



Interaction between small-scale habitat properties and short-term temporal conditions on food web dynamics of a warm temperate intertidal rock pool ecosystem

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Abstract The physical properties of habitats are crucial determinants of community structure with significant effects on food web dynamics. We examined the effects of rock pool physical properties (e.g. pool size, water depth) and short-term temporal (seasonal) change (e.g. temperature, nutrients) on food web structure at small spatial scales (c. 500 m) on the warm temperate coast of South Africa. Using stable carbon and nitrogen isotope signatures, we characterised food web structure with Layman metrics and quantified food web size, defined as the total area in isotopic space occupied by consumer species. The effects of rock pool physical properties and seasonal changes on species counts and food web structure were evaluated using a Bayesian generalised linear mixed model approach. Substratum type, water depth, pool size, phosphate concentrations, salinity and temperature all influenced overall food web dynamics.

A winter reduction of sand cover led to a more heterogeneous substratum and a significant increase in species counts, while consumer niche similarity decreased with increasing pool size in summer. The range of $\delta^{15}\text{N}$ values, or trophic height, was negatively and positively affected by salinity and phosphate levels, respectively. Overall, the effects of pool physical properties on food web structure were moderated by seasonality.

Keywords Stable isotopes · Trophic redundancy · Substratum · Salinity · Seasonality · Food web structure

Introduction

Within the coastal marine environment, species distribution patterns are often attributed to spatio-temporal gradients or discontinuities in abiotic parameters (Bhadja et al., 2014; Castillo-Escrivà et al., 2017). Because of the uniqueness of the physiologies and life history strategies of each species, responses to abiotic parameters are likely species specific (Tilman, 1986). However, abiotic factors also impinge on all trophic levels in food webs with pronounced effects at community and ecosystem levels (Kennedy et al., 2002; Brierley & Kingsford, 2009; Jackson et al., 2020). In most marine environments, ecosystems are

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maintained by the flow of energy from primary producers at the base of the food web to primary consumers, to top predators and back to the base through decomposition and detrital pathways (Doney et al., 2011). Because of this cycle, species persistence is directly and/or indirectly influenced and linked through both environmental and biological interactions to the performance of other species within the community (Pilditch et al., 2015). As a result, changes in food web size and structure along any spatial gradient could highlight key trophic interactions or other consequences elsewhere in the same systems (Pinnegar et al., 2000).

Although significant progress has been made in recent years, understanding the mechanisms through which marine systems persist in nature remains a significant challenge. Amid this complexity though, ecologists have found what seem to be recurring patterns in species diversity (Rosenzweig et al., 1984) and in species composition on gradients (e.g. Tilman, 1986). This similarity in patterns suggests that there may be a few major underlying factors or processes that constrain communities. For example, two main processes primarily affect geographical variation in the southern African marine fauna. This arises from variations in seawater temperature and nutrient concentrations along the coast, reflecting the effects of the major adjacent current systems (Field & Griffiths, 1991) and second, the effects of biogeography, with the presence of both Indo-Pacific and Atlantic species as well as relatively high levels of endemism (Brown & Jarman, 1978; Scott et al., 2012).

Extensive, comparative research has been conducted on large spatial gradients across the three primary biogeographical provinces of South Africa (e.g. Bolton & Stegenga, 2002; Sink et al., 2005). These studies reveal temperature as one of the key drivers of species and community dynamics across meso- and macro-spatial scales. At this stage, it is unclear whether environmental factors such as temperature are important at small scales, as even at these small scales, real food webs can be large and complex enough to describe the networks of interacting species (Twomey et al., 2012). In addition, because most large spatial studies often cover large temporal scales such as inter-annual or decadal changes (Seabra et al., 2011; Dong et al., 2017), it is important to evaluate whether intra-annual or short-term temporal changes in environmental properties are likely to provide information

on changes to the food web structure, which can be masked over extended time periods.

Food webs are theoretical constructs that simplify the many connections among living organisms (Moloney et al., 2011). Traditional food web metrics (e.g. connectance or linkage density) have been based on gut content examination (Madigan et al., 2012), understanding energy flow and nutrient cycling dynamics within the community (Dong et al., 2017) and/or species composition as a function of habitat (Peralta-Maraver et al., 2017). Although such methods as gut content examination likely overemphasise the importance of larger prey items which require longer periods of digestion, they also only provide a snapshot of the actual food ingested at a given time which may not be an accurate representation of an organism's feeding behaviour. Because of this, understanding food web dynamics can be achieved by employing different methodologies such as tracing the architecture of trophic networks (Bersier et al., 2002) and tracing trophic interactions and structure with stable isotope analyses. In this study, we used the latter, i.e. stable carbon ($\delta^{13}\text{C}/\delta^{12}\text{C}$) and nitrogen ($\delta^{15}\text{N}/\delta^{14}\text{N}$) isotope ratios (hereafter $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively) to examine rock pool communities.

Stable isotopic depictions of species' niches reflect temporally (and spatially) integrated data, which is difficult to compile with gut content data alone (Post, 2002). Isotopes also allow for the construction of general community trophic structure by identifying feeding and energy flow patterns, dietary overlaps and allow the estimation of trophic niches as a generalised proxy for assessing the trophic ecology of consumers (Layman et al., 2015; Drazen & Sutton, 2017). Carbon and nitrogen isotopes are especially useful because they provide time- and space-integrated insights into trophic interactions among species and, thus, can be used to develop models of trophic structure.

Our study focus was to evaluate the processes that constrain rock pool communities within small-scale gradients of both space and time. To achieve this, we studied rock pools situated on a c.500 m long transect at a site within the warm temperate coast of South Africa. The warm temperate coast spans c.770 km from Cape Agulhas to the Mbashe River (Fig. 1) and supports high numbers of South African endemic marine species (Procheş & Marshall, 2002; Anderson et al., 2009). Intertidal rock pool environments harbour particularly high biodiversity over small

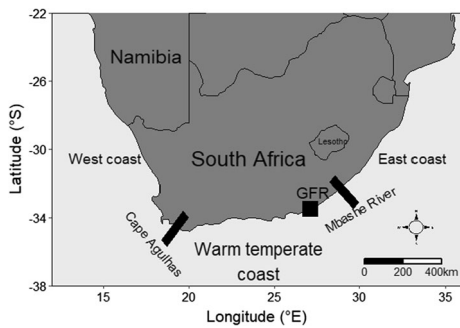


Fig. 1 Location of study site (GFR—Great Fiver River) along the warm temperate coast of South Africa

areas. Their geomorphological similarities render them ideal in situ ‘laboratory’ sites to assess constructs such as community structure, habitat preferences (Sebens, 1991) and trophic diversity (Metaxas & Scheibling, 1993; Johnson, 2001). Rock pools are also characterised by considerable variety in pool geometry and highly variable conditions, which contribute to small-scale environmental heterogeneity (Seabra et al., 2011).

Therefore, to evaluate the significance of changes at small spatial scales and short-term temporal variation (hereafter seasonal changes) on rock pool species counts, food web size and structure, we defined two sets of environmental/habitat properties. For small spatial scales, we defined physical properties such as pool morphometrics (e.g. pool water depth, surface area and substratum heterogeneity influenced by sand accumulation). These habitat characteristics may set constraints on colonisation success, niche occupancy, habitat preference (Menge et al., 1997) and community composition in benthic systems (Jungerstam et al., 2014) with an overall influence on food web attributes over short- and long-time scales. Second, we defined the conditions which potentially vary over the short term (i.e. seasonally) by comparing winter and summer conditions. These parameters included water temperature, salinity, nutrient concentrations (nitrates and phosphates) and chlorophyll-*a* (chl-*a*).

Food web size was defined as the total area in isotopic space of all consumer species based on their isotope signatures. Food web size was measured (i) for individual pools in each season (intra-seasonally) and (ii) for all pools combined across the 2 seasons (inter-seasonally). Food web structure was estimated as the degree of trophic complexity including vertical

structuring (trophic height), species packing and niche diversification within the food web network (Vander Zanden et al., 2006; Tecchio et al., 2013). We did not expect significant differences in short-term temporal conditions (particularly water temperature and salinity) and subsequent changes in species composition in our study area across summer and winter. This was because annual seawater temperatures along the south coast have been reported to vary marginally (Anderson et al., 2009) and because all pools were located at the same shore height.

Materials and methods

Study area

The study was conducted along a rocky shore ecosystem near the Great Fish River (GFR) on the south coast of South Africa ($33^{\circ}34'06.29''\text{S}$ – $33^{\circ}34'08.87''\text{S}$, $27^{\circ}00'33.39''\text{E}$ – $27^{\circ}00'36.06''\text{E}$; Fig. 1). The study site is within an area oceanographically dominated by the Agulhas current, the principal western boundary current of the southern hemisphere, which flows rapidly polewards, channelling warm subtropical water from the Western Indian Ocean (Roberts, 2005). The wind mostly blows from the north-west in winter and the south-east in summer. Annual sea water temperature has been shown to range between 17.2 and 18.2°C (Anderson et al., 2009). In addition, seasonal range in salinity is relatively small (D’Addezio & Subrahmanyam, 2016). The site is minimally disturbed by anthropogenic activities and rare estuarine intrusions from the Great Fish River Mouth Estuary. Rainfall in this area is highly variable, with mean annual precipitation of c.570 mm.

Data collection

Field sampling

Sampling was conducted in the months of July and December (which represented the winter and summer months, respectively). Rock pool physical properties and short-term temporal conditions (hereafter environmental parameters) and biological samples were collected from 12 rock pools (ranging between 0.3 and 2.6 m²). The pools were selected using the stratified

random sampling technique, meaning pools were selected from approximately the same mid shore height with a mean between-pool distance of c.30 m. Further, photographic images of pools were captured using 16 megapixel (Mp) cameras (Nikon AW130 and Olympus TG310). These were later used to compute surface area/pool size (m²) using ImageJ software version 1.47 (Free Software Foundation Inc., USA). Mean water depth was estimated by taking the mean of three random measurements within each pool. Pool substratum embeddedness or substratum type (an estimate of how much of the bed rock of a pool is covered by fine sediment relative to other material such as loose rocks, pebbles or macroalgae) was quantified using a categorical scale of (1) > 75%; (2) 50–75%; (3) 25–50%; (4) 5–25%; and (5) < 5% of surface covered by fine sand (Fischenich, 2002). From this scale, pools in category (1) and (5) were defined as homogenous while (2), (3) and (4) were categorised as heterogeneous.

A portable YSI 500 series multi-parameter water quality sonde (TTT Environmental Instruments & Supplies, USA) was used to measure: total dissolved solids (TDS), conductivity, salinity, oxidation reduction potential (ORP), pH and water temperature in situ while samples of chl-*a*, nitrates and phosphates were collected for laboratory analysis. Dissolved nitrogen (nitrates and nitrites) was measured using a spectrophotometer at 540 μm wavelength (Bate & Heelas, 1975), while phosphates were measured using a multi-parameter photometer (Strickland & Parsons, 1972).

Biological material collected for stable isotope analysis included samples of fish, macroinvertebrates, macroalgae, phytobenthos and suspended particulate organic matter (SPOM). Different sampling strategies were employed for biological data collection. For macroinvertebrates, 4 replicates of each observed species were handpicked into storage containers with filtered seawater. We performed time-based sampling for fish collection, with an average catch effort of 30 min set aside for fish sampling from each pool. In winter, there were 5 pools with fish, while in summer, 4 pools contained fish. From each pool containing at least five fish (i.e. where 5 was the total number of all fish species present), we collected two specimens of each species. The fish were captured using a small hand net within the set sampling time.

For macroalgal species, approximately 20 g of each observed species was collected in a zip lock bag. To

obtain SPOM samples, two (250 ml) water samples from each rock pool were collected. Samples of phytobenthos were obtained by brushing off biofilm from the surfaces of rocks, pebbles, and the pool substratum using a fine brush and rinsed with seawater from the sampled pool into 250 ml jars ($n = 2$). SPOM and phytobenthos samples were then filtered through (GF/F) filters (Carabel et al., 2006) and oven dried at 50°C. The dried filters were stored in aluminium sleeves for later isotope analysis. In addition, two (250 ml) water samples for chl-*a* were collected from each pool and analysed using the Turner design 10AU fluorometer (Thyssen et al., 2015). Chl-*a* concentrations were calculated following the Environmental Protection Agency (EPA) method 445.0 (Arar & Collins, 1992):

$$\text{Chl-}a \text{ (mg/L)} = (\text{C}_3\text{H}_6\text{O}/V) \times (F_0 - F_a) \times C,$$

where Chl-*a* (mg/L) is the chl-*a* concentration in mg/L, C₃H₆O is the quantity of acetone used for extraction in mL, *V* is the quantity of water filtered in ml, *F*₀ is the chl-*a* reading before acidification with 1 N HCl (hydrochloric acid), *F*_a is the chl-*a* reading after acidification with 1 N HCl (hydrochloric acid), and *C* is the constant value (0.325).

Stable isotope analysis sample preparation

Specimens of fish were euthanised using clove oil (10 mg L⁻¹) after which the gut was preserved in 70% ethanol for additional gut content analysis. Fish muscle tissue was excised from the lower lateral line of the organism, and the excised muscle tissue was further cut into 3 parts and prepared for isotope analysis. Macroalgal species were rinsed in seawater to remove epifauna and sand and then preserved in ice coolers. Macroinvertebrate species were kept alive for approximately 24 h in filtered sea water to allow for clearance of the gut contents (Hobson & Welch, 1992). All animals were then sacrificed (ethics permit RU-LAD-16-08-0001) by freezing at -20°C and identified to species level (Day, 1974). For tissue extraction, soft-bodied macroinvertebrates, such as sea anemones (*Actinia ebhayaensis*) and small crustaceans (e.g. sand shrimps *Palaemon peringueyi*), the whole body was processed for isotope analysis while for molluscs, only the soft tissue was considered (Schaal et al., 2010; Marufu et al., 2017). All animal samples were oven dried to a constant weight (60°C,

~ 48 h) and ground into a fine homogenous powder using a pestle and mortar. The ground samples were transferred to tin capsules pre-sterilised with toluene.

The stable isotope analysis procedure involved weighing aliquots of 1–1.1 mg of ground macroalgae, 0.5–0.6 mg of animal samples and 20–25 mg of filters saturated with SPOM or phytobenthos samples. Isotopic analysis was performed on a Flash EA 1112 Series coupled to a Delta V Plus stable light isotope ratio mass spectrometer via a ConFlo IV system (Thermo Fischer, Bremen, Germany) in the Stable Isotope Laboratory at the Mammal Research Institute at the University of Pretoria, South Africa. Two laboratory running standards (Merck Gel: $\delta^{13}\text{C} = -20.26\text{‰}$, $\delta^{15}\text{N} = 7.89\text{‰}$, $\text{C}\% = 41.28$, $\text{N}\% = 15.29$ and DL-Valine: $\delta^{13}\text{C} = -10.57\text{‰}$, $\delta^{15}\text{N} = -6.15\text{‰}$, $\text{C}\% = 55.50$, $\text{N}\% = 11.86$) were used, and a blank sample was run after every 12 unknown samples. These running standards were calibrated against the international standards of National Institute of Standards & Technology (NIST): NIST 1557b (bovine liver), NIST 2976 (mussel tissue) and NIST 1547 (peach leaves). Data corrections were done using the values obtained for the Merck Gel standards during each run. The values for the DL-Valine standard provided the standard error for each run. All results were referenced against Vienna Pee-Dee Belemnite and air for carbon and nitrogen isotope values, respectively (Feuchtmayr & Grey, 2003). Results were expressed in delta notation using the standard equation:

$$\delta X(\text{‰}) = [(R_{\text{sample}} - R_{\text{standard}}) / R_{\text{standard}} - 1] \times 1000,$$

where X is the ^{15}N or ^{13}C , and R represents $^{15}\text{N}/^{14}\text{N}$ or $^{13}\text{C}/^{12}\text{C}$, respectively.

The trophic positions (TP) of consumers were determined using $\delta^{15}\text{N}$ values with a baseline of a primary consumer:

$$\text{TP} = \frac{\text{TP}_{\text{baseline}} + (15\text{N}_{\text{consumer}} - 15\text{N}_{\text{baseline}})}{\text{TEF}},$$

where TP is the trophic position, $\delta^{15}\text{N}_{\text{consumer}}$ is the mean measured $\delta^{15}\text{N}$ of consumer, and $\delta^{15}\text{N}_{\text{baseline}}$ is the mean $\delta^{15}\text{N}$ of the chilli pepper sponge (*Tedania anhelans*). To capture possible spatio-temporal variation at the base of the food web in a particular location, we selected the sponge *T. anhelans* as our baseline species because sponges have a relatively

long life span, limited mobility and the ability to show short-term temporal changes driven by resource availability and temperature (Di Camillo et al., 2011). *T. anhelans* fell into trophic level 2, assuming that primary producers are represented as trophic level 1. A mean $\delta^{15}\text{N}$ trophic enrichment (TEF) value of 3‰ was used following Babaranti et al. (2019). There is a possibility of underestimating trophic position for species feeding on invertebrates, while overestimating trophic position for organisms feeding on vertebrates (i.e. many top predators) when a mean TEF value is applied to all consumers. However, a mean TEF value is appropriate for generalist consumers (including many rock pool species) feeding on a mixture of plant material and microbial or animal material (McCutchan et al., 2003).

Data analysis

Environmental heterogeneity

All environmental data (Table S1) were initially tested for normality and heteroscedasticity using ggpubr package in R (Kassambara, 2018) and Levene's tests, respectively. The seasonal and pool differences in environmental parameters, particularly temperature, salinity, phosphates and pH, were evaluated using the ggbetween stats function in the ggstatsplot package in R (Patil, 2018). Because all data violated normality and heteroscedasticity, non-parametric Mann–Whitney tests were performed.

Species–environment interactions

Multivariate canonical correspondence analysis (CCA) was used to explore the relationship between rock pool species presence/absence and environmental parameters in the two seasons. Data were analysed separately for macroinvertebrates and macroalgal communities. The CCA selects the most influential environmental parameters mapping spatial distribution of biological communities. Prior to using the CCA, a detrended correspondence analysis (DCA) was first conducted to test for heterogeneity in species composition. All ordination analyses were performed in CANOCO version 5 (Šmilauer & Lepš, 2003).

To evaluate the effects of season (measured as changes in different environmental parameters) and pool size on species richness, a Bayesian generalised

linear mixed model (GLMM procedure with Poisson error distribution and a log link function) was performed using the `glmer` function in the package `blme` in R (Dorie & Dorie, 2015). `Bglmer` (a Bayesian approach to GLMM) is recommended for relatively small datasets as in our study (Austin, 2010). Temperature (which was the main parameter distinguishing the 2 seasons) was treated as fixed factor and pool identity as a random factor. High multi-collinearity among continuous (environmental) predictor variables prevented the use of all the predictor variables in the model. Therefore, the results from the CCA plots were used a priori for our mixed models.

Model assumptions were verified by plotting residuals versus fitted values, versus each covariate in the model and versus each covariate not in the model. Where model assumptions were violated, the covariates not in the global model were added (one at a time) into the new model and the model refit again. We used the `dredge` function (which runs all possible model combinations) from the package `MuMIn` in R (Burnham & Anderson, 2002) after which we selected the model with the lowest AIC. To ensure the best fitting model was selected, in cases where the `dredge` output had 2 or more models with AIC values within a range of 2 units, these models were compared against each other (with their respective interactions) and the one with lowest AIC and/or an ecologically meaningful interpretation was selected. Where temperature had any significant effects on any of the dependent variables, we further partitioned the data into summer and winter to better visualise the specific driving the observations.

Food web size and trophic position estimates

The size, structure and length of food webs from our study site were evaluated through isotope biplots and trophic position estimations, respectively. Biplots based on stable carbon and nitrogen isotope values were constructed using `PAST` software (Hammer et al., 2001) while trophic positions were calculated using the package `tRophicPosition` in R (Quezada-Romegialli et al., 2018). Further, using `ANOSIM`, we tested for any significant difference in overall trophic structure between pools with and without fish.

Community-wide isotope metrics and food web structure

Community-wide isotope metrics or simply Layman metrics based on stable isotope data were calculated as a complement to the food web biplots to reveal more quantitative aspects of food web structure and trophic niches of rock pool species (Layman et al., 2007). Our food webs were delineated based on consumer species resident in rock pool systems, and we calculated the following metrics: $\delta^{15}\text{N}$ range (dNr) defined as the trophic height of the food web; dCr ($\delta^{13}\text{C}$ range), the breadth of basal resources; total area (TA) or size of the food web in isotopic space; centroid distance (CD), explained as trophic diversity within a food web; mean nearest neighbour distance (MNND), i.e. the mean Euclidean distance to each species' closest neighbour in bi-plot space, this is a measure of food web packing. Food webs with a large proportion of species occupying almost by similar trophic niches will exhibit a smaller MNND (increased trophic redundancy) than a food web in which species are, on average, more divergent in terms of their trophic niche; standard deviation of nearest neighbour distance (SDNND), i.e. the measure of species evenness, with low values indicating highly uniform distribution of trophic niches and the standard ellipse area correction (SEA_c), defined as the bivariate measure of mean core isotopic niche width (i.e. realised niche), which is used as an estimate of dietary similarity among populations (Layman et al., 2007; Jackson et al., 2012). SEA_c was calculated from consumer isotope data for each season. All the metrics were calculated using the `Stable Isotope Bayesian Ellipses Analysis (SIBER)` package (Jackson et al., 2011) of `MixSIAR` in R (Stock et al., 2018). All metric calculations were bootstrapped ($n = 9999$) to allow comparison among species with different sample sizes. A Bayesian GLMM procedure with Gamma error distribution and a log link function was used to evaluate species community-wide trophic metrics as a function of season (as a fixed factor) and a combination of environmental parameters as explanatory variables. Pool identity was treated as a random factor. Unless specified, all analyses were performed using R version 4.0.2 (R Core Team, 2020).

Results

Seasonal differences in environmental parameters

Temperature significantly varied between the seasons ($\log_e W_{\text{Mann-Whitney}} = 4.97$, $P = 0.0001$, $r = 0.85$, $CI_{95\%} [0.80, 0.95]$), with higher temperature in summer as expected. Phosphate concentrations were also significantly different between summer and winter ($\log_e W_{\text{Mann-Whitney}} = 2.25$, $P = 0.0001$, $r = 0.74$, $CI_{95\%} [-0.99, -0.57]$). Summer showed higher phosphate concentrations than winter. On the other hand, summer showed significantly higher chl-*a* concentrations than winter ($\log_e W_{\text{Mann-Whitney}} = 4.93$, $P = 0.0001$, $r = 0.79$, $CI_{95\%} [0.69, 0.91]$). Lastly, TDS had higher variability in winter than summer ($\log_e W_{\text{Mann-Whitney}} = 2.71$, $P = 0.001$, $r = 0.67$, $CI_{95\%} [-0.94, 0.44]$).

Relationship between species and rock pool environmental parameters

A total of 35 and 30 macroinvertebrate and macroalgal species were recorded in winter and summer, respectively. In addition, there was a total of only three fish species in summer, with six in winter. A Mann–Whitney *U* test revealed no significant differences in total species counts between the 2 seasons. The eigenvalues for the first 2 axes of the CCA explaining the relationship between the measured short-term temporal conditions and species assemblages were low in the macroalgal dataset and particularly the macroinvertebrate dataset (Table 1). For macroinvertebrate communities, axes 1 and 2 together explained only 13.5% of total variation, contributing 6.9% and 6.6%, respectively. All macroinvertebrates were

mainly influenced by salinity, water depth, surface area and chl-*a*. Figure 2a indicates that the presence of species such as the limpet *Siphonaria capensis*, chitons (e.g. *Acanthochitona garnoti*) and the chilli pepper sponge (*Tedania anhelans*) were negatively affected by chl-*a*. Water depth also influenced gastropods such as *Turbo sarmaticus*, which exhibited an affinity for deeper pools. Pool surface area was significantly correlated with negative axis 1, attracting species such as the sand shrimp *Palaemon peringueyi*. Low salinity levels negatively influenced species including the gastropod *Burnupena cincta* and limpets as shown by a negative correlation with both axes. The occurrence of ubiquitous species such as the gastropods *Burnupena lagenaria* and the winkle *Oxystele tigrina* was not influenced by environmental parameters and most were concentrated in pools of low water depth and surface area.

For macroalgal communities, the first two axes of the CCA triplots contributed 7% and 6.3% of total variation, respectively (Fig. 2b). Macroalgae were mainly influenced by salinity, pool depth, conductivity and substratum type. Rhodophytic species such as *Hypnea spicifera* and *Gelidium pteridifolium* were positively associated with high salinity and conductivity (positive axis 1 and 2). The results indicated that depth was positively associated with the second axis while substratum type was negatively correlated to axis 1, influencing the occurrence of opportunistic species such as *Plocamium suhrii*. Further, species such as *Ulva fasciata* and *Codium extricatum* were observed in most pools. Lastly, from our GLMM output an increase in pool size, positive shift in substratum type and the lower winter temperature contributed to increase in overall species richness.

Table 1 Summary of the first two axes of canonical correspondence analysis plots results explaining how environmental parameters influenced species presence/absence (macroinvertebrates and macroalgae) within rock pools

Statistic	Macroinvertebrates		Macroalgae	
	CCA 1	CCA 2	CCA 1	CCA 2
Eigenvalues	0.29	0.28	0.399	0.275
Explained variation (cumulative %)	6.83	13.5	9.50	16.05
Pseudo-canonical correlation	0.91	0.91	0.86	0.78
Explained fitted variation (cumulative %)	34.43	68.19	41.22	69.63

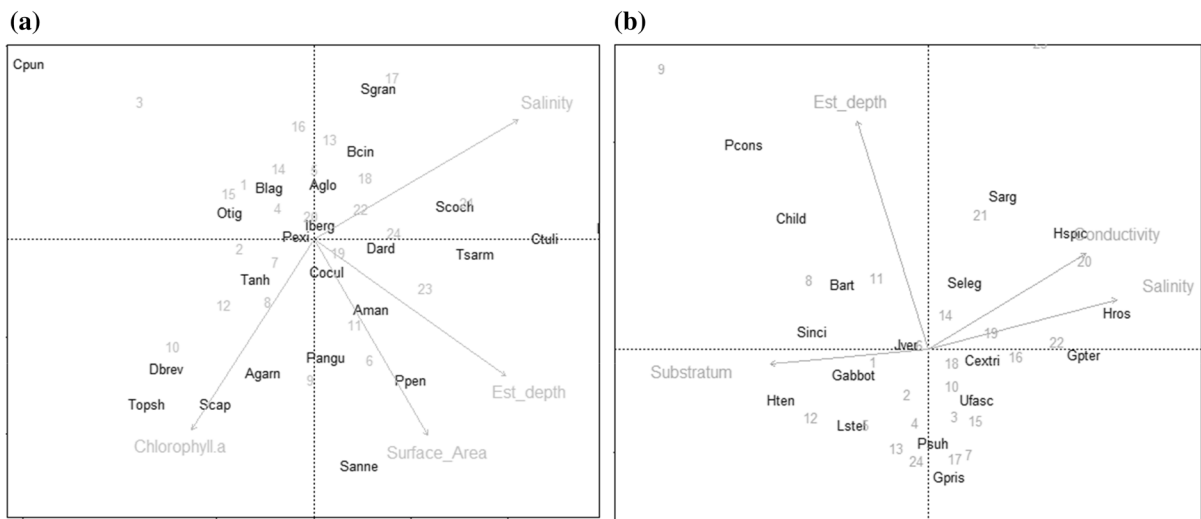


Fig. 2 Canonical correspondence analysis triplots illustrating the relationship between rock pool species presence and the most significant environmental variables: **a** indicates macroinvertebrate communities and **b** represents the macroalgal communities. Pools are labelled as a dark-grey number pools 1–12 represent summer while 13–24 represents the winter season. Quantitative environmental variables are indicated by dark-grey arrows. The species names for macroinvertebrates (**a**) are Agam *Acanthochitona garnoti*, Aman *Actinia equina*; Blag *Burnupena lagenaria*, Bcin *Burnupena cincta*, Cocul *Cymbula oculus*, Cpun *Cyclograpsus punctatus*, Ctuli *Conus tulipa*, Dard *Dardanus arrosor*, Dbrev *Diogenes brevis*, Iberg *Ichnochiton bergoti*, Otig *Oxystele tigrina*, Ovar *Oxystele*

variegata, Ppen *Palaemon peringueyi*, Pangu *Parechinus angulosus*, Pexi *Parvulastra exigua*, Pat *Patiriella sp.*, Sgran *Scutellastra granulata*, Scoch *Scutellastra cochlear*, Scap *Siphonaria capensis*, Tanh *Tedania anhelans*, Socu *Siphonaria oculus*, Tsarm *Turbo sarmaticus*. The species names for macroalgae (**b**) are: Bart *Bartoniella sp.*, Cextr *Codium extricatum*, Hten *Hypnea tenuis*, Gabbot *Gelidium abbotiorum*, Gpter *Gelidium pteridifolium*, Hros *Hypnea rosea*, Hspic *Hypnea spicifera*, Lstel *Lyengaria stellata*, Psuh *Plocamium suhrii*, Pcons *Polyopes constrictus*, Seleg *Sargassum elegans*, Sarg *Sargassum sp.*, Sinci *Sargassum incisifolium*, Ufasc *Ulva fasciata*

Small spatial scale and short-temporal variability in food web size and structure

We attempted to depict the seasonal differences in the trophic structure of species in rock pool communities by analysing intra- and inter-seasonal isotopic changes. Intra-seasonally, the biplots indicated greater food web size and length for most pools in winter than in summer (see same pools juxtaposed for different seasons; Fig. S1, Table S2). Larger pools also exhibited larger food webs in comparison to smaller pools in both seasons.

Further, the fundamental niches for all pools combined (inter-seasonally) were trapezoid shaped, with winter supporting a larger food web than summer (Fig. 3). However, both seasons showed similar realised niches (SEAc). The raw isotope values also indicated that the carbon sources ($\delta^{13}\text{C}$) were more diverse in winter, ranging from -18.26 to -0.74‰ , than in summer (-17.67 to -3.92‰). $\delta^{15}\text{N}$ range is

used to quantify food chain length, and in winter pools, this was larger (2.27 to 14.34‰) than in summer (6.86 and 14.23‰). Overall, pools exhibited higher trophic diversity in winter than summer.

Lastly, species composition comprised mainly herbivorous macroinvertebrates with a trophic position (TP) range of 1.7–3.7 in summer and 1.6–3.9 in winter. Fish species, including *Caffrogobius nudiceps*, *Epinephelus marginatus* and *Clinus agilis*, occupied the upper trophic position ranging between 3.7 and 4.4 in winter, while in summer, the TP for main fish species (*Clinus cottoides*, *Caffrogobius nudiceps*) ranged between 3 and 3.4 (Table S3). The trophic position of gastropods such as the scavenging whelk *Burnupena cincta* also overlapped with that of fish in summer. However, because we used a mean TEF value, it is important to note that these trophic positions are expected to slightly vary within and around these ranges (Hussey et al., 2014).

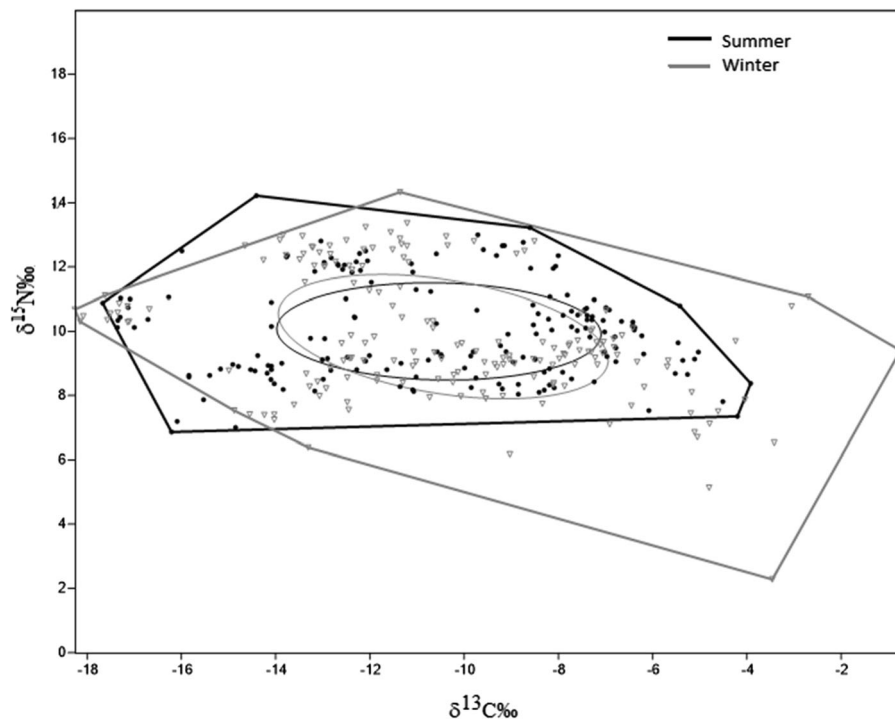


Fig. 3 Inter-seasonal rock pool community-wide metrics based on seasonal $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ isotopic signatures of consumer taxa. Grey indicates winter while black shows the summer season. Thick lines indicate the convex hulls in isotopic space of all

consumer species recorded in each season. The ellipses encompass the SEA_c or realised niche of consumer species within each season

Variation in community-wide food web metrics

The Bayesian GLMMs revealed how different components of the food webs (based on Layman metrics) responded to the local environmental parameters. Contrary to our expectations, there were no significant intra-seasonal interactions between the environmental parameters and all other metrics except for MNND (Table 3). The most influential environmental parameters for most metrics were salinity, pool depth, chl-*a*, substratum type and season, while pH, phosphates and pool size had less effects on food web attributes (Table 2). However, these environmental parameters affected each of the trophic metrics differently. For example, dNr was influenced by depth, phosphates, pool size and salinity with no interactions among any of these parameters. Deeper pools showed high variability in dNr, while higher concentrations of phosphates positively influenced the dNr of all pools. An increase in salinity led to a decrease in the trophic length. In winter, we identified a positive shift in TA,

dNr and dCr across pools (e.g. pools 5, 9, 11, Table S3, Fig. S1). However, the results from the model showed pool size as the only parameter that influenced TA in both seasons (Fig. 4, Table 2).

Further, there was a 3-way interaction among water depth \times salinity \times temperature on MNND. Therefore, to evaluate the effects of temperature on MNND, we partitioned the data by season. The results indicated that higher temperature associated with the summer season had a slightly negative significant effect on MNND while in winter, a significant (positive) interaction between depth \times salinity may have reduced food web packing at pool level in winter (Fig. 4, Table 3). This is based on the observation that MNND slightly decreased as pool size increased in summer relative to winter. All larger pools exhibited lower trophic redundancy (both SDNND and MNND) in summer while in winter, all pools (irrespective of size) exhibited almost similar trophic niches (Fig. 4, Table S3). MNND decreased slightly with pool area in winter (the fitted line is not parallel to the *x*-axis) and

Table 2 Results of fixed effects of the Bayesian generalised linear mixed model (GLMM procedure) obtained from eight separate models for species counts and seven Layman food web metrics

Parameter	Coefficient	Estimate	Standard error	t value	p value
Species counts	(Intercept)	2.5847	0.3533	7.31	<0.0001
	Depth	0.008	0.0956	0.08	0.9298
	Pool size	0.4119	0.1035	3.97	<0.0001
	Temp	− 0.018	0.015	1.19	0.2340
	Substratum	0.2570	0.1066	2.41	<0.01
dNr	(Intercept)	0.2203	0.2889	0.76	0.4456
	Depth	− 0.3855	0.1978	− 1.95	<0.05
	Phosphates	0.8585	0.1861	4.61	<0.0001
	Pool size	0.4311	0.2219	1.94	<0.05
	Salinity	− 0.4874	0.1187	− 4.10	<0.0001
dCr	(Intercept)	1.9987	0.1842	10.85	<0.0001
	Chl- <i>a</i>	− 0.0136	0.1721	− 0.08	0.9370
	Pool size	0.2761	0.1954	1.41	0.1580
	Chl- <i>a</i> × Pool size	− 0.0346	0.1433	− 0.24	0.8090
TA	(Intercept)	2.74571	0.24542	11.188	<0.0001
	Chl- <i>a</i>	− 0.07493	0.24268	− 0.309	0.7575
	Pool size	0.5345	0.24755	2.159	< 0.01
	Chl- <i>a</i> × Pool size	0.02532	0.21033	0.12	0.9042
MNND	(Intercept)	− 0.3448	0.3476	− 0.99	0.3212
	Depth	− 0.0333	0.1167	− 0.29	0.7754
	Salinity	− 0.2513	0.0950	− 2.65	<0.0001
	Temp	− 0.0349	0.0144	− 2.43	<0.01
	Depth × Sal × Temp	− 0.0093	0.0044	− 2.10	<0.001
CD	(Intercept)	0.9597	0.1551	6.19	<0.0001
	Depth	0.0699	0.1544	0.45	0.6510
SDNND	(Intercept)	0.3965	0.4404	0.90	0.368
	Depth	− 0.0662	0.1458	− 0.45	0.6497
	Salinity	− 0.2451	0.1239	− 1.97	<0.05
	Temp	− 0.042	0.018	− 2.26	<0.05
SEAc	(Intercept)	2.2701	0.2222	10.22	<0.0001
	Chl- <i>a</i>	− 0.0994	0.2128	− 0.47	0.6404
	Pool size	0.3952	0.2310	1.71	0.0871
	Chl- <i>a</i> × Pool size	0.0134	0.1802	0.07	0.9407

Coefficients significantly different from zero at $p < 0.05$ are written in bold *Sal* Salinity, *Temp* temperature, *Depth* water depth and × indicates an interaction

was positively related to pool size in summer (fitted line roughly parallel to fitted lines for TA and dNr. Lastly, our results also showed the effects of water depth, salinity and temperature on species evenness (SDNND). After we partitioned the data by season, water depth and salinity independently influenced SDNND only in winter. At pool level, however, SDNND showed a steadier decrease with increase in pool size in winter than summer (Fig. 4), while none of the measured parameters had a significant effect on dCr and CD.

Discussion

Autumn and spring are brief in the study region, and we aimed to describe the trophic structure of rock pool communities in the two main seasons of the year, testing the hypothesis that changes in environmental conditions between summer and winter generate significant variation in food web structure. At the same time, we tested the hypothesis that food web structure varies with habitat characteristics of the pools themselves, specifically the largely fixed

Table 3 Results of fixed effects of the Bayesian generalised linear mixed model (GLMM procedure) partitioned by season for SDNND and MNND

Parameter	Partitioned by season	Coefficient	Estimate	Standard error	<i>t</i> value	<i>P</i> value
SDNND	Summer	(Intercept)	– 0.9089	0.2666	– 3.41	<0.0001
		Depth	0.2202	0.2869	0.77	0.4428
		Salinity	0.2053	0.2869	0.72	0.4742
	Winter	(Intercept)	– 0.3822	0.0001	– 2963.00	<0.0001
		Depth	– 0.0560	0.0001	– 482.00	<0.0001
		Salinity	– 0.1187	0.0001	– 1098.00	<0.0001
MNND	Summer	(Intercept)	– 1.3574	0.2497	– 5.44	<0.0001
		Depth	0.2231	0.3906	0.57	0.5678
		Salinity	– 0.2769	0.4158	– 0.67	0.5054
		Temp	0.5709	0.3019	1.89	0.0586
	Winter	Depth × Salinity	0.0044	0.7096	0.01	0.9951
		(Intercept)	– 1.0162	0.0525	– 19.37	<0.0001
		Depth	0.0806	0.0821	0.98	0.3264
		Salinity	– 0.0227	0.0874	– 0.26	0.7953
		Temp	0.0142	0.0635	0.22	0.8225
		Depth × Salinity	– 0.3025	0.1492	– 2.03	0.0426

Coefficients significantly different from zero at $P < 0.05$ are written in bold. where, *Temp* temperature, *Depth* water depth and × indicates an interaction

physical properties of size and depth, plus substratum type and environmental conditions, which tend to change between seasons.

Abiotic drivers of rock pool communities

Our results indicated increases in species richness, food web size and overall trophic diversity in winter, indicating that summer rather than winter is the more stressful season in these temperate systems (Seuront et al., 2019). Computing of the Layman metrics revealed notable shifts in the trophic niches of consumer species, where niche similarity (MNND) decreased with increases in pool size in summer but not winter. Further, although little variation was explained by habitat characteristics in the CCA, the triplots highlighted how they contributed to the persistence of certain species. For example, in winter, the gastropod *Turbo sarmaticus* exhibited an affinity for deeper pools, while the shrimp, *Palaemon peringueyi*, favoured smaller pools with a sandy substratum in both winter and summer (Fig. 2a). Other species were not influenced by any seasonal parameters, for example, the gastropods *Oxyste-*

tigrina, and *Burnupena cinta*, the cnidarian *Actinia equina*, the echinoderm *Parechinus angulosus* and the crustacean *Dardanus arrosor*. We speculate that based on their functional traits (Martins et al., 2007), these species may have evolved to tolerate short-term variability in rock pool conditions.

A relationship between chl-*a* and limpets (*S. capensis*), chitons (*I. bergoti*, *A. garnoti*) and sponges (*T. anhelans*) was observed from the CCA triplots. Previous work on the coast of South Africa at both large (100 km) and local (100 m) spatial scales revealed a positive correlation between chl-*a*, nutrients and the abundance of most macroinvertebrate species (Bustamante et al., 1995). Although nitrate concentrations in most pools across both seasons were almost below detection limits, the indirect influence of phosphates in our study was realised through dNr which increased with an increase in phosphate concentrations. The presence of phosphate may explain the shifts recorded in the carbon isotope signatures of SPOM and the proliferation of macroalgal species observed in summer. Nutrient flux dynamics are strongly influenced by seasonal variation of temperature, and higher phosphate availability in

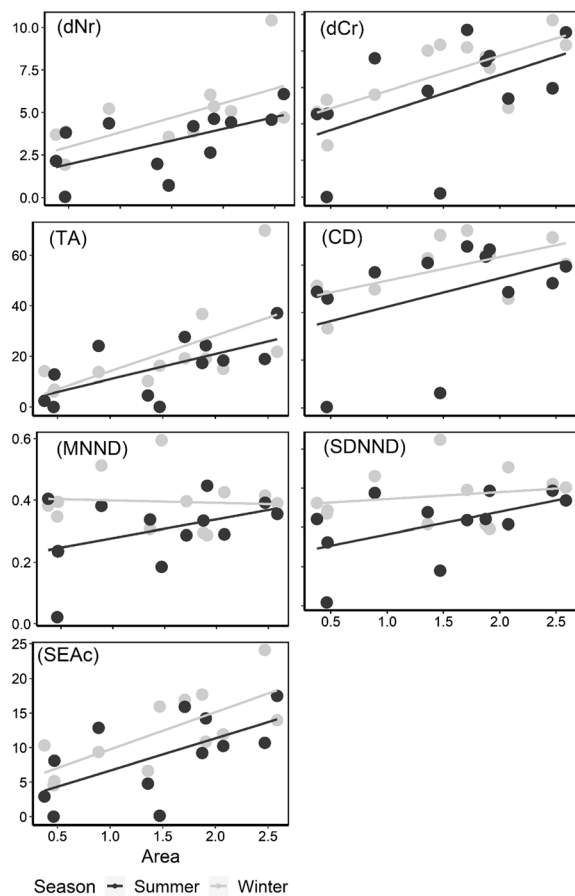


Fig. 4 Layman metrics results for intra-seasonal consumer communities in the 12 rock pools sampled in summer (black) and winter (grey). dNr ($\delta^{15}\text{N}$ range), dCr ($\delta^{13}\text{C}$ range), TA (trophic diversity), CD (mean distance to centroid), MNND (mean nearest neighbour distance), SDNND (species evenness across populations) and SEA_c (realised niche), Area rock pool surface area in m^2

temperate regions is associated with higher temperatures (Asmus et al., 2000). In summer, the lower abundance of epiphytes and the higher temperatures in the rock pools potentially enhance phosphate flux, while during winter, lower temperatures may inhibit this process. Gervais & Riebesell (2001) also showed that algal carbon:nitrogen:phosphate ratios were strongly affected by phosphate concentrations. Similarly, an earlier study performed in laboratory microcosms, showed that phosphate addition positively affected chl-*a* concentrations (Gusha et al., 2019).

In addition, we also speculate that some seasonal changes in species composition were caused by pool-

to-pool variation in short-term temporal conditions. For example, although the mean temperature difference between the two seasons was approximately 5°C , an inspection of the raw data revealed larger differences in water temperatures between pools across seasons, e.g. pool 1 had a temperature variation of up to 14°C between winter and summer. This variation highlights some of the actual temperatures experienced by rock pool species. This in turn can contribute to differences in species richness and changes in species composition between seasons. Other possible factors contributing to pool-to-pool species variation include ecological effects such as competition, territoriality and predation and seasonal differences in algal cover which can provide camouflage for predators and/or prey (Macieira & Joyeux, 2011).

An unexpected seasonal effect involved a shift in substratum type, which had notable effects on the presence of certain species. The most common substratum type across all pools in summer was type 2, while in winter, type 3 predominated. Type 2 indicates an almost homogenous sandy substratum, which is assumed to promote colonisation by certain psammophilic macroalgal species as more were recorded in summer (13) than in winter (10), with the colonisation of pools by opportunistic psammophilic species such as *Hypnea tenuis* and *Gelidium abbotiorum* in summer. These findings are consistent with those of previous studies (McQuaid & Dower, 1990; Fischenich, 2002; Nejrup & Pedersen, 2012) who identified substratum type as a key component in the proliferation of certain macroalgal species, thus, raising the possibility of new colonists or species mortality depending on seasonal changes in substratum. Increased sand can promote mortality or smothering due to reduced light (Littler et al., 1983), while the absence of soft sediment cover ($< 5\%$) on rocky substratum can negatively affect species with a holdfast system that requires sand for anchorage (Fischenich, 2002). This corroborates the importance of substratum type to benthic species composition (Zardi et al., 2008).

Trophic position estimations and food web length

The marginal differences in food web length between summer (1.7–3.7) and winter (1.6–4.4) suggest subtle shifts in diet of species with season. These shifts in trophic position may indicate a change in the food

available, i.e. seasonal differences in material ingested as indicated by seasonal shifts observed in phyto-benthos isotope values and/or different assimilation efficiencies (dos Santos et al., 2019). We predict that such shifts in diets can restructure energy flow within the system.

We assume that pool size, substratum type and resource availability (as indicated by increased dCr) and overall habitat heterogeneity attracted fish to some pools, resulting in increased food web sizes (Fig. S1). This in turn led to an expected positive increase in the total area (TA) and niche area of pools containing fish in comparison to those without fish. Moreover, the presence of fish (as predators) may have led to potential top-down trait-mediated indirect cascading effects (Gravem & Morgan, 2019) on prey species. Gut content analysis indicated the sand shrimp *Palaemon peringueyi* as the primary prey of several fish, particularly *Clinus* spp. (M. N. C. Gusha, *unpub. data*), and pools without fish at the time of sampling contained higher numbers of sand shrimps. Conversely, based on the CCA (Fig. 2), sand shrimps exhibited an affinity for smaller pools, also suggesting a possible habitat induced cascading effect on this prey species. Lastly, due to the project limitations, we could not exhaustively untangle the potential interactions between other aspects of pool geometry (e.g. edge effect) and the presence or absence of fish.

Seasonal variability in carbon sources

The broader carbon source of primary producers observed in summer (-26.22 to -4.16%) vs in winter (-16.88 to 3.8%) suggests that a combined effects of rock pool size and seasonal changes, particularly temperature, water depth and salinity, may have played a critical role in increasing the similarity of trophic niches (lower MNND) of consumer species in summer (Fig. 4, Table 3). Catry et al. (2016) suggested that increased carbon sources influence secondary production, promoting lower MNND within the food web which, ultimately, can impact ecosystem resilience. This is because the loss of one species can be compensated by another species with a similar ecological niche, thereby buffering potential losses in terms of overall ecosystem functioning (Ojwang et al., 2010). Therefore, we speculate that during the summer season, when there is high variability in environmental parameters (and

potentially desiccation stress), macroinvertebrates tend to aggregate in similar trophic niches as a survival mechanism.

Nevertheless, broader carbon sources may be due to the fact that stable isotope ratios in primary producers are determined by photosynthetic reactions (Farquhar et al., 1989) based on factors such as irradiance and are often affected by temporal variation (Legrand et al., 2018). Hence, the observed variations in $\delta^{13}\text{C}$ isotope signatures may not necessarily reflect a broadening carbon base or increase in the number of food sources but rather a change in photosynthetic pathways, growth conditions and irradiance levels, resulting in variation in the isotopic values of primary producers that are assimilated with different efficiencies. This could explain why none of our models were able to fully explain the mechanisms driving the carbon breadth of basal sources.

Lastly, none of our models were able to account for the variation in the core isotopic niche width (SEAc). Presumably, other factors that were not included in this study contributed to the determination of the SEAc. Such factors could include species' functional traits, the influence of oceanographic and hydrodynamic processes on larval settlement and recruitment, the influence of temperature on larval development and interspecific interactions such as predation and competition (Perkins et al., 2015). It is known that temporal variability in hydrographic processes along the South African coastline profoundly affects the composition and distribution of nearshore SPOM and subsequently its carbon signature (Hill et al., 2008). As we did not sample nearshore waters, we may have missed its influences on the carbon breadth of basal sources.

Conclusion

This study highlighted how the species counts and realised niches of rock pool species remained fairly conserved across summer and winter. However, the community-wide metrics highlighted the main environmental effects which drove subtle changes in overall food web length, size and structure. As with spatio-temporal drivers observed across large-scale gradients, our findings showed that, even within small, localised geographical ranges, variability in temperature, salinity and nutrients (particularly phosphates)

are evident and strong enough to affect food web dynamics. Shifts to lower temperatures in winter were significant enough to promote species evenness among pools while an increase in phosphates had a significant positive effect on trophic height. We suggest that the interaction between the physical structure of rock pools and seasonal changes especially in temperature is important in explaining shifts in trophic niches. In summer, the mean nearest neighbour distance notably increased with pool size, i.e. larger pools contained species with less similar trophic niches than smaller pools. We conclude that local hydrography plays an important role in the ecosystem dynamics of rocky pool communities. As our study was done at a single locality, it would be useful to conduct similar small-scale studies across many sites and various temporal scales to allow more robust generalisation on the drivers of carbon sources and trophic diversity in warm temperate systems.

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Author contributions TD, CDM and MNCG conceptualised and designed the methodology; MNCG and TD collected the data; MNCG analysed the data and wrote the original draft; TD, CDM and MNCG reviewed and edited the drafts; CDM provided funding for the research. All authors gave final approval for publication.

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Data availability All data and material generated during the present study are available from the corresponding author upon request.

Compliance with ethical standards

Conflict of interest The authors declare that there are no competing interests.

Consent for publication The authors give consent to publish this article.

Ethical approval An ethics permit (RU-LAD-16-08-0001) was granted to conduct this study.

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