Frondose and turf-dominated marine habitats support distinct trophic pathways: evidence from ^{15}N and ^{13}C stable isotope analyses

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Marine vegetation plays an important structuring role, delivering key functions and services to coastal systems the extent of which depends on the foundation species and their architecture. In increasingly urbanised coastlines, turf-forming macroalgae are replacing frondose morphotypes. Trophic relationships within these systems can be studied through stable isotope analysis of the different food web compartments. In the present study, we investigated trophic pathways in two distinct macroalgal assemblages: one dominated by small brown frondose algae, and one dominated by low-lying turf-forming species. ^{15}N and ^{13}C isotopic signatures were determined for selected macroalgae and sedentary animals from distinct trophic levels, collected from two habitats on São Miguel Island (Azores, Portugal). In frondose habitats macroalgae appeared to make up the primary carbon source for the entire food web, whilst in turf-dominated habitats there was a decouple between macroalgae and higher trophic levels.
Because canopy replacement by algal turf may affect the structure of the littoral food webs, coastal biodiversity conservation strategies should give priority to natural areas rich in canopy-forming algae.

Key words*: Trophic pathways; Habitat; Macroalgae; Food web; Stable isotopes*

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INTRODUCTION

The functioning and complexity of services provided by marine vegetated ecosystems depend on the assemblage and architecture of foundation species. In temperate areas, for instance, large forests of brown seaweeds are the structural element of coastal ecosystems (Steneck et al. 2002). Warmer temperate and/or subtropical communities are characterized by two algal morphotypes, a canopy type of growth composed by associations of two or more species of frondose algae, and algal turfs, which are complex assemblages of macroalgae with

compact growth, about 5 cm in height, and well developed entangled prostate axes (Lawson & Norton 1971; Price & Scott 1992; Neto 2001; Wallenstein et al. 2009; Martins et al. 2016). Canopy-forming algae modify several biotic and abiotic factors of rocky shore ecosystems, and are fundamental in creating and maintaining habitats and their assemblages and ecological processes (Bulleri et al. 2002; O'Brien et al. 2018). They are, however, considerably vulnerable to anthropogenic disturbances, and are being increasingly replaced by turf-forming algae in urbanised coastlines (e.g. Benedetti-Cecchi et al. 2001), due to the latter's rapid lateral vegetative growth (Airoldi 1998) and consequently high rates of colonisation under high sedimentation and nutrient input (Worm et al. 2001). Along with the fact that this type of algal growth can hinder the recruitment of its canopy-forming counterpart (Kennelly 1987), these characteristics enable turf-forming algae to dominate urbanized coasts, which poses a major threat to the biodiversity of those ecosystems (Gorgula & Connell 2004).

In the subtropical Azores archipelago, kelps occur only in limited deep water habitats (Tittley et al. 2001), and there are no records of seagrass and other warm-water vegetated habitats. Instead, the Azorean shallow subtidal (up to 40 m depth) supports extensive beds of frondose vegetation generally dominated by associations of brown algae, namely *Dictyota* spp., *Halopteris filicina* and, most commonly, *Zonaria tournefortii* (Neto 2000a, 2000b, 2001; Tittley & Neto 2000). Even though these macroalgae have not traditionally been designated as canopies, they can attain substantial sizes (>30 cm) and effectively shadow the understory assemblage (e.g. Martins et al. 2016). Comparatively little is known about the ecological and functional role of the habitats dominated by these smaller brown algae. Another benthic coastal habitat in the Azores is structured by low-lying multispecific turf-forming algae, such as the red seaweeds *Ellisolandia elongata* and *Gelidium* spp. (Martins et al. 2016). Thus the Azorean coastal habitats, which are increasingly subject to human pressure and activities, match the basic conditions for the dynamics of canopy replacement. For instance, the dominance of turf-forming algae in the Azores intertidal was seen to be related with the overexploitation of herbivores

(e.g. limpets) suggesting that human exploitation may have shifted the community to an alternative stable state, and that continued exploitation of limpets is the key driver allowing turfs to dominate (Martins et al. 2010).

Stable isotopes of Nitrogen and Carbon have been successfully used for a range of applications in marine ecology (Behringer & Butler IV 2006; Carvalho 2008; Gillies et al. 2012), such as comparative studies of aquatic food chains (Cabana & Rasmussen 1996; Behringer & Butler IV 2006) and investigating human impact on coastal ecosystems (e.g. Page et al. 2013; Mancinelli & Vizzini 2015). Following considerable methodological and technological advances in this rapidly growing field, stable isotopes have become reliable tools for studying food chain structure (Peterson 1999; Phillips et al. 2014).

The Carbon-13 stable isotope may be effectively used to identify the food chain's carbon sources, as there is considerable variation in the ratio of ^{13}C to ^{12}C ($\delta^{13}C$) among producers, and little variation once incorporated in the higher levels of the trophic pathways (Layman et al. 2011). The ratio of ^{15}N to ^{14}N ($\delta^{15}N$), on the other hand, increases predictably from one trophic level to the next (Post 2002), and may thus be employed to infer an organism's position in the food chain. Therefore, the combined analysis of Carbon and Nitrogen stable isotope ratios is an effective approach to investigate trophic pathways and energy flow within marine food webs (Lepoint et al. 2003).

Here we employ stable isotopic analysis to investigate whether there are functional differences between two distinct habitats, one dominated by frondose and the other by turf-forming macroalgae, in order to better understand the potential consequences of canopy replacement on the dynamics and structure of coastal ecosystems.

MATERIALS AND METHODS

Study site and sampling method
This work was carried out on two distinct shallow-water habitats in the south coast of São Miguel Island, Azores (Fig. 1), one dominated by
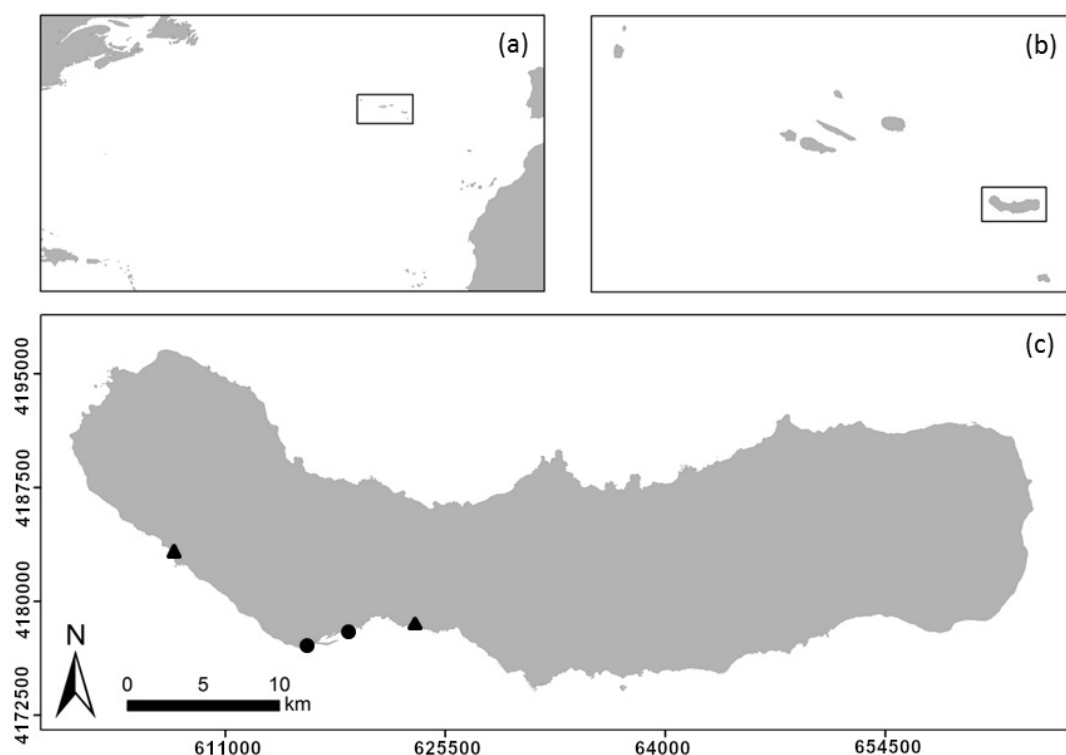
Fig. 1. Map of Azores Archipelago (a), São Miguel Island (b) and sampling locations (c): two frondose-dominated (Feteiras and Lagoa, black triangles) and two turf-dominated habitats (Santa Clara and São Roque, black circles).

small frondose macroalgae (*Asparagopsis* spp., *Dictyota* spp. and *Halopteris* spp.) and one dominated by low-lying turf-forming red algae (corresponding to macroalgae with <5 cm height forming dense mats), mostly short strands of *Ellisolandia elongata* (see Martins et al. 2016 for further description of the studied communities). Two sites were chosen for each habitat, similar in depth (5-15 m), seawater temperature, wave exposure and other physical factors. The selection of species (biotic entities) for this study took into consideration two main criteria; their sedentary life style, which ensured habitat representation; and their abundance in both habitats, which ensured trophic level representation and facilitated specimen collection. Herbivores were represented by the sea urchin *Sphaerechinus granularis* (Verlaque 1981), omnivores by the hermit crab *Calcinus tubularis* (Kunze & Anderson 1979; Schembri 1982) and the Canary damselfish *Similiparma lurida* (Frédérich &

Parmentier 2016), and carnivores by the predatory gastropod *Stramonita haemastoma* (Carriker 1981) and the ambush predator rockfish *Scorpaena maderensis* (La Mesa et al. 2007). Hermit crabs have a generalized omnivorous mode of feeding on benthic particles, detritus and moderately macroscopic material, depending, therefore on a reasonable amount of scavenging (Kunze & Anderson 1979; Schembri 1982). *S. lurida* maintains farms of turf-forming algae (personal observation), and like all the members of the Stegastinae subfamily feeds upon the algae, as well as on the detritus and invertebrates caught up in them (Frédérich & Parmentier 2016).

Macroalgae were scraped off from three haphazardly-selected 0.15 x 0.15 m replicate quadrats into fine mesh net bags. Three specimens of each invertebrate and fish species were collected, by hand and spearfishing, respectively.

Sampling took place in May 2014, in a short 4-

day period (9th – 13th) in order to reduce temporal variations in isotopic composition (Heminga & Mateo 1996; Jennings et al. 1997). Samples were stored on ice immediately after arrival on the boat and no later than 30 minutes after collection.

At the laboratory, algae were gently rinsed with tap water in order to remove all visible macrofauna and detrital fragments, and oven-dried at 60ºC until constant weight (about 48 h). Following the instructions of the certificated MARINNOVA Laboratories of Porto, Portugal where the stable isotope ratios were determined, sea urchin gonads, fish muscle and skin samples, and whole gastropods and crustaceans were frozen, accommodated, and sent for analysis. The isotope analysis results were expressed relative to the primary patterns, air N_2 for nitrogen and the Peedee belemnite marine limestone (PDB) standard for carbon. ^{15}N:^{14}N and ^{13}C:^{12}C ratios were calculated following Wieser & Schwieters (2005) and Bahlmann et al. (2010).

Data analysis
The ^{15}N and ^{13}C isotopic compositions of consumers and producers on frondose- and turf-dominated communities were compared using a

3-way mixed model analysis of variance with the following factors: habitat (2 levels, fixed), site (2 levels, random and nested within habitat) and biotic entities (algal morphotypes and animal species; 6 levels, fixed). Prior to analysis, Cochran's test was used to assess heterogeneity of variances and transformations were applied when necessary. When required, *a posteriori* Student-Newman-Keuls (SNK) tests were used. All analyses were run using GMAV5 (University of Sydney). At one of the sites (Santa Clara) only two (instead of three) replicates of *S. haemastoma* were available. In order to keep the analysis balanced, the missing value was replaced by the mean of the other two replicates, and one degree of freedom was subtracted from the residual.

RESULTS

Although no $\delta^{13}C$ differences were observed between habitats, both the differences between biotic entities and the interaction of habitat and biotic entities were significant (P<0.001 and P<0.01 respectively, Table 1) and are illustrated in Fig 2. Although the signatures of *S. maderensis*, *S. haemastoma* and *C. tubularis*
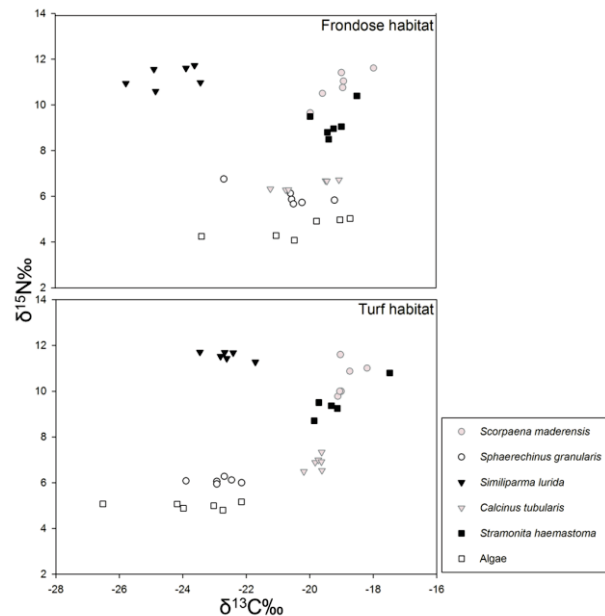

Fig. 2 – Relationship between $\delta^{13}C$ and $\delta^{15}N$ (‰) of producers and consumers in frondose and turf-dominated communities.

show no variation, those of the macroalgae and *S. granularis* were higher in the frondose habitat, where they aligned with the previously enumerated entities, then in the turf habitat, where they matched that of *S. lurida*. The $\delta^{13}C$ signature of the latter varied in the opposite direction, with higher values in turf than in frondose habitats, where it formed a separate group from the remainder of the biotic entities (Fig 2). SNK tests confirmed the significance of entity isotopic variations among habitats, and yielded two isotopic groups for each habitat, separating *S. lurida* from all other biotic entities in the frondose habitat, and grouping *S. lurida*, *S. granularis* and macroalgae apart from the remaining entities in the turf habitat (Table 1).

As for $\delta^{15}N$, neither the difference between habitats nor the interaction of habitat and biotic entities was significant, but the difference between biotic entities was highly significant (P<0.001, Table 1), which is clearly displayed in Fig 2. Macroalgae exhibited the lowest $\delta^{15}N$ signature, just below that of the herbivore *S. granularis*, which was followed by those of the omnivore *C. tubularis* and the carnivores *S. haemastoma* and *S. maderensis*. The omnivore *S. lurida* had on average the highest $\delta^{15}N$ values of all the biotic entities. This ordering was confirmed by SNK analysis of $\delta^{15}N$ among biotic entities (Table 1).

Table 1 - ANOVA testing the effects of habitat (frondose- versus turf-dominated) on the ^{15}N and ^{13}C isotopic composition of biotic entities (algal morphotypes and animal species). Significant differences noted in bold. SNK pair-wise tests assessing the effects of habitat on the ^{13}C isotopic composition of each biotic entity, and comparing the $\delta^{15}N$ of the biotic entities.

Source	df	$\delta^{13}C$			$\delta^{15}N$			F-ratio
		MS	*F*	P	MS	*F*	P	
Habitat	1	5.01	1.58	0.34	0.68	0.35	0.61	Site (Habitat)
Site (Habitat)	2	3.17	4.46	**0.02**	1.95	13.20	**<0.001**	Residual
Biotic entities	5	39.62	32.75	**<0.001**	87.13	337.72	**<0.001**	Site (Habitat) x Biotic entities
Habitat x Biotic entities	5	10.77	8.90	**<0.01**	0.21	0.80	0.57	Site (Habitat) x Biotic entities
Site (Habitat) x Biotic entities	10	1.21	1.70	0.11	0.26	1.75	0.10	Residual
Residual	47	0.71			0.15			
Cochran´s test		C = 0.21 (Not significant)			C = 0.32 (P<0.01)			

	$\delta^{13}C$		$\delta^{15}N$
	Among habitats within biotic entities		**Among biotic entities**
	S. maderensis	Frondose = Turf	*S. lurida* > *S. maderensis* > *S. haemastoma* > *C. tubularis* > *S. granularis* > Algae
	S. granularis	Frondose > Turf	
	S. lurida	Frondose < Turf	
	C. tubularis	Frondose = Turf	
	S. haemastoma	Frondose = Turf	
	Algae	Frondose > Turf	
SNK	**Among biotic entities within habitats**		
	Frondose habitat:		
	S. lurida < all other biotic entities		
	Turf habitat:		
	S. maderensis = *S. haemastoma* = *C. tubularis* > *S. granularis* = *S. lurida* = Algae		

DISCUSSION

The significant macroalgal $\delta^{13}C$ variation between habitats reflects their different species composition. The ^{15}N isotopic signature of the sea urchin is consistent with its strictly herbivorous diet, and its ^{13}C isotopic signature suggest that it feeds on the dominant macroalgal assemblage in each habitat. In both habitats, the omnivore damselfish *S. lurida* exhibited a ^{13}C isotopic signature similar to that of the turf macroalgae, which is consistent with its diet of turf-forming algae. Surprisingly, it showed the highest $\delta^{15}N$ values, above even those of the carnivorous rockfishes, with trophic shifts as high as +5.9‰. This apparently higher ^{15}N accumulation rate may arise from differential digestion or fractionation during assimilation and metabolic processes (McCutchan et al. 2003).

The hermit crabs and the carnivorous gastropods and fish exhibited no significant variation in $\delta^{13}C$ or $\delta^{15}N$ across habitats. In frondose habitats the ^{13}C isotopic composition was similar among all those species and the local macroalgae, suggesting that the latter provide the main carbon source for the remainder of the benthic food web. However, in turf-dominated habitats there was a clear decouple between macroalgae/sea urchins and the three species mentioned above. This implies that the higher trophic levels in these habitats rely on exogenous carbon sources, possibly from the adjacent frondose habitats. It should be noted that the suspension- and deposit-feeding pathways were not considered in this study, and that sampling the particulate organic matter pool (POM) could improve these results and explain part of the observed decoupling.

These findings add to literature indicating that habitats dominated by frondose macroalgae play an important ecological role in coastal ecosystems (Benedetti-Cecchi et al. 2001; Gorgula & Connell 2004; Martins et al. 2016; Smale et al. 2013). Their fundamental contribution to the energy flows on the food webs is not matched by that of the increasingly dominant turf communities. Therefore, the current trends of reduction of algal canopies pose a threat to coastal biodiversity, which should be taken into consideration when devising conservation strategies.

REFERENCES

Airoldi, L. 1998. Roles of disturbance, sediment stress, and substratum retention on spatial dominance in algal turf. *Ecology* 79: 2759–2770. https://doi.org/10.1890/0012-9658(1998)079[2759:RODSSA]2.0.CO;2

Bahlmann, E., S.M. Bernasconi, S. Bouillon, M. Houtekamer, M. Korntheuer, F. Langenberg, C. Mayr, M. Metzke, J.J. Middelburg, B. Nagel, U. Struck, M. Voß and K.C. Emeis 2010. Performance evaluation of nitrogen isotope ratio determination in marine and lacustrine sediments: An inter-laboratory comparison. *Organic Geochemistry* 41: 3–12. https://doi.org/10.1016/j.orggeochem.2009.05.008

Behringer, D.C. and M.J. Butler IV 2006. Stable isotope analysis of production and trophic

relationships in a tropical marine hard-bottom community. *Oecologia* 148: 334–341. https://doi.org/10.1007/s00442-006-0360-0

Benedetti-Cecchi, L., F. Pannacciulli, F. Bulleri, P.S. Moschella, L. Airoldi, G. Relini and F. Cinelli 2001. Predicting the consequences of anthropogenic disturbance: Large-scale effects of loss of canopy algae on rocky shores. *Marine Ecology Progress Series* 214: 137–150. https://doi.org/10.3354/meps214137

Bulleri, F., L. Benedetti-Cecchi, S. Acunto, F. Cinelli and S.J. Hawkins 2002. The influence of canopy algae on vertical patterns of distribution of low-shore assemblages on rocky coasts in the northwest Mediterranean. *Journal of Experimental Marine Biology and Ecology* 267: 89–106. https://doi.org/10.1016/S0022-0981(01)00361-6

Cabana, G. and J.B. Rasmussen 1996. Comparison of aquatic food chains using nitrogen isotopes. Proceedings of the National Academy of Sciences of the U.S.A. 93: 10844–10847. https://doi.org/10.1210/endo-63-5-707

Carriker, M.R. 1981. Shell penetration and feeding by Naticacean and Muricacean predatory gastropods: a synthesis. *Malacologia* 20: 403–422.

Carvalho de Carvalho, M. 2009. Use of the stable isotopes of carbon, nitrogen and sulfur for studies on coastal ecology. *Oecologia Aust*alis 12(4): 694–705.

Frédérich, B. and E. Parmentier 2016. Biology of Damselfishes. CRC Press. 340 pp.

Gillies, C.L., J.S. Stark and S.D.A. Smith 2012. Small-scale spatial variation of $\delta^{13}C$ and $\delta^{15}N$ isotopes in Antarctic carbon sources and consumers. *Polar Biology* 35: 813–827. https://doi.org/10.1007/s00300-011-1126-7

Gorgula, S.K. and S.D. Connell 2004. Expansive covers of turf-forming algae on human-dominated coast: The relative effects of increasing nutrient and sediment loads. *Marine Biology* 145: 613–619. https://doi.org/10.1007/s00227-004-1335-5

Hemminga, M.A. and M.A. Mateo 1996. Stable carbon isotopes in seagrasses: Variability in ratios and use in ecological studies. *Marine Ecology Progress Series* 140: 285–298. https://doi.org/10.3354/meps140285

Kennelly, S.J. 1987. Inhibition of kelp recruitment by turfing algae and consequences for an Australian kelp community. *Journal of Experimental Marine Biology and Ecology* 112: 49–60. https://doi.org/10.1016/S0022-0981(87)80014-X

Kunze, J. and D.T. Anderson 1979. Functional Morphology of the Mouthparts and Gastric Mill in the Hermit Crabs *Clibanarius taeniatus* (Milne Edwards), *Clibanarius virescens* (Krauss),

Paguristes squamosus McCulloch and *Dardanus setifer* (Milne-Edwards) (Anomura: Paguridae). *Australian Journal of Marine and Freshwater Research* 30: 683–722.

La Mesa, G., M. La Mesa and P. Tomassetti 2007. Feeding habits of the Madeira rockfish *Scorpaena maderensis* from central Mediterranean Sea. *Marine Biology* 150: 1313–1320. https://doi.org/10.1007/s00227-006-0414-1

Lawson, G.W. and T.A. Norton 1971. Some observations on littoral and sublittoral zonation at Tenerife (Canary Isles). *Botanica Marina* 14: 116–120.

Layman, C.A., M.S. Araujo, R. Boucek, C.M. Hammerschlag-Peyer, E. Harrison, Z.R. Jud, P. Matich, A.E. Rosenblatt, J.J. Vaudo, L.A. Yeager, D.M. Post and S. Bearhop 2012. Applying stable isotopes to examine food-web structure: An overview of analytical tools. *Biological Reviews* 87: 545–562. https://doi.org/10.1111/j.1469-185X.2011.00208.x

Lepoint, G., P. Dauby, M. Fontaine, J.M. Bouquegneau and S. Gobert 2003. Carbon and Nitrogen Isotopic Ratios of the Seagrass *Posidonia oceanica*: Depth-related Variations. *Botanica Marina* 46: 555–561. https://doi.org/10.1515/BOT.2003.058

Mancinelli, G. and S. Vizzini 2015. Assessing anthropogenic pressures on coastal marine ecosystems using stable CNS isotopes: State of the art, knowledge gaps, and community-scale perspectives. *Estuarine, Coastal and Shelf Science* 156: 195–204. https://doi.org/10.1016/j.ecss.2014.11.030

Martins, G.M., R.C. Thompson, A.I. Neto, S.J. Hawkins and S.R. Jenkins 2010. Exploitation of intertidal grazers as a driver of community divergence. *Journal of Applied Ecology*, 47: 1282-1289, DOI 10.1111/j.1365-2664.2010.01876.x.

Martins, G.M., C. Hipólito, F. Parreira, A.C.L. Prestes, M.A. Dionísio, J.M.N. Azevedo and A.I. Neto 2016. Differences in the structure and functioning of two communities: Frondose and turf-forming macroalgal dominated habitats. *Marine Environmental Research* 116: 71–77. https://doi.org/10.1016/j.marenvres.2016.03.004

McCutchan, J.H., W.M. Lewis, C. Kendall and C.C. McGrath 2003. Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. *Oikos* 102: 378–390. https://doi.org/10.1034/j.1600-0706.2003.12098.x

Neto, A.I. 2000a. Observations on the biology and ecology of selected macroalgae from the littoral of São Miguel (Azores). *Botanica Marina* 43: 483–498. https://doi.org/10.1515/BOT.2000.049

Neto, A.I. 2000b. Ecology and dynamics of two

intertidal algal communities on the littoral of the island of São Miguel (Azores). *Hydrobiologia*. https://doi.org/10.1023/A:1004042808901

Neto, A.I. 2001. Macroalgal species diversity and biomass of subtidal communities of São Miguel (Azores). *Helgoland Marine Research* 55: 101–111. https://doi.org/10.1007/s101520100074

O'Brien, B.S., K. Mello, A. Litterer and J.A. Dijkstra 2018. Seaweed structure shapes trophic interactions: A case study using a mid-trophic level fish species. *Journal of Experimental Marine Biology and Ecology* 506: 1–8. https://doi.org/10.1016/j.jembe.2018.05.003

Page, H.M., A.J. Brooks, M. Kulbicki, R. Galzin, R.J. Miller, D.C. Reed, R.J. Schmitt, S.J. Holbrook and C. Koenigs 2013. Stable Isotopes Reveal Trophic Relationships and Diet of Consumers in Temperate Kelp Forest and Coral Reef Ecosystems. *Oceanography* 26: 180–189. https://doi.org/10.5670/oceanog.2011.65

Peterson, B.J. 1999. Stable isotopes as tracers of organic matter input and transfer in benthic food webs: A review. *Acta Oecologica* 20: 479–487.

Phillips, D.L., R. Inger, S. Bearhop, A.L. Jackson, J.W. Moore, A.C. Parnell, B.X. Semmens and E.J. Ward 2014. Best practices for use of stable isotope mixing models in food-web studies. *Canadian Journal of Zoology* 92: 823–835. https://doi.org/10.1139/cjz-2014-0127

Post, D.M. 2002. Using Stable Isotopes to Estimate Trophic Position: Models, Methods, and Assumptions. *Ecology* 83: 703–718. https://doi.org/10.1890/0012-9658(2002)083[0703:USITET]2.0.CO;2

Price, I.R. and F.J. Scott 1992. The Turf Algal Flora of the Great Barrier Reef. Part I. Rhodophyta. James Cook University: Townsville, North Queensland.

Schembri, P.J. 1982. Feeding behaviour of fifteen species of hermit crabs (Crustacea: Decapoda: Anomura) from the otago region, southeastern new zealand. *Journal of Natural History* 16: 859–878. https://doi.org/10.1080/00222938200770691

Smale, D.A., M.T. Burrows, P. Moore, N. O'Connor and S.J. Hawkins 2013. Threats and knowledge gaps for ecosystem services provided by kelp forests: A northeast Atlantic perspective. *Ecology and Evolution* 3: 4016–4038. https://doi.org/10.1002/ece3.774

Steneck, R.S., M.H. Graham, B.J. Bourque, D. Corbett, J.M. Erlandson, J.A. Estes and M.J. Tegner 2002. Kelp forest ecosystems: Biodiversity, stability, resilience and future. *Environmental Conservation* 29: 436–459. https://doi.org/10.1017/S0376892902000322

Tittley, I. 2000. A provisional classification of algal-characterised rocky shore biotopes in the Azores. *Hydrobiologia* 440: 19–25.

Tittley, I., A.I. Neto, W.F. Farnham and M.I. Parente 2001. Additions to the marine algal (seaweed) flora of the Azores. *Botanica Marina* 44: 215–220. https://doi.org/10.1515/BOT.2001.028

Verlaque, M. 1981. *Preliminary data on some Posidonia feeders. Rapp PV Réun Commiss Internatl Explor Sci Méditerr* 27(2): 201–202.

Wallenstein, F.M., M.R. Terra, J. Pombo and A.I. Neto 2009. Macroalgal turfs in the Azores. *Marine Ecology* 30: 113–117. https://doi.org/10.1111/j.1439-0485.2009.00311.x

Wieser, M.E. and J.B. Schwieters 2005. The development of multiple collector mass spectrometry for isotope ratio measurements. International *Journal of Mass Spectrometry* 242: 97–115. https://doi.org/10.1016/j.ijms.2004.11.029

Worm, B., H.K. Lotze and U. Sommer 2001. Algal propagule banks modify competition, consumer and resource control on baltic rocky shores. *Oecologia* 128: 281–293. https://doi.org/10.1007/s004420100648