunne et al. (2004); ^fTownsend et al. (1998), Romanuk et al. (2006); ^gPolis (1991), Goldwasser & Roughgarden (1993), Waide & Reagan (1996), Memmott et al. (2000)

The most connected nodes in these networks were often detritus (SW Indian Ocean and South Pacific), large macrobenthic groups, such as Amphipoda and Polychaeta (SW Indian Ocean and South Pacific), and a generalist euryhaline fish, *Pomatoschistus microps* (NE Atlantic and the Mediterranean). The important role of detritus in estuarine food webs is well documented for larger open estuaries (e.g. Simenstad & Wissmar 1985, Riera et al. 2002, Vinagre et al. 2008, 2011, 2012); it is thus not surprising that this node is also highly connected in small intermittent estuaries. Terrestrial run-off in wet periods should foster an important detritivorous community within these systems, similar to what happens in larger open estuaries (Peterson et al. 1985). During wet periods, the estuary will be open and flushing detritus to the sea, but it will also be accumulating inside the estuary because its shallow waters have low hydrodynamism. The higher input of detritus that occurs in wet periods will foster abundant populations of various species of benthic organisms forming a detritivorous community that is a pivotal link in the detrital energy pathway that occurs in estuarine food webs (e.g. Simenstad & Wissmar 1985, Vinagre et al. 2011). This has been accessed in large estuaries, permanently open to the sea, so it can be assumed that it also happens in smaller intermittent estuaries.

The identification of large macrobenthic groups, such as Amphipoda and Polychaeta, as highly connected nodes is due to the high aggregation of species into such nodes caused by the low definition of their predator's diets, and is a common feature in most food web networks. The fish *P. microps* also appears as a highly connected node in the study sites of the NE Atlantic and Mediterranean. This is a small gobiidae, which is euryhaline and eurythermal, and thus a very

common species in European estuaries. On the Mediterranean coast, another gobiidae fish *Gobius niger* was also among the most-connected food web nodes. These fish are not only generalist predators but also easy prey for higher trophic levels due to their small size (e.g. Salgado et al. 2004, Leitão et al. 2006), which justifies their high connectivity in these food web networks.

The food web network properties analysed for these systems generally fall within the range of other ecosystems, both marine and terrestrial; however, they stand out in terms of omnivory, with remarkably high values (83–92%). The percentage of omnivory in larger open estuaries varies from 53 to 84%; thus, small intermittent estuaries seem to have an even higher level of omnivory than larger open estuaries.

This is probably due to a prevalence of opportunistic feeding by marine fish and crustaceans that enter these systems in search of additional feeding grounds. A biased definition at the fish level could also be at play, given that omnivorous fish are better represented in the diet literature than other animal groups. Fishes are easier to identify and study than lower-trophic-level organisms, such as macrobenthos, zooplankton, phytoplankton, etc. Various studies have pointed out that a better resolution at the basal level, where the aggregation is higher, should mitigate current high omnivory levels in marine food webs (Cohen et al. 1993, Dunne et al. 2004, Vinagre & Costa 2014). This also applies to estuarine food webs, which present similar resolution biases. However, high omnivory may also be the result of opportunistic feeding based on mouth opening size being widespread and prevalent in marine and estuarine systems (Polis & Strong 1996, McCann et al. 1998, Closs et al. 1999, Link 2002). Resolution biases have the potential to hinder food web network structure analyses, especially when integrating or comparing ecosystems from different parts of the world, as done in the present study. Different levels of difficulty in identifying different biological compartments, different levels of expertise, different methods, and different logistical problems in the field may all have some effect in the final resolution of the food webs. Therefore, care should be taken when selecting the reference studies and species lists to ensure that the methodologies and expertise behind the studies are similar and comparable.

Mean niche model predictive success (62–83%) was very similar to that previously found for large open estuaries, which range from 47 to 80% and can be considered a poor fit (Dunne et al. 2013). Dunne et al. (2004) found that niche model predictive success

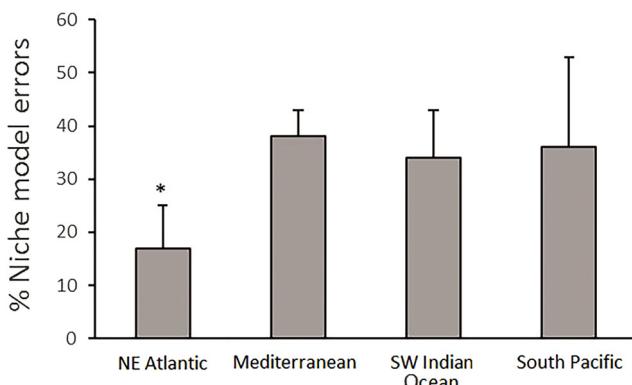


Fig. 3. Percentage of niche model errors for 18 network structure properties (defined in Table 1) that are greater than 1%. Error bars indicate standard deviation and the asterisk indicates a significant difference.

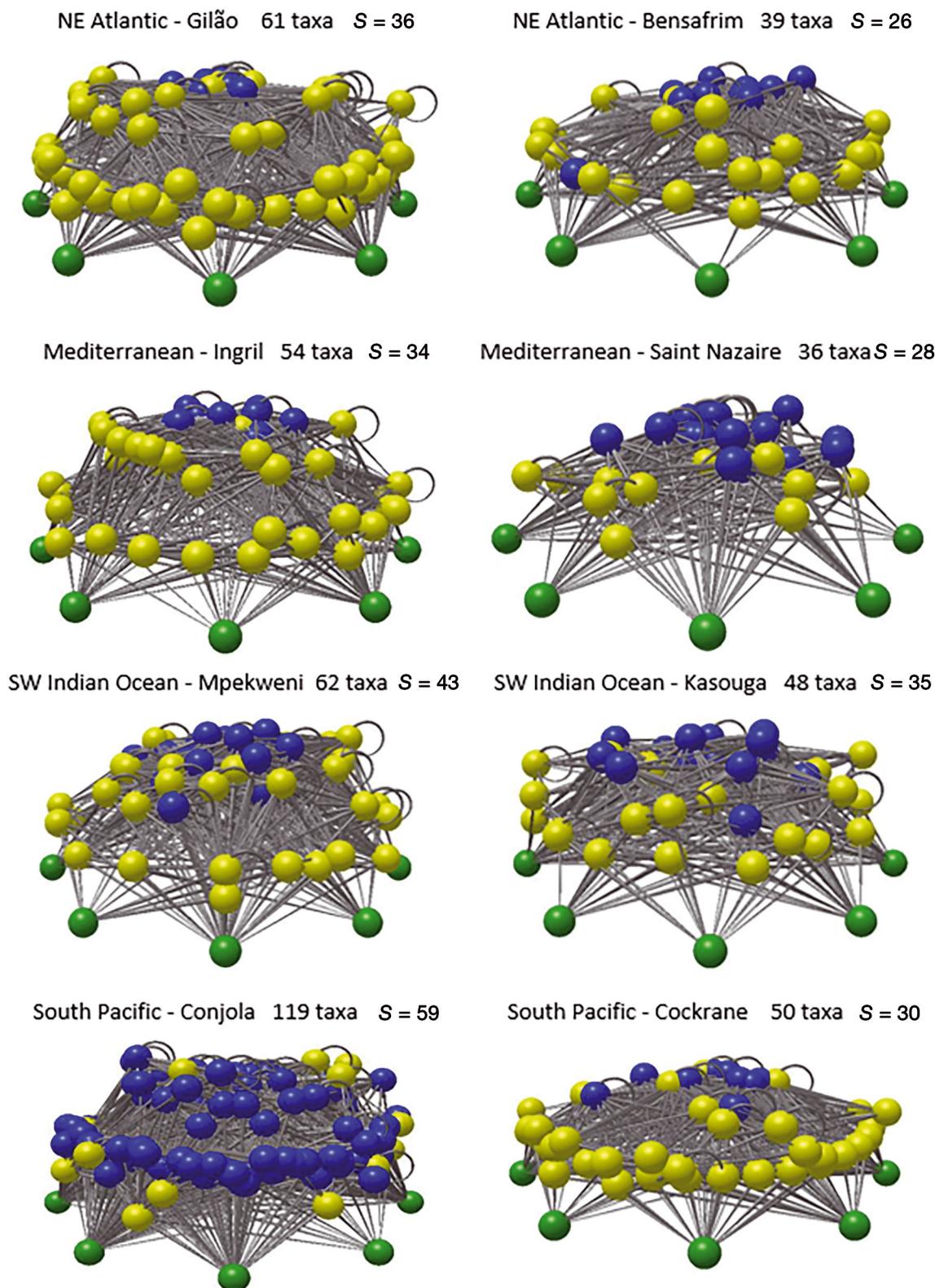


Fig. 4. Network3D images of selected small estuaries' trophic species food webs. Green nodes: basal taxa; yellow nodes: invertebrates; blue nodes: vertebrates. Trophic species are groups of taxa whose members share the same set of predators and prey and are thus aggregated in single nodes. On the left the food webs with the highest number of taxa, while on the right the ones with the lowest number of taxa, at each location are presented

was 87% for 3 highly resolved marine food webs. It can thus be concluded the niche model has a poorer fit to estuaries in general, both large and small, when compared with marine food webs.

The most important finding of the present study is that the food web networks of small intermittent estuaries present important differences to those of larger open estuaries. The networks of small intermittent estuaries have higher connectance, higher cannibalism, and lower chain lengths. Cannibalism is usually the result of a very wide size gap between adults and juveniles and larvae, and should be more common in areas where early life stages concentrate, such as nursery areas. Estuarine waters attract larvae and juveniles of fish because of their warm waters and richness in macrobenthic prey (Haedrich 1983), particularly in spring and summer; however, this also attracts the adults of some species, which end up feeding on their own young. Although this is a common feature of estuaries, it seems to be more pronounced in small intermittent estuaries, possibly because adults may have less space to forage and have higher encounter rates with their young.

Lower chain lengths mean that disturbance is more likely to rapidly affect many food web nodes through predator-prey links (Williams et al. 2002). This has been previously reported for marine food webs (Dunne et al. 2004). In the case of small intermittent estuaries, it is probably due to the absence of larger top predators in these low depth waters. Low depth and restricted estuarine mouths make it very hard for large predators to enter these systems, giving way for short chain lengths. This knowledge is very important from a management perspective. Although larger open estuaries are much better studied, their management strategies should not be directly applied to smaller intermittent estuaries since their shorter chains lengths make them more susceptible to disturbances. In fact, it would be more effective to compare them with seagrass beds, which have similar values of chain length (Table 4) and are known to be fragile ecosystems (e.g. Halpern et al. 2007, Jordá et al. 2012).

The vulnerability associated with shorter chain lengths may, however, be counterbalanced by the higher connectance found for these systems, since previous studies have shown that high connectance leads to higher robustness to species loss (Albert et al. 2000, Solé & Montoya 2001, Dunne et al. 2002, 2004).

Network analysis, as conducted in the present study (a first description of an ecosystem type), will not inform on any particular management actions effectiveness. However, our results highlight the

importance of not applying management strategies used in larger open estuaries in small intermittent estuaries because their basic food web organization is different. Small intermittent estuaries should be regarded as systems that work differently from larger open estuaries and more research should be focused on them.

CONCLUSION

Given that the food web network properties of small intermittent estuaries are within the ranges reported for other marine and terrestrial ecosystems, this study adds to the evidence that indicates that there are general rules in the organization of food web networks possibly due to common evolutionary and thermodynamic mechanisms that shape the general complex structure of all food webs (Williams & Martinez 2000, Camacho et al. 2002, Dunne et al. 2004). However, the differences in food web network properties found between these small intermittent estuaries and large open estuaries mean that caution should be taken when transposing management strategies from larger open estuaries to smaller intermittent estuaries.

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