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Changing webs—Variation of complex networks over a tidal cycle in an intertidal rocky reef

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ABSTRACT

Incorporating temporal variation in models is one of the most important challenges in food web research. One of the environments where time causes profound changes is the intertidal zone, where the immersion-emersion cycle drastically changes the abiotic and biotic conditions. Intertidal rocky shores have been intensively studied, however the variation in the complex food web network that occurs during a tidal cycle remains undescribed. Highly resolved food web networks were assembled for an intertidal reef depicting the food web during low and high tide, and with and without tide pools. It was concluded that high tide adds new species to the web, but it does not add complexity since network connectance was not changed. This occurs because incoming species are mostly highly generalist fish, which add many new links to the web. Tide pools, however, add not only diversity but also complexity. Webs were dominated by intermediate species, with the proportion of top consumers fluctuating throughout the tidal cycle, being lowest during low tide and highest at high tide, due to the incoming larger vertebrate predators. Consumer taxa outnumbered resource taxa, except at low tide when pools are present. Mean trophic level was lowest at low tide (2.3) and highest at high tide with pools (2.6). Omnivory was high and showed little change. "Chain", the number of links connecting top to basal species, was stable but low. This implies that disturbance can rapidly travel bottom-up or top-down through predator-prey links. The increased connectance given by the addition of tide pools likely increases robustness to disturbances, an important feature in coastal areas so often impacted by human action.

1. Introduction

The emergence of network theory and the increase in computational power has allowed the integration of food web ecology and complex networks analysis in a promising field, called food web network theory, that enables the investigation of ecological processes at different organizational scales – from the species level to the ecosystem level (e.g. Thompson et al., 2012). The reductionist approach to community ecology - at the individual, species or population level - can thus be merged with the holistic approach, that allows the study of fluxes of energy and matter between large ecological compartments but lacks species-level detail (e.g. Loreau et al., 2001; Montoya et al., 2003; Thompson et al., 2012).

In the analysis of complex food web networks, species are represented by nodes and predator-prey links are symbolized by lines between those nodes. The structure of these networks depicts food web topology, which can be analysed, modelled and compared. Knowing the basic topology of complex food webs in a crucial first step for the understanding of food web organization, functioning and potential responses to disturbances (e.g. Williams and Martinez, 2000, 2004; Solé and Montoya, 2001; Bascompte, 2009). Additionally, the comparison of food web topology over vastly different ecosystems enables the search for universal features of food web organization (Dunne et al., 2002a, 2004; Brose et al., 2019; Mendonça et al., 2019; Mendonça et al., 2018; Vinagre et al., 2019).

Thompson et al. (2012) identified the incorporation of time as one of the most important challenges in food web research. It has been shown that intra-annual variation alters food web topology (Tavares-Cromar and Williams, 1996; Thompson and Townsend, 1999). It is also well-known that top predators are usually larger and long-lived animals, in contrast to single-cell organisms such as those included in the phytoplankton, which are extremely short-lived. This means that there is a general trend where the temporal-scale of response increases from the bottom to the higher levels of the food web. This has been modelled

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using a complex food web networks approach to examine the effect of climate warming on energy dynamics and species persistence in food webs (e.g. Petchey et al., 1999; Woodward et al., 2010; Gauzens et al., 2020).

However, much remains to be studied concerning the temporal variation of complex food web network structure. One of the environments where time causes profound changes is the intertidal zone, where the immersion-emersion tidal cycle drastically changes the abiotic conditions within a daily and semi-lunar timescale. Intertidal rocky shores have been intensively studied. Their easy access makes them natural laboratories for the study of biological patterns and biotic interactions (e.g. Underwood, 1980; Menge et al., 1995; Navarrete and Menge, 1996; Hawkins et al., 2008). The complex food webs structure occurring in intertidal environments have been described in temperate intertidal mudflats in New Zealand and Germany-Denmark (Thielgtes et al. 2011; Mouritsen et al., 2011), in the temperate rocky shores of Chile (Kéfi et al., 2015) and in the Sub-Arctic Sanak Islands (Maschner et al., 2009; Dunne et al., 2016). Recently, Mendonça et al. (2018) presented an extensive study of the complex food webs occurring in intertidal rock pools, in different parts of the world, including Canada, United Kingdom, Portugal and Brazil, using a highly-resolved database. However, none of these studies incorporated the temporal variation that occurs in these environments with the tidal cycle, where important top consumers are excluded from the web during low tide, and only organisms that can withstand some level of desiccation can occur. Tide pools are important in these webs because they allow animals that cannot live out of the water to extend their distribution into the intertidal (Metaxas and Scheibling, 1993), however they still exclude the larger top consumers due to their low depth and restricted area.

Given this gap in the knowledge of the complex topology of food webs, the present study set out to investigate the variation of the complex food web occurring in rocky intertidal environments over the tidal cycle. Given the ecological importance of tide pools, their presence/absence was also incorporated into the food web network models produced. Because there is a scarcity of studies in tropical marine environments, Brazil's tropical coast with its easily accessible rocky reefs, was chosen for this study. Highly resolved datasets, where taxa were identified to the species-level whenever possible, were used in this work, to allow an analysis within the food web network theory framework and produce outcomes (network properties) directly comparable to similar analyses previously published for marine ecosystems, such as J.A. Dunne et al. (2004), Maschner et al. (2009), Mendonça et al. (2018), Mendonça and Vinagre (2018), Dunne et al. (2016).

The main objectives of this work were to investigate 1) the temporal variation in network properties in a tropical intertidal rocky reef by assembling the complex food web network occurring during high tide and low tide, 2) the role of tide pools in increasing diversity and complexity by assembling food webs with and without tide pools, 3) to compare the network properties of this tropical intertidal food web with other food webs from different ecosystem types, and 4) to evaluate how these food webs fit the theoretical niche model proposed by Williams and Martinez (2000). The niche model incorporates scale-dependence, thus allowing the comparison of the structure of food webs with different levels of diversity and complexity (e.g. J.A. Dunne et al., 2004, 2013).

2. Methods

2.1. Study area

The study area is located in the northeast of Brazil, State of Ceará, where the climate is predominantly tropical semi-arid (Leão and Dominguez, 2000). The coastline is mainly composed by long sandy beaches, oftentimes bordered by elongated and discontinuous shallow sandstone rocky reef platforms that extend from the beach nearly two hundred meters seaward (Maida and Ferreira 1997; Leão and Dominguez, 2000). Tides are semidiurnal (Leão and Dominguez, 2000) and sea temperature typically varies between 26 °C and 30 °C (see www.seatemperature.org).

For this study, two locations were chosen, Flexeiras and Guajiru, distanced 2.25 km apart. At each location, two sites were surveyed, Flexeiras A (3°13′04,55′’S, 39°16′06,63′’W), Flexeiras B (3°13′02,30′’S, 39°15′58,70′’W), at Flexeiras, and Guajiru A (3°13′23,29′’S, 39°15′00,00′’W) and Guajiru B (3°13′26,23′’S, 39°14′56,72′’W) at Guajiru. Both beaches are sandy with shallow, flat, and discontinuous rocky reef platforms that start in the lower intertidal zone and extend ~150 m into the sea at its farthest points. During low tides the reefs are partially emersed leading to the formation of numerous intertidal pools.

2.2. Sampling

Sampling was conducted at two spring tides, in December of 2014. At each site, two 10 m transects were sampled, perpendicular to the coastline, during ebb tide. At each meter a 25 cm x 25 cm quadrat was scraped from the rock surface. A total of 8 transects were sampled. During high tide, similar transects were carried out starting at the same points, using snorkeling equipment, for the video recording of species that swim into these areas (visual non-destructive survey). Gopro Hero3 cameras were used. Water depth was approximately 1 m during high tide.

At each site, four intertidal rock pools were chosen for sampling, within the first 10 m of the reef platform. A total of 16 pools were sampled. All pools were located in the lower intertidal. The size range of the selected pools ensured a minimum patch size for benthic community development, yet still allowing a complete record of all macro-organisms found in each pool (depth, 0.11 m-0.58 m; surface area, 0.16–18.78 m^2, as estimated from scaled digital photographs using the software ImageJ). Main composition of substrate cover was registered, as well as water temperature (±0.1°C) and salinity (±1‰) (see supplementary Table 1 for pool characteristics).

For pools with an area $\leq$0.5 m^2, one 50 ml sample of bottom sediment was taken (whenever there was sediment at the bottom), for pools with an area >0.5 m^2 and $\leq$ 2 m2 two samples, and for pools >2 m^2, three samples. Additionally, three 5 cm x 5 cm quadrats were scrapped from the rock surface, in each pool. Macro-organisms were collected by hand or using hand-nets and identified *in situ* (and returned alive to the pool), except when taxonomic issues demanded that the species was taken to the laboratory for detailed observation, consultation of identification keys and/or taxonomic experts. All sediment and scrapping samples were preserved in 70° alcohol with Rose Bengal. Organisms were later identified in the laboratory, using a stereomicroscope or a microscope. Microorganisms were not included in the food web, with the exception of zooplankton and phytoplankton – included as aggregates and assumed to always be present – due to the low resolution of their predators' diets in the published literature. This results in aggregate nodes for phytoplankton and zooplankton, meaning that the web is unevenly resolved, which is a limitation for the understanding of the whole complexity of the network. However, this limitation is shared with all other studies done in the context of food web network theory so it does not hinder the comparisons done in the discussion. No terrestrial animals (e.g. marine birds, rodents) were observed over the study area.

2.3. Food web assemblage

A cumulative platform-wide food web was compiled encompassing all species sampled in this intertidal zone, to ensure a good description of the complex food web network in the area. This is a common procedure in the description of complex food web networks (e.g. J.A. Dunne et al. 2004, 2016; Wood et al., 2015). This web was produced using the complete species lists (Supplementary Table 2), from all the sampling, at all sites, encompassing the species present in the transect quadrats, in the video records and in the intertidal rock pools, to obtain the full web of the shallow reefs' habitat during high tide.

Another three webs were assembled, one that contained all of the species except the ones exclusively registered in the pools, to obtain the web of the platform during high tide over the platform; another excluding the videorecording done at high tide to assemble the web that occurs during low tide, and another that excluded not only the videorecording but also the species that occur exclusively in tide pools to obtain the food web of the rocky platform during low tide with no pools. Published information on each species diet anywhere in the world (Supplementary Table 3) was used to assemble the predator-prey matrices that are the basis of the food webs, following the methodology used in other food web network theory works (e.g. J.A. Dunne et al. (2004), Maschner et al. (2009), Coll et al., 2011, Mendonça et al. (2018), Dunne et al. (2016)), to allow direct comparison of web structure. All taxa that are prey to each node were included throughout their life span. The highest possible taxonomic resolution in both feeding data and species identifications was used.

2.4. Food web networks

The food web networks assembled in this work were based on trophic species, also called trophospecies. This means that groups of taxa with the same predators and prey are aggregated into one trophic species (Briand and Cohen, 1984). This is a convention used in the analyses of structural food web networks to reduce methodological biases related to uneven resolution of taxa within and among food webs (Briand and Cohen, 1984; Williams and Martinez, 2000; Dunne et al., 2013).

For all food webs, 18 structural properties were estimated and compared (description of each property in Table 1). A biodiversity metric was estimated; number of trophic species (S). Metrics of trophic interaction richness were investigated (Table 1), links per species (L/S) and connectance (C), along with metrics that indicate the proportion species types (Table 1), top (T), basal species (B), intermediate species (I), cannibal species (Can), herbivores plus detritivores (H), and omnivore species (Omn). Additionally, resource and consumer count were calculated for each trophic species. Network structure properties were also estimated (Table 1), mean number of links connecting top species to basal species (Chain); characteristic path length (Path); mean short-weighted trophic level (TL); clustering coefficient (Clust); standard deviation of mean generality (GenSD); vulnerability (VulSD); and normalized standard deviation of links (LinkSD).

Food web network properties were compared throughout the tidal cycle (Table 2). Network properties were estimated for each node (trophic species) to allow the analysis of the top 5 trophic species with the highest TL and vulnerability, throughout the tidal cycle and the impact of the presence of pools in that list (Tables 3, 4) Network properties were also compared with the range of values previously published for other intertidal rocky reefs, as well as for other marine and terrestrial food webs (Table 5).

Table 1
Definition of the food web properties calculated.

Food-web properties		Description
Number of trophic species	S	Number of species in the food web after being converted into a trophic web
Links per species	L/S	Number of pred/prey links per species
Connectance	C	Proportion of actual trophic links to all possible links (L/S^2)
Top species	T	Species with prey and not predators or parasites
Intermediate species	I	Species with both predators and prey
Basal species	B	Species with predators and no prey
Herbivores plus detritivores	H	Species who prey on primary producers
Cannibals	Can	Species which prey on their own species
Omnivores	Omn	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	TL	Trophic level averaged across taxa
Mean food chain length	Chain	Mean number of links in every possible food chain or sequence of links connecting top species to basal species
Mean shortest path length	Path	The mean shortest set of links between species pairs
Generality standard deviation	GenSD	Resources per taxon, how many prey items a species has
Vulnerability standard deviation	VulSD	Consumers per taxon, how many predators a species has
Normalized standard deviation of links	LinkSD	Links per taxon
Clustering coefficient	Clust	The mean shortest set of links between species pairs

2.5. Fit to the niche model

The fit to the niche model of all the food web networks produced in this work was investigated by calculating the percentage of niche model errors (taking into account all food web network properties). The niche model was applied after trophic webs were assembled (the initial highly resolved webs are modified so that species/taxa with the same predators and prey are aggregated into one trophic species). Detritus was considered a basal node, with no prey, but with many links to all species that have detritus in its dietary items. The niche model has two input parameters, S, number of trophic species and C, connectance of the food web. The model designates to each species a random 'niche value' (ni) within the interval (1,0). This way, every species is restricted to consume all prey species within an interval of values (ri) whose randomly chosen center (ci) is less than the consumer's niche value. The niche model allows looping (cycles of >1 length (e.g. A eats B, which eats A, or longer like A eats B, which eats C, which eats A) and cannibalism (cycles of length 1 (A eats A). Additionally, the consumer must feed on all species that fall within its feeding range (ri).

For each food web, 1000 niche model webs with the same S and C as the empirical web were generated using Monte Carlo simulations, allowing the estimation 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 with ± 1 model SD, the model is

Table 2
Food web network properties throughout the tidal cycle in the rocky reef platform, with and without tide pools.

	Platform without pools - high tide	Platform with pools - high tide	Platform without pools - low tide	Platform with pools - low tide
S	51	73	33	55
L/S	6.96	10.1	5.4	10.3
C	0.14	0.14	0.16	0.19
T	25	18	15	5
I	67	76	73	87
B	8	6	12	7
H	14	11	18	11
GenSD	0.9	1.0	0.9	1.0
VulSD	1.3	1.1	1.1	0.9
LinkSD	0.7	0.7	0.7	0.6
TL	2.5	2.6	2.3	2.5
Chain	1.9	1.9	1.9	1.9
Omn	80	85	73	84
Can	27	35	36	40
Path	1.8	1.8	1.8	1.7
Clust	0.3	0.3	0.4	0.4
ResourceCount	38	59	28	52
ConsumerCount	47	68	29	51

Table 3
Top 5 trophic species with the highest trophic level (TL) throughout the tidal cycle over the rocky reef platform, with and without tide pools.

Trophic species Platform without pools - high tide	TL	Trophic species Platform with pools - high tide	TL
Lutjanus jocu (commercial fish)	3.05	*Lutjanus jocu* (commercial fish)	3.23
Mugil curema (commercial fish)	3.05	*Mugil curema* (commercial fish)	3.23
Anemonia sargassensis (anemone)	3.05	*Pachygrapsus transversus* (crab)	3.20
Mangelia sp. (sea snail)	3.04	*Anemonia sargassensis* (anemone)	3.16
Eucinostomus melanopterus (commercial fish)	3.02	*Panopeus occidentalis* + *Panopeus herbstii* (crabs)	3.15
Platform without pools - low tide		Platform with pools - low tide	
Mangelia sp. (sea snail)	3.04	*Pachygrapsus transversus* (crab)	3.19
Eurypanopeus sp. (crab)	3.01	*Anemonia sargassensis* (anemone)	3.18
Olivella minuta (sea snail)	3.01	*Neogonodactylus* sp. (mantis shrimp)	3.14
Stramonita haemastoma+ Muricopsis necocheana +Morula nodulosa (sea snails)	2.99	*Menippe nodifrons* (crab)	3.14
Aurantilaria aurantiaca + Leucozonia nassa (sea snails)	2.99	*Bathygobius soporator* (fish)	3.13

Table 4
Top 5 trophic species with the highest vulnerability (Vul) throughout the tidal cycle over the rocky reef platform, with and without tide pools.

Trophic species Platform without pools - high tide	Vul	Trophic species Platform with pools - high tide	Vul
Detritus	6.75	Detritus	6.71
Zooplankton	5.03	Zooplankton	4.83
Macroalgae	3.16	Macroalgae	3.45
Gammaridae (amphipods)	2.44	Talitridae (amphipods)	2.37
Ampithoidae (amphipods) + Sphaeromatidae (isopods) + Colomastigidae (amphipods) + Aoridae (aamphipods) + Hyalidae (amphipods) + Photidae (amphipods) + Tylidae (isopods)	2.44	Gammaridae (amphipods)	2.37
Platform without pools - low tide		Platform with pools - low tide	
Detritus	5.41	Detritus	4.96
Zooplankton	3.36	Zooplankton	3.69
Macroalgae	2.80	Macroalgae	2.72
Phytoplankton	1.68	Talitridae (amphipods)	1.94
Polychaeta	1.68	Gammaridae (amphipods)	1.94

considered to have a good fit to the empirical data (Williams and Martinez, 2000). The software Network3D was used in all the analyses of the food web networks, visualization of networks, and in the determination of the niche model fit (Yoon et al., 2004; Williams, 2010).

3. Results

The web encompassing all the sampling (benthic quadrats over the platform at low tide, videorecordings in the water column at high tide, and tide pool sampling) had 118 taxa, corresponding to 73 trophic species (Table 2). This reduction is due to some species having exactly the same predators and prey and thus being aggregated into one trophic species, as described in the methods (Briand and Cohen, 1984). This occurred for various filtrating bivalve species, some small gastropod species, Porifera, chitons and fishes of the genus *Haemolon*.

Number of species is lowest at low tide, when no pools are present, with only 33 trophic species present, corresponding to 94 original taxa (before agglomeration into trophic species). Both high tide and pools add to the diversity of species (Fig. 1). High tide adds 18 trophic species to the web, mostly of fish, while the presence of pools, adds 22 trophic species, encompassing macroalgae, Porifera, Cnidaria, Gastropoda, Bivalvia, Decapoda, ascideans and fish (supplementary Table 2).

Complexity of the food web networks, as given by connectance, peaks during low tide, with a value of 0.19 for the platform with pools, in contrast to 0.14 for the platform at high tide, with or without pools (Table 2). Tide pools increase the complexity of the low tide trophic network, given that when the food web is assembled without pools, connectance is only 0.16 (Table 2).

The proportion of top consumers (T) was lowest at low tide, 15%, dropping to only 5% when tide pools were not considered. High tide increases this proportion, reaching 25%, when tide pools are not considered. Intermediate species assumed the highest proportion of the species occurring in these webs, at all times during the tidal cycle (Table 2). Tide pools contributed to increase this proportion, both at high tide and low tide (Table 2). The proportion of basal species was low throughout the tidal cycle, with pools having a decreasing effect over these values. The proportion of basal species peaked at low tide, when no pools were considered, reaching 12% (Table 2).

Omnivory remains stable over the tidal cycle (85% at high tide, 84% at low tide, Table 2). When pools are not considered the proportion of omnivory decreases to 80% at high tide and 73% at low tide (Table 2). Cannibalism is higher during low tide (40% versus 35% at high tide). When pools are not considered, the proportion of cannibalism decreases (Table 2).

A low proportion of herbivores was observed throughout the tidal cycle, with tide pools having a decreasing effect on this proportion (Table 2). The proportion of herbivores was highest at low tide over the platform with no pools, reaching 18%. The presence of pools greatly increases the number of resources (prey species), but also of consumers (predator species), both during low and high tide (Table 2). Throughout the tidal cycle the number of consumer taxa was always higher than that of resource taxa, except for the low tide web with pools, that presented more resource taxa than consumer taxa (Table 2).

The variability (given by the standard deviation - SD) of the generality (number of prey per node), was stable throughout the tidal cycle (Table 2). The variability (given by the SD) of the vulnerability (number of predators per node) was higher at high tide. Inclusion of tide pools decreased these values (Table 2). The variability of the number of links per node (LinkSD) was higher at high tide. Inclusion of tide pools in the webs had little or no effect on these values (Table 2).

The trophic level (TL) did not suffer a marked variation over the tidal cycle, reaching a maximum of 2.6 during high tide, when pools were considered, and a lowest value of 2.3 during low tide, without pools (Table 2). “Chain” and “Path” suffered almost no variation over the tidal cycle, while clustering (Clust) was slightly higher during low tide. The inclusion of pools did not affect the clustering of the networks (Table 2).

The top 5 trophic species in terms of TL were mostly seasnails of different species and one species of crab in the intertidal platform during low tide (Table 3). High tide adds new species at higher TLs, among them three species of fish, all of them belonging to commercial species, and the anemone *Anemonia sargassensis* (Table 3). The presence of pools adds various crustaceans to the higher TLs, among them two species of crabs and one mantis shrimp. The anemone *A. sargassensis* is also among the top 5 species with the highest TL, as is the fish *Bathygobius soporator* (Table 3).

The top 5 trophic species in terms of vulnerability were mostly the same over the tidal cycle, detritus, zooplankton, macroalgae and small invertebrates, polychaeta over platforms at low tide and amphipods and isopods at high tide. The presence of pools does not add much alterations to this list, with detritus, zooplankton and macroalgae at the top levels followed by amphipods of the families Talitridae and Gammaridae, with no alteration brought to this list by high tide (Table 4).

Comparison of the food web properties estimated for the intertidal tropical rocky reef under study here, with the Sub-Arctic Sanak Islands

Table 5

Ranges of commonly reported network food-web properties for various ecosystem types and for the tropical intertidal rocky reefs of the present study (platform with pools at high tide).

Ecosystem	N	S	C	L/S	T	I	B	Can	Omn	TL	Chain	Path	Source
Intertidal tropical rocky reef	1	72	0.14	10.1	18	76	6	35	85	2.6	1.9	1.8	Present work
Intertidal Sub-Arctic (rock + sand)	1	232	0.03	7.8	7	76	17	20	64	2.4	–	2.4	Dunne et al. (2016)
Rock tide pools	116	7–52	0.11–0.39	1.6–7.0	0–46	14–88	7–43	14–60	43–84	1.7–2.5	1.6–2.0	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	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	a
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)
Estuarine	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	b
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	c
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	d
Terrestrial	4	29–155	0.03–0.31	1.6–9.0	0–31	56–90	13–18	0–66	21–76	2.4–3	3.2–8.4	1.4–3.7	e

Footnote.

[a] J.A. Dunne et al. (2004), Link (2002), Opitz (1996), Yozdis (1998).

[b] Vinagre and Costa (2014), Huxham et al. (1996), Lafferty et al. (2006), Hechinger et al. (2011), Zander et al. (2011), Thielgtes et al. (2005), Mouritsen et al. (2005).

[c] J.A. Dunne et al. 2004, Warren (1989), Havens (1992), Martinez (1991).

[d] Townsend et al. (1998), Romanuk et al. (2006).

[e] Polis (1991), Goldwasser and Roughgarden (1993), Memmott et al. (2000), Waide and Reagan (1996).

intertidal ecosystem (Dunne et al., 2016) (the only other intertidal food web network published) showed a lower number of taxa and a much higher connectance for the tropical web. The proportion of intermediate taxa was similar for the two food webs (Table 5). The tropical intertidal food web exhibited a higher proportion of top consumers and a lower proportion of basal taxa. Cannibalism and omnivory were higher for the tropical food web (Table 5)

All food web properties estimated for the intertidal tropical rocky reef were within the ranges previously reported for other ecosystem types, including rock tide pools, seagrass beds, marine ecosystems, small intermittent estuaries, large estuaries, lakes, ponds, streams and terrestrial non-aquatic food webs (Table 5).

Niche model fit was 44% at high tide and it did not change with the inclusion of pools. At low tide it was 72%, dropping to 61% with the inclusion of pools.

4. Discussion

This work showed, for the first time, the changing topology and network properties of the food webs that occur in an intertidal rocky reef over a tidal cycle. It also revealed the important role of tide pools in structuring intertidal food web networks and increasing, not only their diversity, but also their complexity.

As expected, species diversity increased with high tide and the addition of pools. While high tide added 18 species to the food web, mostly incoming fish, pools added a much greater variety of organisms, with 22 new species encompassing macroalgae, sponges, cnidarians, gastropods, bivalves, crabs, shrimp, ascideans and fish. Numerous studies have shown that tide pools allow subtidal species to extend their distribution into the intertidal and offer a tridimensional habitat where macroalgal stands often develop, allowing various species to find refuge, feeding and nursery grounds (e.g. Underwood, 1980; Metaxas and Scheibling, 1993, 1994; Martins et al., 2007; Noël et al., 2009; Seabra et al., 2020).

Firth et al. (2013, 2014a,b) highlighted the importance of the addition of pools to man-made structures, as a habitat enhancement strategy to increase coastal biodiversity. Here, we show that pools not only increase diversity but also complexity, given that network connectance increased during low tide with the inclusion of pools. It has been shown that connectance increases the robustness of food web networks to species loss (Dunne et al., 2002a). This way, the present study provides another strong argument to protect natural tide pools and add water retaining depressions to artificial structures built in coastal areas, since they add connectance which likely increases robustness to the local food web network, an important feature especially in coastal areas which are so often disturbed by human impacts.

Complexity of the food web changes over the tidal cycle. The intertidal food web peaks in complexity during low tide, when pools are present, as shown by the higher connectance of 0.19, versus 0.17 for low tide without pools, and 0.14 for high tide, with or without pools. High tide adds species yet does not change connectance. This happens because most of the incoming species are highly generalist fish, which add an important number of new links to the web, thus keeping connectance stable even though number of species increases ($C=L/S^2$).

Low tide offers the potential for coastal birds and land animals to forage over the reef platform, however that was not observed during the study period (one month), nor was any published evidence found, so they were not included in the food web. In this study site there is no continuity between the terrestrial environment and the reef. The bordering terrestrial environment is semi-arid, dominated by coconut trees and very scarce vegetation, the beach is circa 150 m of sand, and only after that sand belt starts the water line, meaning that terrestrial animals like rats would need to cross 150 m of sand and then swim to reach the reef. We believe that habitat discontinuity is the reason for the absence of terrestrial land animals in our observations.

The proportion of top consumers was lowest at low tide, especially when pools are considered, with only 5% of top predators, confirming shallow rocky reefs as important refuges from predators, especially when they include tide pools (e.g. Bennett et al., 1987; Delany et al., 1998; Vinagre et al., 2015; Dias et al., 2016). The webs analysed are highly dominated by intermediate consumers, both at high tide (67–77%) and low tide (74–88%), with pools contributing to increase these proportion, both at low and high tide. Cannibalism is higher at low tide and increases with the presence of pools.

Throughout the tidal cycle the number of consumer taxa is always higher than that of resource taxa, except for the web during low tide with pools, where more resource taxa exist than consumer taxa, thus highlighting one of the most important features of pools, being refuge areas with abundant food resources (e.g. Noël et al., 2009; Mendonça et al., 2019). TL does not suffer marked changes over the tidal cycle. This is probably because this is a low depth reef, where large predators such as sharks do not venture during high tide, otherwise a greater increase in TL would be expected at high tide.

Nevertheless, the top predators varied markedly with the tidal cycle.

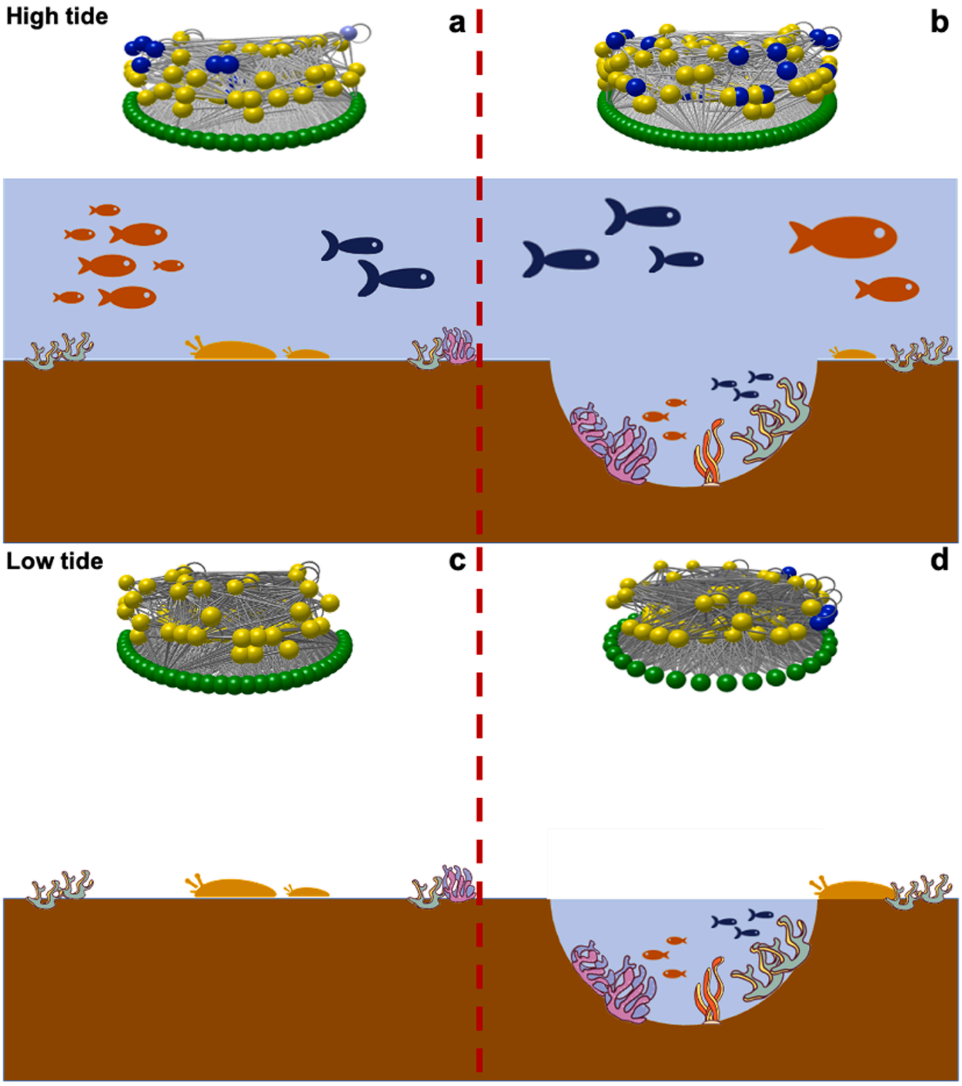

Fig. 1. Schematic representation of the changing food web in the intertidal zone, representing the food web occurring over the rocky platform during high tide (A), during high tide when pools are present (B), during low tide (C) and during low tide when pools are present (D). Spheres represent taxa and lines between them represent feeding links. Primary producers, invertebrates, and vertebrates are shown in green, yellow, and blue, respectively. The vertical axis indicates short-weighted trophic level.

The food web that occurs over the platform is dominated by invertebrate predators, mostly seasnails, and the crab *Eurypanopeus* sp, also a top predator in this environment. The incoming tide brings larger vertebrate predators, with several commercial fish entering the food web, such as the Dog snapper, *Lutjanus jocu*, the White mullet, *Mugil curema* and the Flagfin mojarra, *Eucinostomus melanopterus*. Pools add the crabs, *Pachygrapsus marmoratus* and *Mennipe nodifrons*; the anemone *Anemonia sargassesis*, the mantis shrimp *Neogonodactylus* sp. and the resident goby, *Bathygobius soporator*, to the food web as top predators.

Although, there are no studies using topological complex networks that allow a direct comparison, these findings are generally aligned with the observations of other studies from other parts of the world (albeit most of them from temperate regions), which describe predation in intertidal platforms by seasnails (e.g. Paine 1966, 1984; Connel, 1970; Dayton, 1971; Menge, 1978; Janke, 1990), and predation in tide pools by crabs (Lubchenco, 1978), anemones (Dethier, 1980) and fish (Dethier, 1980; Coull and Wells, 1983; Ranta et al., 1987). Several authors also refer to sea stars as dominant predators over intertidal platforms, all over the world, (e.g. Paine, 1966, 1971, 1974; Dayton, 1971; Lubchenco and Menge, 1978; Paine et al., 1985; Robles et al., 1995). Although there is an important diversity of sea stars in the northeast coast of Brazil, and some species have been recorded in the intertidal (Gondim et al., 2014), they were not found in the present study's sampling, only brittle stars were found, which are much smaller and do not occupy top predator positions.

The species with the highest vulnerability (highest number of predators) suffered very little change over the tidal cycle. They are mostly aggregate taxa representing compartments of the food web with low definition, detritus, zooplankton, macroalgae and small invertebrates, polychaeta over the platforms at low tide and various families of amphipods and isopods at high tide. Tide pools do not add great alterations to this list, with detritus, zooplankton and macroalgae being the most vulnerable taxa, followed by the families of amphipods Talitridae and Gammaridae (with high tide causing no alteration at this level). The need to agglomerate macroalgae in the food web network is due to their low resolution in the published diets of their consumers, certainly has an important effect in this analysis. Several studies report that tide pools typically support more diverse macroalgal assemblages than the emergent platform (Goss-Custard et al., 1979; Chapman and Johnson, 1990; Metaxas and Scheibling, 1993), which is also confirmed in the present study (see species list, supplementary Table 2), thus, consumers that use tide pools during low tide are exposed to a different availability of macroalgae at the species level, than when they feed in the emergent platform at high tide. Additionally, not all macroalgal species are necessarily edible by their potential consumers. This way, at this food web level an important amount of uncertainty exists and is shared by all studies of this kind. This knowledge gap, that hinders a better understanding of complex food web networks, can only be overcome with future feeding ecology studies for a large number of species.

To the best of our knowledge our study is the first to examine how the complex food web network changes with the tidal cycle over an intertidal rocky platform. However, other complex food web networks have been assembled for rocky shores in other parts of the world. The intertidal rocky shores of Chile are among the best studied in the world and a complex food web network model has been assembled for this ecosystem by Kéfi et al. (2015). However, it does not include pools, and many taxonomic groups were not sampled such as amphipods, isopods, mobile polychaetes, porcellanid crabs, urchins, mites, insects, filter-feeding limpets and fish, and thus, it cannot be directly compared to the present work.

The food web study that is more directly comparable to the present one is that of the intertidal rocky shores of the Sanak Islands (Alaska) described by Dunne et al. (2016), because it followed a similar methodology, although it did not examine changes due to the tidal cycle. The Sanak Islands study, however, has a much higher sampling effort, including a much wider area and a much longer time period (3 years versus just 1 month in the present study). Additionally, it encompassed not only rocky platforms but also boulder fields and sand substrate. For this reason, the intertidal food web of the Sanak Islands presents a much higher number of species and a much lower connectance (Table 5). The lower connectance is probably due to the higher resolution of the web, which leads to lower link density (Dunne et al., 2002b).

Both the present tropical web and the Sub-Arctic web of the Sanak Islands are dominated by intermediate species, in a very similar proportion. However, the tropical web has a higher proportion of top predators (18% versus 7% for the Sub-Arctic web). In turn, basal taxa assumed a smaller proportion in this tropical web, only 5%, compared to 17% for the Sub-Arctic web. This could be part of a latitudinal trend or not, since the only available study that replicated food web networks over different latitudes was that of Mendonça et al. (2018), with tide pools, spanning from 50°N to 3°S, and it did not detect such a trend.

Mean trophic level (TL) was 2.3–2.6 in the present study, lower than that estimated for deeper marine ecosystems, like the Benguela system off the Southwest coast of South Africa with a TL of 3.2, the Northeast US Shelf ecosystem, with a TL of 3.1, or the Puerto Rico-Virgin islands coral reef ecosystem, with a TL of 3.1 (J.A. Dunne et al., 2004), but within the same range as that calculated for the intertidal of the Sanak Islands, with a TL of 2.4 (Dunne et al., 2016) and for shallow coastal lagoons, with TLs of 2.4 to 2.7 (Mendonça and Vinagre, 2018). Deeper marine ecosystems have the necessary water column space to harbor predators with a larger body size, like large teleosts, sharks and marine mammals (J.A. Dunne et al., 2004), and thus have food webs with higher TLs.

All food web network properties were within the ranges previously reported for other ecosystem types, confirming the idea that food web networks are ruled by universal organizational rules (Solé and Montoya, 2001; Montoya et al., 2006; J.A. Dunne et al., 2004; Bascompte, 2009; Mendonça et al., 2018; Mendonça and Vinagre, 2018). However, the "Chain" value observed in the present study, 1.9, is among the lowest ever registered. A lower value, of 1.6, was reported for tide pools by Mendonça et al. (2018) and similar 1.9 values were observed in seagrass beds Coll et al. (2011) and shallow coastal lagoons (Mendonça and Vinagre 2018), all of them very shallow ecosystems. Given that "Chain" indicates the number of links in any possible food chain connecting top to basal species, it is not surprising that such low depth ecosystems, that naturally exclude large predators, present such low "Chain" values, since probably at least one upper level of predators is absent. Small chains imply that disturbance can rapidly travel all the way through the web bottom-up or top-down through predator-prey links (Williams et al., 2002), a particularity that should be taken into account in the management of these ecosystems.

Niche model fit was 44–72%, which can be considered a relatively low fit when compared to some other marine food webs like the Benguela coastal system food web (88%) (J.A. Dunne et al., 2004). However, it is well within the range calculated for other marine systems like the NE US Shelf web with 69% or the Caribbean reef web with 46% (J.A. Dunne et al., 2004).

The present study is a purely structural perspective which is inherently limited in its scope of conclusions, as previously noted by Winemiller (1990), who demonstrated the low sensitivity of web metrics for detecting seasonal community response to the marked seasonality of tropical swamp and stream ecosystems. A dynamical view of the present webs, taking into account energy and mass transfer, intensity of predator-prey interactions, prey-switching and population dynamics changes throughout the tidal cycle, would certainly reveal interesting insights into the functioning of this intertidal food web and how it changes over the tidal cycle (de Ruiter et al. 2005). That kind of study would demand observation of feeding behavior and gut content analysis.

5. Conclusions

This study revealed the changing structural complexity occurring in the intertidal environment over a tidal cycle. It showed that although high tide adds new species, it does not add complexity to the web. Pools, however, add not only species diversity but also network complexity. The webs were dominated by intermediate species, with the proportion of top consumers fluctuating throughout the tidal cycle, being lowest during low tide and highest at high tide, due to the incoming larger vertebrate predators. Consumer taxa always outnumbered resource taxa, except for low tide when pools are present, when there was more resource than consumer taxa. The low "Chain" values observed throughout the tidal cycle have implications for conservation, since it means that disturbance can rapidly travel bottom-up or top-down the food web through predator-prey links. This means that, like other shallow marine ecosystems, intertidal rocky reefs should be carefully monitored and protected. Addition of pools to the web increases connectance, which likely increases web robustness, highlighting the particularly important role of pools in intertidal environments, and adding a strong argument for their protection, maintenance and, even, its addition to artificial structures, so often built in these areas.

CRediT authorship contribution statement

Catarina Vinagre: Conceptualization, Formal analysis, Funding acquisition, Methodology, Project administration, Resources, Writing – original draft, Writing – review & editing. **Vanessa Mendonça:** Conceptualization, Methodology, Data curation, Formal analysis, Writing – original draft.

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.

Data availability

Data will be made available on request.

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Supplementary materials

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