Associations in ephemeral systems: the lack of trophic relationships between sandhoppers and beach wrack

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ABSTRACT: In ephemeral systems, material subsidies can play a key role in the persistence and connectivity of populations, especially if the organisms living within them are trophically dependent on imported resources. Sandy beaches are heavily subsidized by organic material of both terrestrial and marine origin. For highly mobile supratidal fringe species, such as amphipods, which are marine but with a high tolerance of aerial conditions, such material potentially provides both food and shelter. We investigated the relationship between beach wrack and amphipods by examining the trophic contribution of allochthonous food sources to sandhopper diets using stable isotope analysis. Replicate samples of the sandhopper *Talorchestia capensis* and several types of beach wrack (including seagrass, wood and different macrophytes) colonized by these amphipods were collected from 11 sites within one biogeographical region along the south coast of South Africa. Analysis of variance showed that the $\delta^{13}C$ and $\delta^{15}N$ signatures of sandhoppers were significantly affected by the type of wrack with which they were associated, but stable isotope mixing models showed that there was no close relationship between *T. capensis* diet and the material under which they were found. Thus sandhopper isotope signatures differed with wrack type, but were not clearly derived from wrack. This was interpreted as an indication that amphipod feeding was extremely opportunistic, with different sandhopper populations feeding at different trophic levels (based on $\delta^{15}N$ signatures) and obtaining their $\delta^{13}C$ signatures from material associated with specific wrack types, rather than directly from the wrack itself or from imported suspended particulate material. These results suggest alternative links in sandy beach food webs, with amphipods obtaining their carbon indirectly from wrack via bacterial communities that are specific to different types of imported material.

KEY WORDS: Allochthonous resources · Stable isotopes · Diet · *Talorchestia capensis* · Sandy beaches · Trophic ecology

INTRODUCTION

Flow of material between markedly separate systems, such as land and water, is the most extreme example of cross-boundary trophic subsidisation (Polis et al. 1997, Paetzold et al. 2008, Schlacher & Connolly 2009). Smaller-scale differences in subsidisation are also common within systems, such as the different proportions of autochthonous and allochthonous inputs within estuaries (Mann 2000), which are characterised by an upstream to downstream gradient of terrestrial and marine inputs (Vannote et al. 1980). Globally, the effect of river discharges on the sea provides a strong functional coupling between terrestrial and marine systems through the export of terrestrial organic carbon to the ocean (Schlünz & Schneider 2000), and it has been suggested that the energetic dependence of nearshore marine systems on continental sources is likely to be much greater than previously estimated (Schlacher & Connolly 2009). Cross-boundary flow from sea to land is also a common process that operates at different scales depending on vector mobility (Polis

& Hurd 1996, Stapp & Polis 2003, Paetzold et al. 2008), but marine inputs to terrestrial systems seem generally to be weaker (Paetzold et al. 2008), with the possible exception of isolated islands (Smith & Froneman 2008). Cross-boundary exchanges are common within marine systems, like subtidal kelp inputs to intertidal grazers (Bustamante et al. 1995), and rocky shores dominated by filter-feeders or macroalgae may act respectively as sinks or sources of detrital food (McQuaid & Branch 1985).

Sandy beaches are the most widely distributed transitional coastal systems and rely heavily on energy sources from both land and sea (McLachlan 1980, Talbot & Bate 1987, Brown & McLachlan 1990, van der Merwe & McLachlan 1991). The flux of material between land and sandy shores can be dynamic, with beaches transferring nutrients to terrestrial communities (e.g. Polis & Hurd 1996, Stapp & Polis 2003), as well as land providing a strong energy contribution to sandy beach ecosystems (Schlacher & Connolly 2009). Beach-stranded material from the sea and from rivers can support a range of intertidal primary consumers, which in turn influence secondary productivity by becoming food sources for terrestrial consumers (Polis & Hurd 1996, Stapp & Polis 2003, Catenazzi & Donnelly 2007). However, stranded material can also form the habitat for many species and it can be difficult to separate the relative importance of such material as either shelter or food.

Semi-terrestrial amphipods are ubiquitous and abundant decomposers (Griffith et al. 1983) on sandy beaches; they are often recognised as bioindicators of pollution (Rainbow et al. 1989, Ugolini et al. 2005) and ecological indicators of disturbance (e.g. beach grooming; Dugan et al. 2003), making them ideal models for investigating trophic dependency in ephemeral systems. Stable isotopes have been widely used to examine food web structure and time-integrated trophic relationships that link marine and terrestrial systems (e.g. Peterson & Fry 1987, Hobson 1999, Dunton et al. 2006), and to incorporate trophic spatial heterogeneity (McGlynn et al. 2009). In the present study, isotopic signatures of carbon and nitrogen were used to assess the role of beach wrack in the diet of the supralittoral sandhopper *Talorchestia capensis* from several populations supplied by a series of different subsidies on the south coast of South Africa. *T. capensis* occurs from the South African-Namibian border to Durban, on the east coast (Branch et al. 2002). While numerous studies show that sandhopper diet is heavily dependent on macrophytes (e.g. Adin & Riera 2003, Crawley et al. 2009), evidence of alternative food sources, including diatoms (Johnston et al. 2005), carrion (Blankenship & Levin 2007) and, with severe food limitation, conspecifics (Duarte et al. 2010), also suggests opportunis-

tic foraging strategies. The material deposited on these shores tends to be reasonably consistent over time, largely reflecting the nature of neighbouring macrophyte communities. For example, the wrack on shores close to kelp beds is almost exclusively kelp material (Koop et al. 1982), while near estuaries the angiosperm *Zostera capensis* is abundant, and on open coast shores away from kelp beds there is usually a mixture of algae consisting largely of rhodophytes, with some sponges and ascidians (F. Porri pers. obs.).

South African beaches generally experience high levels of wave exposure (McLachlan et al. 1981) and high nutrient input by macrophyte decomposition (Griffiths & Stenton-Dozey 1981). In addition, while amphipods in the northern hemisphere (Scapini et al. 1992) and on the west coast of South Africa (Griffiths & Stenton-Dozey 1981, F. Porri pers. obs.) are usually found buried along the wrack line during the day, in the study region they are strictly associated with the wrack itself during daylight hours, with virtually no sandhoppers under the sand along the detritus line (F. Porri pers obs., Baldanzi et al. unpubl data). Consequently, we hypothesised that the amphipods on each shore would feed exclusively on the wrack under which they were found, producing clear signals in their stable isotope composition. The implications of tight trophic dependency include high sensitivity to disturbance of these ephemeral habitats, with likely local extinction of sandhopper populations in the event of the interruption of food supplies.

MATERIALS AND METHODS

Study sites. Eleven sandy beach study sites were chosen within the warm temperate south coast bioregion of South Africa (Fig. 1). To minimize temporal variability and maximize geographic coverage within the region, as recommended by McLachlan & Dorvlo (2005), sampling of sites was done over a single week (during April 2009). These shores are similar in their morphodynamics, characterized by a semidiurnal tidal regime (with a tidal range of from 0.05 to 2.36 m for the studied region), high wave energy dissipated within the surf zone, moderate slopes and sands of fine to medium grain size (our Table 1; McLachlan et al. 1981). Although the amount of wrack deposition is variable in time, shores tend to consistently receive the same type of subsidy, depending on shore exposure (Ochieng & Erftemeijer 1999, Orr et al. 2005) and on the closest source of wrack (e.g. estuaries, kelp beds or rocky shores), except when extreme winter storms disrupt this pattern (F. Porri pers. obs.). Sites were selected according to the type of wrack present as determined from familiarity with the sites and repeated visits over
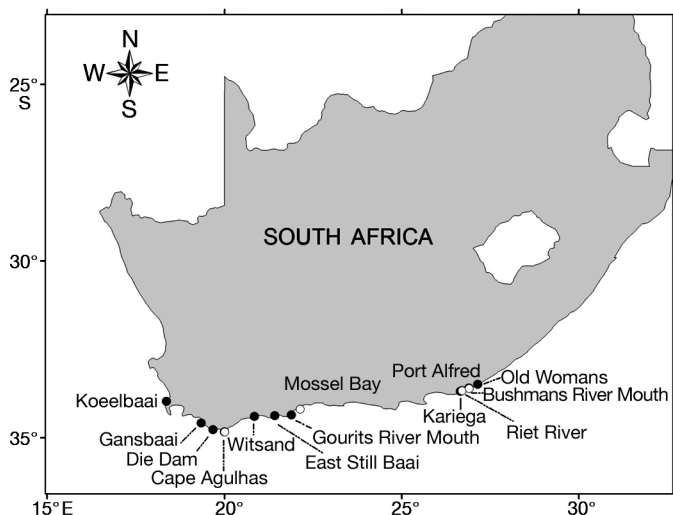
Fig. 1. South coast bioregion South Africa. Sites: ● = sandhopper collection, ○ = POM values taken from Hill et al. (2006)

a number of years (F. Porri pers. obs., S. Baldanzi pers. comm.): seagrass (*Zostera capensis*), kelp (*Ecklonia maxima*), wood and a mixture of macroalgae and small brown macroalgae with large inputs by *Zonaria subarticulata* or *Anthophycus longifolius* (which differ from kelp in terms of absolute and seasonal biomass; Bolton & Anderson 1997). Although all the permanently open estuaries considered in this study are marine-dominated (Allanson & Baird 1999, Vorwerk & Froneman 2009), a subset of sites was also partitioned according to the proximity of an open estuary, to account for a possible, even if limited, effect of river discharge.

Sample collection and preparation. *Talorchestia capensis* (5 samples, each pooled from the whole bodies of 5 individuals) and beach wrack (n = 5) under which the sandhoppers were found were collected from each of the 11 sandy beaches. The sandhoppers were kept in fresh seawater (30 ± 1 ppt, at ambient temperature) for 8 h to allow the evacuation of gut contents. All

sandhoppers and beach wrack were rinsed in distilled water to remove potential contaminants, including trapped particulate organic matter (POM) and/or microbial communities. Samples were subsequently oven dried (60°C, 48 h) and ground into fine powder. Sandhoppers and samples of coralline algae were acidified to remove $CaCO_3$ in accordance with Fry (1988) and Cloern et al. (2002) by adding 2 N hydrochloric acid (HCl) drop-by-drop until CO_2 release stopped. Samples were then re-dried at 60°C without rinsing to minimize loss of dissolved organic matter (DOM) and were ground again as described by Jacob et al. (2005).

Isotope analysis. $\delta^{13}C$ and $\delta^{15}N$ signatures of all samples were determined using a continuous-flow Isotope Ratio Mass Spectrometer (IRMS), after sample combustion in an on-line Flash EA 1112 series elemental analyser at the University of Cape Town, South Africa. Beet sugar and Merck gelatine were used as standards, calibrated against International Atomic Energy reference materials (PeeDee Belemnite and air for $\delta^{13}C$ and $\delta^{15}N$, respectively). Results are expressed in standard delta notation, $\delta X = ([R_{sample} / R_{standard}] - 1) \times 1000$, where X is the element in question and R is the ratio of the heavy to light isotope. Precision of replicate determinations for both carbon and nitrogen was ±0.05‰.

Data analysis. To evaluate the site-specific dietary contribution of beach wrack to amphipod diet, the stable isotope analysis in R (SIAR) package was used (Parnell et al. 2008 available at http://cran.r-project.org/web/packages/siar/index.html). This program employs a Bayesian framework based on Gaussian likelihood with a mixture dirichlet-distributed prior on the mean. The SIAR package was run for (1) all shores characterised by essentially monospecific subsidies (i.e. seagrass, kelp, wood, *Anthophycus longifolius* or *Zonaria subarticulata*), and (2) the more complex, mixed-shore sites. Each mixing model was run as a multigroup dataset (i.e. multiple sites and sources), with no concentration correction factors, and only site-

Table 1. Physical features of all sites selected for analysis. Shore type: dissipative for all sites

Site	Source type	Source	Sand	Tidal range (m)	Adjacent to estuary
Old Womans	Mixed	Macroalgae East	Fine	0.07–2.06	No
Riet River	Mixed	Macroalgae East	Fine	0.07–2.06	No
Kariega	Monospecific	*Zostera capensis*	Fine	0.07–2.06	Yes
Bushmans	Monospecific	*Z. capensis*	Fine	0.07–2.06	Yes
Gourits River Mouth	Monospecific	Wood	Fine	0.05–2.36	Yes
Witsand	Monospecific	Wood	Fine	0.05–2.36	Yes
Die Dam	Monospecific	*Ecklonia maxima*	Fine	0.05–2.36	No
Cape Agulhas	Mixed	Macroalgae West	Fine/medium	0.07–1.80	No
East Still Baai	Monospecific	Wood	Fine	0.07–1.80	Yes
Gansbaai	Monospecific	*E. maxima*	Fine	0.07–1.80	No
Koeelbaai	Mixed	Macroalgae West	Fine/medium	0.07–1.80	No

specific results are presented. As there is some evidence to suggest that amphipods obtain their organic carbon from trapped POM rather than from the habitat in which they live (de Robertis et al. 2001), isotopic signatures (δ^{13}C and δ^{15}N) of nearshore POM from nearby geographic locations (taken from Hill et al. 2006) were included in both mixing models. Due to variable fractionation, especially amongst herbivores (Van der Zanden & Rasmussen 2001), 2 sets of fractionation values were applied: (1) the traditional fractionations of 1.0 and 3.4‰ for carbon and nitrogen, respectively (DeNiro & Epstein 1978, 1981, Fry & Sherr 1984), and (2) the fractionations based on the results of amphipod feeding experiments run by Crawley et al. (2007) of −3.0‰ and 0.6‰ for δ^{13}C and δ^{15}N, respectively.

To assess the effects of source and river proximity on the δ^{13}C and δ^{15}N signatures of sandhoppers, two 1-way ANOVAs were performed for each element, using source and river proximity as independent fixed factors. In order to balance the data, Gourits River Mouth was excluded for ANOVA of source effect, while Old Womans and Koeelbaai were removed from the analysis of the effect of river proximity. Using Cochran's test, δ^{13}C variances were determined to be heterogeneous, although no transformations were applied because ANOVA is robust to heterogeneous data when large datasets are balanced (i.e. for source, but not for proximity to a river). In small heterogeneous studies significant results could lead to Type 1 errors. Therefore an additional conservative precaution in data interpretation was applied by accepting p-values of 0.01, rather than 0.05 (Underwood 1997). Significant differences were screened using the Student Newman Keuls post-hoc test (Zar 1996).

An additional 1-way ANOVA was performed after review of the SIAR mixing model results on the C:N ratios of all the source contributors to monospecific shores in order to compare the quality of the different potential food sources. The dataset was balanced to n = 4. Homogeneity of variances was confirmed after log transformation using Cochran's test, while significant differences were screened using the Student Newman Keuls post-hoc test (Zar 1996).

RESULTS

Isotopic box plots from both mixed and monospecific (Fig. 2) shores incorporate a large range of values. At the mixed-shore Riet River for example, the range of values for beach wrack was −32.85 to −7.12‰ for δ^{13}C and 3.24 to 6.46‰ for δ^{15}N. Wrack from monospecific shores ranged from −26.25 to −8.44‰ for δ^{13}C and from 0.14 to 6.69‰ for δ^{15}N.

Results from the SIAR mixing models, which included nearshore POM signatures taken from Hill et al. (2006), showed that *Talorchestia capensis* does not appear to feed exclusively on beach wrack. The proportions returned by the SIAR mixing model using traditional fractionation values (Fry & Sherr 1984) and those from Crawley et al. (2007) for mixed shores were similar (Riet River and Old Womans; Fig. 3),
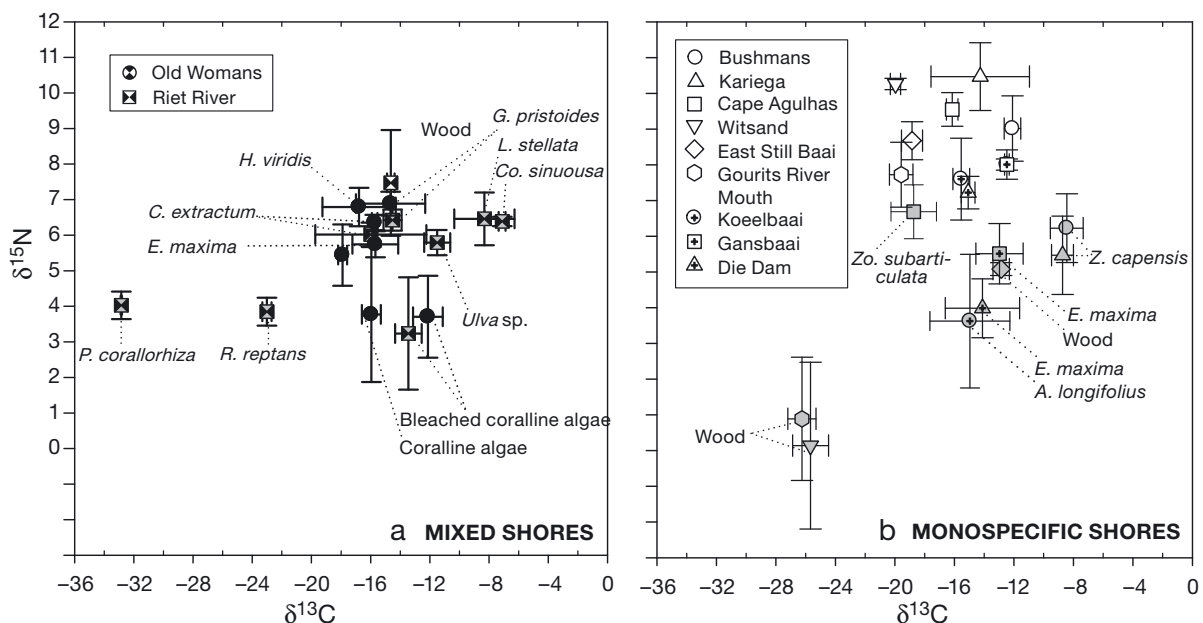

Fig. 2. Isotopic biplots of sandhoppers *Talorchestia capensis* (white symbols) and beach wrack (grey symbols) subsidies for (a) mixed and (b) monospecific shores. *A.* = *Anthophycus*; *C.* = *Codium*; *Co.* = *Colpomenia*; *E.* = *Ecklonia*; *G.* = *Gelidium*; *H.* = *Hypnea*; *P.* = *Plocamium*; *R.* = *Rhodophyllis*; *Z.* = *Zostera*; *Zo.* = *Zonaria*

suggesting a range of minimum values of from 0 to 35%, a maximum value of 40% and a mean of ~10% for the contribution of all sampled beach wracks and POM to sandhopper diet. Results for the monospecific shores (Fig. 4) were somewhat different. *Ecklonia maxima*, *Anthophycus longifolius* or *Zonaria subarticulata* contributed a minimum of 0 to 50%, and a maximum of 65% (with a mean of 10 to 30%) to the diet, with potentially higher contributions by POM (a mean of 10 to 20%, a range of minimum values from 0 to 80%, and a maximum value of 90%). Shores subsidised by seagrass showed mean *Zostera capensis* contributions of 30% (range from 0 to 90%) compared to a 20% contribution of POM to sandhopper diet (range from 0 to 80% minimum, and up to 90% maximum). Sandhoppers found under wood subsidies were different again, with similar dietary contributions of wood (a mean of 37%, with a range from 0 to

65%) and nearshore POM (a mean of 15 to 18%, with a range from 0 to 80%).

The ANOVA results showed a significant effect of source for carbon and nitrogen. The carbon signatures separated into 4 homogenous groups ($F_{4,45}$ = 55.42, MS = 71.89, p < 0.01): mixed macroalgae, wood, seagrass and kelp (Fig. 5). $\delta^{15}N$ signatures ($F_{4,45}$ = 14.32, MS = 18.52, p < 0.01) separated into 3 groups: mixed macroalgae; small brown macroalgae and mixed with seagrass and wood; and kelp (Fig. 5). Nitrogen signatures from sites adjacent to estuaries were also significantly more enriched than those far from estuaries ($F_{1,38}$ = 23.063, MS = 23.81, p < 0.01), while carbon showed no significant differences.

C:N ratios in beach wrack in monospecific shores fell into 3 homogenous groups, with ratios in wood > ratios in all brown macroalgae > ratios in seagrass and POM ($F_{4,20}$ = 693.81, MS = 16.63, p < 0.001).
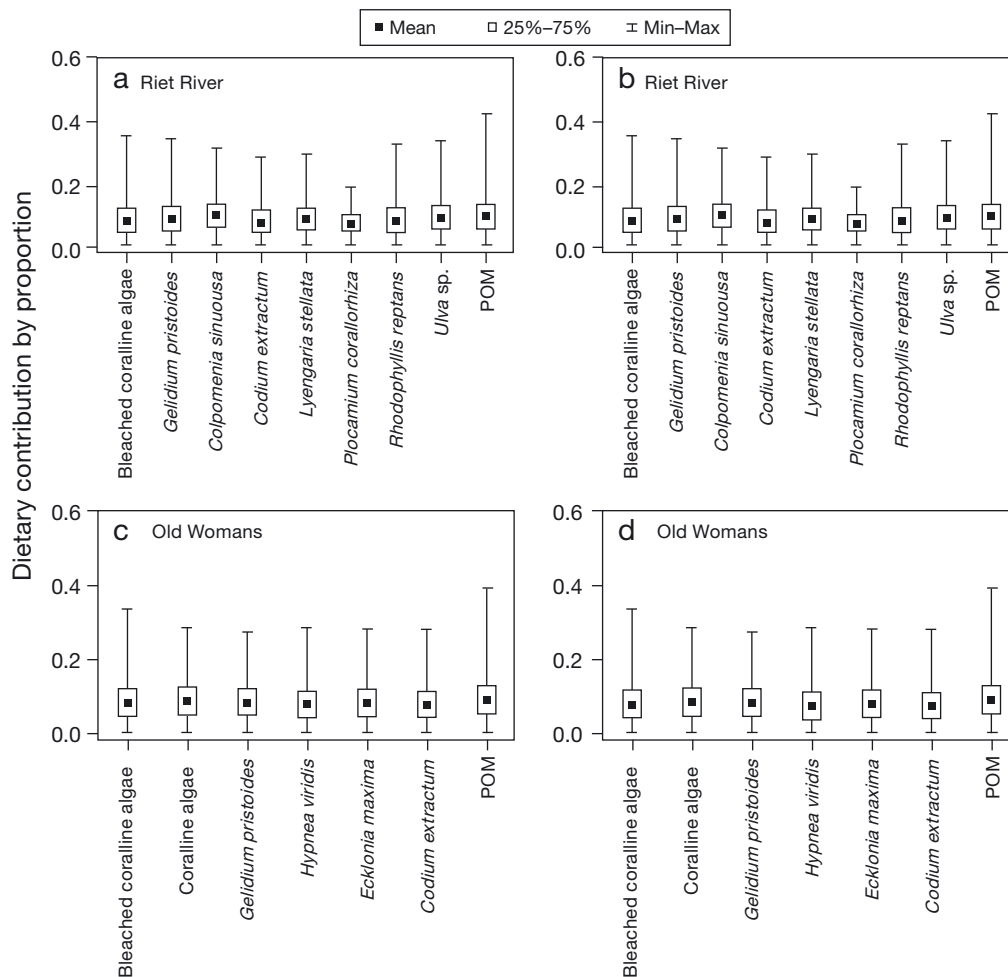

Fig. 3. *Talorchestia capensis.* Source contributions at (a,b) Riet River and (c,d) Old Womans by proportion to sandhopper diet as determined by stable isotope mixing models for mixed-shore sites. (a,c) Results using traditional fractionations; (b,d) results using fractionations suggested by Crawley et al. 2007. POM particulate organic matter
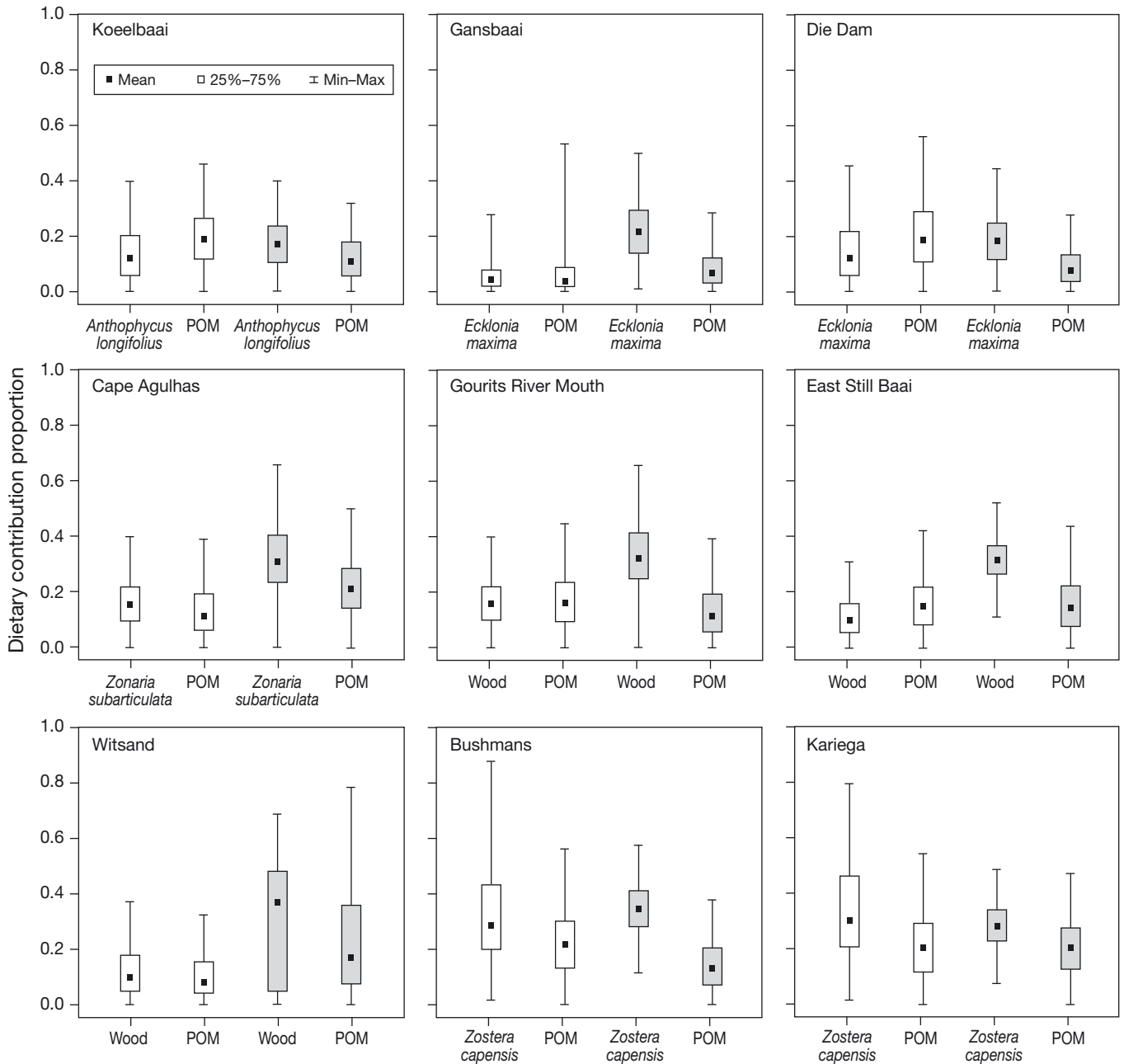
Fig. 4. *Talorchestia capensis.* Source contributions by proportion to sandhopper diet as determined by SIAR mixing models for sites with monospecific subsidies. Boxes: white = fractionations suggested by Crawley et al. (2007); grey = traditional fractionations. POM: particulate organic matter

DISCUSSION

Mixing models of stable isotope ratios for sandhoppers collected from 11 sites along the south coast of South Africa, and predominantly receiving different types of beach wrack, including seagrass, wood and different macrophyte species, indicated that sandhoppers did not feed exclusively or even predominantly on the material under which they were found. The hypothesis of an exclusive trophic association with material subsidies to the shore was therefore rejected.

Although the mixing models incorporated a large range of potential dietary contributions, the variability of the values (CI of 25 to 75%) suggested minimal trophic dependency on wrack subsidies or nearshore POM at most sites (Figs. 3 & 4). In fact, macroalgal or
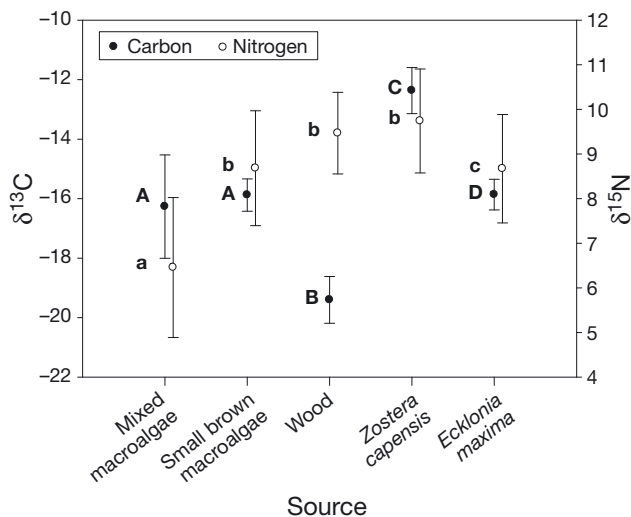
Fig. 5. *Talorchestia capensis.* $\delta^{13}C$ and $\delta^{15}N$ signatures (means ± 1 SD) of sandhoppers in relation to source type. Letters indicate homogenous groups (Student Newman-Keuls, p < 0.05) for carbon (uppercase) and nitrogen (lowercase)

POM subsidies at mixed-shore sites accounted only for a range from 0 to 35 % (mean ~10 %; Fig 3) of sandhopper diet. The situation was similar for sandhoppers living on shores with monospecific subsidies (Fig. 4). If we consider these data in conjunction with the C:N ratios of each subsidy (which reflect the quality of organic matter; Russel-Hunter 1970), inferences can be made on the probability of a certain macroalga being a substantial contributor to the diet of *Talorchestia capensis*. Mixed-shore subsidies showed C:N ratios >12, with the exception of coralline algae (bleached or fresh) which showed ratios of 8.17 ± 1.21 for bleached and 10.99 ± 2.37 for fresh coralline algae, respectively. Material with a lower C:N ratio forms higher quality food that is generally easier to assimilate (Cruz-Rivera & Hay 2001). For example, although mixing models from monospecific shores (using traditional fractionations) demonstrated high contributions of wood to diet, the C:N ratio range was from 43.66 to 158.58, making it an extremely unlikely food source. Mid-range ratios combined with the relatively low potential contributions returned by mixing models suggest that sandhoppers from all communities are not tightly linked trophically to the beach wrack under which they are found. Earlier studies have shown that other factors may also affect macroalgal palatability, including physical structure (Pennings et al. 1996, Wessels et al. 2006) and secondary compounds (e.g. $CaCO_3$, phenolics; Estes & Steinberg 1988, Levinton et al. 2002), which act to deter grazing. The high levels of $CaCO_3$ in coralline algae and the phenolic levels in kelp, for example, make their assimilation by sandhoppers even more unlikely. All other sources from monospecific shores

showed high C:N ratios (>20), with the exception of *Zostera capensis* (mean ± SD = 15.24 ± 3.36). POM, however, showed a mean C:N ratio of 7.36 ± 0.96, making it a more probable food. Overall, we suggest that *T. capensis* shows no strong dependence on a specific subsidy (Figs. 3 & 4), but instead demonstrates an opportunistic feeding response. Indeed Brown (1996) suggested that behavioural plasticity is directly related to population survival on sandy beaches. However, flexible foraging strategies complicate interpretation of stable isotope ratios, as opportunistic diets result in increased mixing of isotope ratios when there is a wide range of signatures in food sources.

Amphipods have been shown to shift their mode of feeding from grazing to detritivory to scavenging (e.g. Cruz-Rivera & Hay 2001, Riisgård & Schotge 2007). Our results support these findings, as the 3 $\delta^{15}N$ groups identified suggest that *Talorchestia capensis* may be feeding at multiple trophic levels. Furthermore, the identification of 4 homogenous groups within sandhopper $\delta^{13}C$ signatures suggests that *T. capensis* may make use of different organisms and/or microbial communities associated with different species of wrack (Fig. 5). The higher nitrogen signatures seen in sandhoppers living adjacent to estuaries, on the other hand, can be related to available nitrogen pools. In systems where there is a reliance on recycled nitrogen for growth (e.g. estuaries), $\delta^{15}N$ isotope ratios will be significantly more enriched than in those that depend on upwelled "new" nitrogen (Miyake & Wada 1967, Schubert & Calvert 2001). The observed isotopic differences among sandhopper populations suggest that trophic relationships for *T. capensis* are highly variable and are influenced by multiple factors, necessitating plastic dietary responses to available subsidies.

The lack of a clear relationship between the stable isotope signatures of these amphipods and the beach wrack that provides their habitat is in contrast to the extensive literature that reports close trophic relationships between amphipods and beach wrack (e.g. Griffiths et al. 1983, Adin & Riera 2003, Dugan et al. 2003, Crawley et al. 2009). There is also some debate as to the role of talitrids in wrack decomposition, with some studies suggesting low sandhopper impact (Inglis 1989, Jędrzejczak 2002) and others suggesting a higher influence, depending on wrack age and species (Mews et al. 2006). Historically, stable isotope analysis has helped to distinguish between ingested and assimilated material (Fry & Sherr 1984) and the application of mixing models (e.g. IsoSource, Phillips & Gregg 2003; SIAR; Parnell et al. 2008) has helped to clarify isotopic contributions to consumer diets when dealing with multiple sources. It is important, however, to recognise that metabolic isotope fractionations as well as isotopic equilibration rates are often species-specific

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(Burkhardt et al. 1999, Vander Zanden & Rasmussen 2001). Quantifying these factors prior to analysis is important to the interpretation of trophic relationships and, due to fractionation variability amongst herbivores (Vander Zanden & Rasmussen 2001), two sets of fractionations were applied: the traditional values (DeNiro & Epstein 1978, 1981, Fry & Sherr 1984), and those previously determined for a semi-aquatic amphipod by Crawley et al. (2007), an approach also taken by Rossi et al. (2010). If we assume isotopic equilibration rates of 2 to 3 wk on average, as reported for rapidly growing small arthropods (Fry & Arnold 1982, Crawley et al. 2007), the results then suggest that for the sampled month, there were very weak trophic relationships between sandhoppers and beach wrack. Although temporal variability of deposited material was not quantified on these shores, we believe species composition to be relatively consistent (Orr et al. 2005, F. Porri pers. obs., S. Baldanzi pers. comm.). Food quality is another factor that must be considered; however, there is evidence that meiofauna is strongly linked with successional changes in microbial communities (Jędrzejczak 2002), rather than with physical wrack breakdown and general variability, suggesting that food quality in wrack communities is relatively stable. Coupled with the stable isotope results, this suggests that, in general, sandhopper populations on the warm temperate South African coast have little direct dietary association with the material under which they live.

As sandy shores, particularly dissipative beaches, are often regarded as semi-enclosed systems with a large input of primary production from the surf zone (McLachlan 1980), the trophic link could lie in blooms from the local surf-zone diatom *Anaulus birostratus* (Talbot & Bate 1987). Although *A. birostratus* commonly occurs within South African surf zones, the input from diatoms on the nearshore does not seem to contribute as much as detritus (Talbot & Bate 1987). In addition, sandhoppers in the present study showed isotopic signatures that vary according to wrack source (Fig. 5). If we accept then that none of the subsidies under which these sandhoppers are found contribute significant amounts of organic matter to their diet (Figs. 4 & 5), it is plausible that the missing trophic link may lie in additional organic material indirectly associated with the subsidy itself. This additional source of organic carbon would be ubiquitous around the coastline, but would possess variable $\delta^{13}C$ signatures. Additionally, microbial and bacterial communities colonising the decomposing beach wrack are likely to provide a nitrogen-rich food source to *Talorchestia capensis*. Furthermore, it is possible that talitrids ingest, but do not assimilate, beach wrack along with wrack-associated organic material or microbial communities, which may reconcile the current results with the past literature describing close trophic associations (e.g. Griffiths et al. 1983, Duarte et al. 2010). Since the composition of the bacterial community can vary among types of detritus (Simon & McQuaid 1999), a scenario where sandhoppers obtain their carbon from bacterial populations that differ among wrack types would explain our results. The importance of epibenthic detritus (de Robertis et al. 2001) and diatoms on leaf litter (Lepoint et al. 2006) in amphipod diet underlines the potential for detritivorous feeding strategies. On sandy beaches, where the arrival of macrophyte material is stochastic at best, a detritivorous approach to feeding is warranted, and flotsam may be more important as a structural refuge (Covi & Kneib 1995).

Weak trophic relationships between sandhoppers and their subsidies or habitats in this region opens a new range of questions for future work that should focus on clarifying alternative uses of allochthonous material subsidies, their link with sandhopper diet and the source of assimilated material. Further investigations may also unravel trophic dynamics in sandy beach ecosystems, and clarify the role of detritus-based food webs.

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