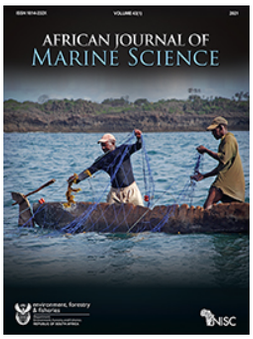

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Cross-shelf movement of *Chrysaora fulgida* (Scyphozoa; Discomedusae) off Namibia inferred from stable isotopes (δ^{15}N and δ^{13}C)

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Large and small specimens of two species of metagenic Scyphozoa (true jellyfishes) can be found in nearshore waters off central Namibia throughout the year. Whereas populations of *Chrysaora africana* are largely restricted to inshore waters, *C. fulgida* occurs across the shelf, with small individuals found inshore and large individuals primarily found offshore. We examined stable isotopes δ^{15}N and δ^{13}C of both species in Walvis Bay and found that large-sized *C. fulgida* have lower δ^{15}N values than small individuals and *C. africana* throughout the year. These differences are interpreted to reflect cross-shelf changes in δ^{15}N baseline levels, with greater nitrogen recycling (and hence lower δ^{15}N values) occurring offshore. The occasional/seasonal nearshore appearance of large *C. fulgida* with low δ^{15}N values therefore implies routine, onshore advection. The values of δ^{13}C did not show cross-shelf differences, which suggests that jellyfish populations across the shelf are supported by phytoplankton-based food chains. This study emphasises the value of using stable isotopes to examine the mesoscale structuring of jellyfish populations.

Keywords: *Chrysaora africana*, coastal upwelling, eastern boundary currents, energy flow, jellyfish, metagenesis, molecular markers

Online supplementary material: The Supplemenary Information, available at https://doi.org/10.2989/1814232X.2021.1879268, includes a map of surface-current flow in Walvis Bay, figures that show the relationship between winds and the size-frequency distribution of *Chrysaora fulgida* in the bay, as well as seasonal changes in the size-frequency distribution, and tables detailing sampling of the *C. fulgida*, *C. africana* and various non-jellyfish organisms for stable isotope analysis.

Introduction

Tracking the mesoscale movement of marine animals can be done in several ways. Large and robust species can be physically tagged with passive markers (e.g. Oosthuizen 1991) or with acoustic (Attwood et al. 2007) or satellite (Sherley et al. 2013) tags, and molecular methods can be employed, in conjunction with Lagrangian modelling, when taxa are more fragile and short-lived (e.g. Lee et al. 2013). Stable isotopes (δ^{15}N, δ^{13}C) can also be used if there are pronounced differences in the baseline values between different geographic areas (e.g. Cruz-Flores et al. 2018).

In a well-cited work, Costanzo et al. (2001) were able to detect and map sewage impacts in Moreton Bay (eastern coast of Australia) through the determination of δ^{15}N in a variety of macrophytes. This approach focusing on determining δ^{15}N in primary, rather than secondary, producers has been widely adopted because it can accommodate the complexities associated with trophic enrichment. Heavier isotopes accrue in an organism's body tissues through time since lighter isotopes are metabolised (faster) and excreted, which leads to an enrichment of the heavier isotope from diet to consumer (Post 2002). The ^{15}N/^{14}N ratio (termed δ^{15}N) has pragmatically been assumed to become enriched by ~3.4‰ per trophic step, and the ^{13}C/^{12}C ratio (δ^{13}C) by ≤1‰ per trophic step (Post 2002).

Only four jellyfish species with large medusae are regularly encountered off central Namibia: the hydrozoan *Aequorea forskalea*, the cubozoan *Chirodropus gorilla*, and two species of scyphozoan jellyfishes—*Chrysaora africana* and *C. fulgida* (Pagès et al. 1992; Ras et al. 2020). *Chrysaora africana* is largely restricted to nearshore environments north of Walvis Bay, whereas *C. fulgida* occurs across the shelf to the shelf break, from Angola to Cape Town, South Africa. Although the ephyrae of *C. fulgida* appear to be released in a seasonal manner (Skrypzeck and Gibbons 2021), animals of a wide size range are present year-round (Fearon et al. 1992; Buecher et al. 2001). The continental shelf off central Namibia comprises mostly soft sediments, but hard seabed substrates are located close to the shore (Rogers and Bremner 1991), where polyps of both species are presumed to be found (they have never been observed *in situ*). Ephyrae of both species can be collected in very shallow waters (Skrypzeck and Gibbons 2021), and as individuals of *C. fulgida* mature and increase in size so they are thought to be moved progressively offshore by Ekman transport: the largest *C. fulgida* occur towards the edge of the shelf (Fearon et al. 1992; Buecher et al. 2001) but may occasionally be found close inshore.

The Namibian coastline is subject to coastal upwelling; the ecosystem is very productive, and short food chains lead to

industrial-scale fisheries (Hutchings et al. 2009). The shelf is relatively wide off Walvis Bay, and is characterised by a double-circulation cell (shelf break and continental slope) that effectively traps water (Barange et al. 1992). This in turn leads to an accumulation of phytoplankton over the inner shelf, and diatom-dominated assemblages experience significant self-shading and display comparatively deep chlorophyll maxima (Brown et al. 1991). Primary production downstream of upwelling centres is, for an upwelling ecosystem, relatively low (Brown et al. 1991) and a significant amount of that by siliceous phytoplankton is based on recycled nitrogen (Dittmar and Birkicht 2001). The high biomass of phytoplankton fuels populations of euphausiids and large herbivorous copepods (Hutchings et al. 1991, 2009). Historically, populations of small pelagic fishes (e.g. sardine *Sardinops sagax*, anchovy *Engraulis encrasicolus*) were abundant in the area, but their overexploitation during the late 1960s has led to fundamental changes in the structure of the entire ecosystem (Roux et al. 2013). Jellyfishes, especially *C. fulgida* and *A. forskalea*, are now common (Venter 1988; Lynam et al. 2006) and play an important role in the way that energy and matter move through the northern Benguela ecosystem (Roux et al. 2013). *Chrysaora fulgida* is known to feed on a wide variety of plankton (Flynn and Gibbons 2007) and is suspected of acting as both a competitor with, and predator of, commercially valuable pelagic fishes and their eggs and larvae (Bakun and Weeks 2006; Flynn et al. 2012; Roux et al. 2013).

Given that large *C. fulgida* are routinely encountered offshore only (Fearon et al. 1992), the source of planulae for nearshore polyps remains unknown. Are they released at depth in offshore waters and then advected shoreward during upwelling? Or are they released inshore by the few large individuals that are advected shoreward in those same currents? Although we cannot answer those questions directly, using stable isotopes we can determine whether the large specimens of *C. fulgida* occasionally encountered in the nearshore waters of Walvis Bay originated from waters farther offshore. Recently upwelled water close to the coastline is rich in new nitrogen, and this typically leads to primary producers that are isotopically heavier (higher $\delta^{15}N$ values) than those using recycled nitrogen encountered farther offshore (Mullin et al. 1984; Hill et al. 2006; Hill and McQuaid 2008; Reddin et al. 2015).

Materials and methods

Study site

Walvis Bay is located midway along the Namibian coast and supports the country's largest—and only deep-water—commercial harbour. Organic-rich sediments line the floor of the bay, which is generally less than 15 m in depth, and the area is prone to hypoxia (Aquafact 2012). Surface currents are predominantly wind-driven (Aquafact 2012) and create a clockwise flow in the bay (Supplementary Figure S1). Current velocities are ~0.12 m s^{-1}, and the residence time of water in the bay is estimated at between 3 and 7 days (Aquafact 2012).

Sample collection

Samples of *C. africana* and *C. fulgida* were collected in Walvis Bay between May 2012 and January 2016 (Supplementary Table S1). Dipnets were used to collect medusae that were at or close to the sea surface, while ephyrae were caught using a weighted plankton net of 50 cm mouth diameter (180 µm mesh size), fitted with a 1-l plastic codend jar. All specimens were kept at 16 °C overnight to evacuate their stomachs.

To contextualise the jellyfish data, specimens of common organisms (Supplementary Table S2) were collected from Walvis Bay at the same time as the jellyfish and their stable isotope values were also determined (see below). Comparative isotope data from the bell tissue of *C. fulgida* collected at depths of 120–180 m off Walvis Bay in 2008 have been taken from van der Bank et al. (2011).

Tissue processing and sample analysis

Within 24 h of collection, individual maximum bell diameters (mm) were determined, and tissue samples were taken from the umbrella of larger medusae (following D'Ambra et al. 2014; Javidpour et al. 2016). In the case of ephyrae and small medusae, multiple individuals of similar maximum diameter were pooled to provide sufficient material for analysis. Tissue and whole ephyrae samples were washed with 0.2 µm-filtered seawater, then quickly rinsed with distilled water to remove surface salt. Thereafter they were dried to constant weight at 60 °C and pulverised to a fine powder using a clean mortar and pestle. Subsamples of 2.1–2.3 mg were then weighed, sealed in tin cups and frozen for later analysis. Tissue samples from other common organisms from Walvis Bay were processed in a similar manner.

The values of $\delta^{13}C$ and $\delta^{15}N$ were determined using either a FlashEA 1112 elemental analyser coupled to a Delta V Plus stable isotope ratio mass spectrometer (IRMS) via a ConFlo IV system, or a Flash 2000 organic elemental analyser connected to a Delta V Plus IRMS via a ConFlo III gas control unit (all equipment supplied by Thermo Fischer, Germany). In the case of the former, Merck Gel and DL-Valine standards were applied, calibrated against National Institute of Standards and Technology (NIST) 1557b, NIST 2976 and NIST 1547; measurement error (SD) was 0.09‰ for $\delta^{13}C$ and 0.07‰ for $\delta^{15}N$. In the case of the latter, Merck Gel, seal bone and DL-Valine standards were used, calibrated against the International Atomic Energy Agency (IAEA) standards; measurement error (SD) was 0.102‰ for $\delta^{13}C$ and 0.034‰ for $\delta^{15}N$.

Nitrogen is expressed in terms of its value relative to atmospheric nitrogen, whereas carbon is expressed in terms of its value relative to Vienna Pee-Dee Belemnite (VPDB). All stable ratios are expressed in delta notation using a per-mille scale and the standard equation (e.g. Post 2002). Lipids were not extracted prior to analysis to prevent any bias of $\delta^{15}N$ (Post et al. 2007). However, the presence of lipids can cause depletion in $\delta^{13}C$ irrespective of the carbon source; therefore the lipid-normalisation equation derived by D'Ambra et al. (2014) for *Aurelia* was used when the C:N ratio of individual samples was >3.5. For the other common taxa collected in Walvis Bay (non-jellyfish), the lipid normalisation of Post et al. (2007) was employed.

Statistical methods

Medusae of *C. fulgida* appear to reach sexual maturity at a diameter of ~300 mm (Skrypzeck 2019), and animals of this

size dominate populations offshore of Walvis Bay (Buecher et al. 2001). Individuals of this species were classified into three size classes: ephyrae and small medusae (≤100 mm bell diameter); medium-sized medusae (101–299 mm); and large medusae (≥300 mm). One-way analyses of variance (ANOVAs) were computed to test for differences in the mean values of both δ^{15}N and δ^{13}C of the small, medium and large specimens of *C. fulgida* collected in Walvis Bay. Too few *C. africana* (n = 12) were sampled to allow division into size classes, and therefore data for all individuals (average bell diameter 223.9 mm [SD 99.6], range 62–330 mm, median 273.5 mm) were combined, and comparisons were also made between the mean values of δ^{15}N and δ^{13}C of *C. africana* and large *C. fulgida* from Walvis Bay, and between the large *C. fulgida* collected in Walvis Bay and those collected from farther offshore in 2008 by van der Bank et al. (2011). In all cases, normality was inspected visually from probability plots, and homogeneity of variances was tested using Levene's test (F = 1.61, p > 0.05). Selected comparisons with other biotic components of the ecosystem were also made (see below).

Results

The average values of δ^{15}N observed for the bell tissue of *C. africana* and *C. fulgida* were 10.82‰ (SD 1.06‰, n = 12) and 10.41‰ (SD 1.35‰, n = 72), respectively, and the average values of δ^{13}C were −15.63‰ (SD 0.87‰) and −16.33‰ (SD 1.25‰), respectively. The isotopic biplot (Figure 1) shows a clear separation in values of δ^{15}N between large and small specimens of *C. fulgida* in Walvis Bay (ANOVA; F[1, 42] = 9.47, p < 0.005), and also between large and medium specimens (F[1, 61] = 9.54, p < 0.005), but no difference between small and medium specimens (F[1, 37] = 1.00, p > 0.05) (pooled hereafter). There was a significant difference in δ^{15}N between large specimens of *C. fulgida* and *C. africana* (F[1, 44] = 5.12, p < 0.05) in Walvis Bay, but not between *C. africana* and small/medium specimens of *C. fulgida* (F[1, 49] = 0.12, p > 0.05). No significant differences (F[1, 51] = 1.56, p = 0.22) were observed in δ^{15}N between the large specimens of *C. fulgida* collected in Walvis Bay (this study) and those reported for specimens collected farther offshore in 2008 (van der Bank et al. 2011). Across the different seasons, there were no differences in the δ^{15}N values either of small/medium individuals (F[2, 26] = 2.87, p > 0.05) or of large individuals (F[2, 28] = 2.24, p > 0.05) of *C. fulgida* in Walvis Bay (Table 1).

There were no significant differences in δ^{13}C in any comparisons between the jellyfish, and all values are characteristic of source production from marine phytoplankton (Bouillon et al. 2011, and references cited therein). Note similarities in the δ^{15}N of the marine macroalga *Ulva* (10.64‰) and the terrestrial *Sarcocornia* (10.91‰) collected from Walvis Bay; the differences in δ^{13}C between those two genera (−12.3‰ and −26.59‰, respectively) are in accordance with Bouillon et al. (2011) and the references cited therein.

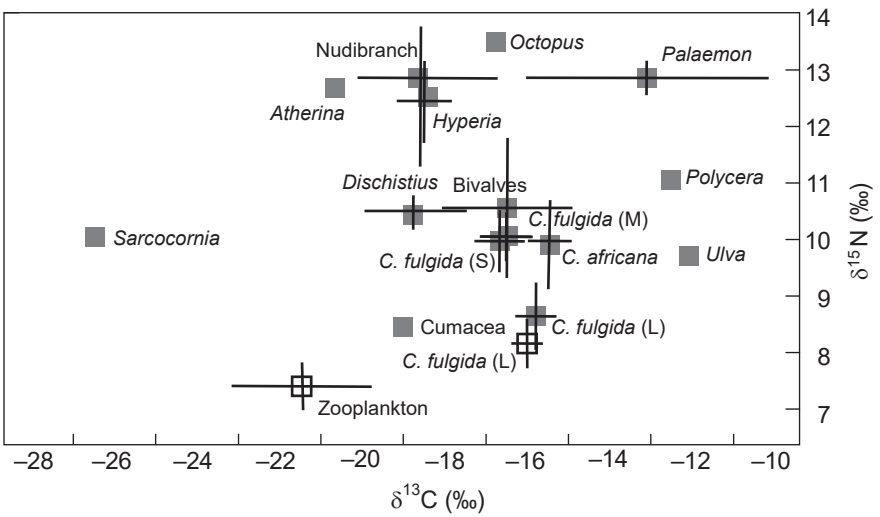

Figure 1: Stable isotope biplot (δ^{13}C and δ^{15}N, mean values ±95% confidence intervals) of organisms collected in Walvis Bay, Namibia (filled squares), and in waters farther offshore (open squares). Data for the jellyfish *Chrysaora fulgida* are subdivided by size class based on bell diameter: large (L: ≥300 mm), medium (M: 100–299 mm) and small (S: <100 mm). Offshore data from van der Bank et al. (2011)

Table 1: Seasonal average values of isotopes δ^{15}N and δ^{13}C recorded for *Chrysaora fulgida* of different size groups (bell diameter) collected in Walvis Bay, Namibia

Size class	δ^{15}N (‰)					δ^{13}C (‰)				
	Spring	Summer	Autumn	Winter	Average	Spring	Summer	Autumn	Winter	Average
Small (<100 mm)	10.96	11.08	10.54	10.50	10.87	−16.50	−17.41	−16.81	−18.14	−16.78
Medium (100–299 mm)	9.95	9.80	10.85	11.78	10.91	−16.12	−16.09	−16.39	−16.89	−16.49
Large (≥300 mm)	9.78	9.15		10.54	9.77	−15.79	−15.74		−16.56	−15.93

Discussion

Studies of trophic flow use $\delta^{13}C$ to indicate the source of production as different autotrophs tend to have different stable isotope values: angiosperms have more-negative values of $\delta^{13}C$ than phytoplankton, which in turn have more-negative values than macroalgae (Bouillon et al. 2011). Diatoms dominate phytoplankton communities in upwelling regions (e.g. Lassiter et al. 2006), and the values of $\delta^{13}C$ observed here for jellyfish indicate that phytoplankton formed the main base of the food webs inshore and offshore (see Bouillon et al. 2011, and references therein). Evidence to suggest that macrophytes (algae or angiosperms) materially contributed to the base of the pelagic food web inshore, as has been shown elsewhere (Miller et al. 2008), is scant (Figure 1). Our data in this regard are similar to those reported by others (i.e. D'Ambra et al. 2014; Fleming et al. 2015; Tilves et al. 2018).

Given the absence of any cross-shelf change in $\delta^{13}C$ within *C. fulgida*, how do we explain the significant reduction in the values of $\delta^{15}N$ from small to large individuals and from inshore to offshore? Two possible explanations may account for the patterns we have observed, and these are discussed below.

Small C. fulgida *and their ephyrae feed at a higher trophic level than large individuals*

Using the enrichment values of Post (2002), it could be argued that ephyrae and small medusae of *C. fulgida* feed at a higher trophic level than do large individuals—even though as jellyfish increase in size, so too generally does their $\delta^{15}N$ (as in *Lychnorhiza lucerna*: Nagata et al. 2015; *Aurelia aurita*, *Cyanea capillata*: Fleming et al. 2015; *Cyanea nozakii*: Wang et al. 2020), though in the case of *Cyanea lamarckii* there does not appear to be any size-related change in $\delta^{15}N$ (Fleming et al. 2015).

Flynn and Gibbons (2007) did not detect significant size-related changes in the diet of *C. fulgida* in Walvis Bay lagoon, from their analysis of the stomach contents of 55 animals collected in September 2003. Although those authors did note that larger individuals consumed greater numbers of some prey items than did the smaller animals, and that the overall evenness of their diet was higher, this relationship was observed only at night. The lack of any clear size-related difference in diet likely reflects the size of the animals examined, which had a mean diameter of 240 mm (SD 55 mm, range 150–380 mm). None of the individuals inspected fell into the category recognised here as 'small,' and few (n = 10) were 'large.'

The small size of ephyrae limits what they can consume (Sullivan et al. 1997; Gordoa et al. 2013), and there will be a tendency for their diet to be dominated by microplankton and components of the microbial loop (e.g. Båmstedt et al. 2001). Zoccarato et al. (2016) have recently shown that the ephyrae of *Aurelia aurita* can influence the microplankton community by causing large declines in the abundances of the more-motile groups, with smaller reductions in less-motile groups. Olesen et al. (1994) have demonstrated that rotifers such as *Brachionus plicatilis* can be an important prey source for the ephyrae of *A. aurita,* while ciliates may serve as a food source for the ephyrae (but not meta-ephyrae) of *A. coerulea* (Kamiyama 2018).

As individual *C. fulgida* increase in size, their food entrapment surfaces (tentacles and oral arms) become progressively larger and more robust and more widely spaced, and, although not tested, it is likely that in the presence of otherwise abundant food, bigger prey items would comprise a dominant component of the diet. Larger medusae can thus tap into mesozooplankton as a food source. Although most copepods are likely to be omnivorous (Schukat et al. 2014), communities in the northern Benguela upwelling region are dominated by herbivores (see Mauchline 1998: Table 13), such as species of *Calanoides*, *Calanus*, *Pseudocalanus* and *Rhincalanus* (Jarre et al. 2015). Consequently, the food chains leading to larger jellyfish have the potential to be shorter than the microplankton food chain utilised by ephyrae and the smaller jellyfish inshore, which could result in the observed decline in $\delta^{15}N$ with body size.

However, the (scant) literature does not support this logic but indicates that $\delta^{15}N$ enrichment from phytoplankton to ciliates or heterotrophic dinoflagellates is negligible (Décima et al. 2017). This would suggest that the nearshore food chain (phytoplankton → ciliate → copepod → jellyfish) is, from the perspective of $\delta^{15}N$, no lengthier than that over the shelf (phytoplankton → copepod → jellyfish). Although the enrichment from bacteria through protists to copepods is high (Berglund et al. 2007), the food chain leading to jellyfish in Walvis Bay is phytoplankton-based and not bacteria-based, as evidenced by the $\delta^{13}C$ data.

The same conclusion of negligible difference in the trophic position of large and small *C. fulgida* is reached if we interpret our data using the enrichment values of D'Ambra et al. (2014). Those authors determined that $\delta^{15}N$ becomes enriched by ~0.1‰ per trophic step and $\delta^{13}C$ by ~4‰ per trophic step for *Aurelia* in the Gulf of Mexico, implying that $\delta^{13}C$ may be more robust and useful in trophic studies of jellyfish than measures of $\delta^{15}N$. This latter conclusion was also reached by Frost et al. (2012) from their study of gelatinous plankton in the North Sea, which led D'Ambra et al. (2014) to suggest that "jellyfish may have atypical fractionation values compared to other species" (D'Ambra et al. 2014, p 478).

Bode et al. (2003) showed a significant negative relationship between $\delta^{15}N$ and size for large (total length ≥180 mm) *Sardina pilchardus* in the upwelling ecosystem off northwest Spain and interpreted this to be the consequence of the increasing consumption of phytoplankton by larger fish. Carlisle et al. (2012) reported a negative relationship between individual length and $\delta^{15}N$ of muscle tissue of the white shark *Carcharodon carcharias* from the northeastern Pacific. This was suggested to reflect ontogenetic changes in habitat: small sharks reside in the coastal waters of the California Current ecosystem where they forage on food webs enriched with $\delta^{15}N$, and after attaining maturity they move offshore and consume less-enriched prey (Carlisle et al. 2012). Similar observations were made by Li et al. (2016) for the silky shark *Carcharhinus falciformis* in the northeastern/central Pacific. The latter authors suggested that, after birth, juvenile sharks switched from coastal waters to offshore and pelagic habitats, and their diets changed from being dominated by jumbo squid *Dosidicus gigas* to chub mackerel *Scomber japonicus*.

Cross-shelf changes in the baseline of $\delta^{15}N$

An alternative, and perhaps more parsimonious, explanation for the pattern observed is that the large *C. fulgida* found in Walvis Bay did not originate there but from farther offshore. This is supported by the fact that the isotope values of the large (≥300 mm) *C. fulgida* in Walvis Bay ($\delta^{15}N$ = 9.75‰ [SD 1.30]; $\delta^{13}C$ = −15.91‰ [SD 1.31]) barely differ from those of animals of the same size obtained by van der Bank et al. (2011) in waters deeper than 120 m off Walvis Bay in 2008 ($\delta^{15}N$ = 9.40‰ [SD 0.86]; $\delta^{13}C$ = −16.07‰ [SD 0.75]). These values in turn are similar to those of the planktivorous sardine *S. sagax* off Namibia, as reported by Iitembu et al. (2012: $\delta^{15}N$ = 9.2‰ [SD 0.7], $\delta^{13}C$ = −15.9‰ [SD 0.7]).

The argument here is based on differences in the baseline levels of $\delta^{15}N$ between the nearshore and shelf waters off Walvis Bay. Recently upwelled water is rich in new nitrogen (Chapman and Shannon 1985), and this typically leads to primary producers that are isotopically heavier than those using recycled nitrogen (Hill et al. 2006; Hill and McQuaid 2008; Reddin et al. 2015). When that upwelled water matures and moves offshore, nutrients (including nitrate) are progressively stripped from the surface by developing diatom blooms (Pitcher et al. 1992); the depth of the chlorophyll maximum deepens, and a significant amount of the production by siliceous phytoplankton becomes based on recycled nitrogen (Dittmar and Birkicht 2001).

As noted earlier, ephyrae of *C. fulgida* are released from polyps located on hard substrates that are naturally restricted to very nearshore environments around Walvis Bay (Rogers and Bremner 1991; Skrypzeck and Gibbons 2021). When animals increase in size, they might be advected offshore in the surface Ekman layer; available evidence shows that offshore animals are larger than those close inshore (Fearon et al. 1992; Buecher et al. 2001). In Walvis Bay, ephyrae and small jellyfish are feeding in an environment characterised by new nitrogen with a heavier isotopic value than that occupied by large medusae offshore, where nitrate is scarce in surface waters (Chapman and Shannon 1985) and nitrogen recycling is more pronounced. Although the $\delta^{15}N$ of seston was not determined here, it can be inferred in Walvis Bay from the near-identical values of $\delta^{15}N$ noted in both *Ulva* and *Sarcocornia*. Large *C. fulgida* may be reintroduced into the nearshore environment following either advection in the surface layer by onshore winds from the west or northwest, or they may be entrained in upwelled water following alongshore wind stress predominantly from the south. The latter route is more likely, as significantly greater numbers of large individuals (>300 mm bell diameter) tend to be recovered nearshore during periods of southerly winds than during westerly or northwesterly winds (Supplementary Figure S2).

Research on *Aurelia* sp. in the Gulf of Mexico determined that it takes 18–20 days for jellyfish tissues to reach a stable-isotope steady state (D'Ambra et al. 2014). If we accept differences in the $\delta^{15}N$ baseline between inshore and offshore areas, this implies that the large jellyfish collected in Walvis Bay were advected shoreward shortly prior to collection. This agrees with the findings of Flynn and Gibbons (2007), who noted no significant difference in the diet of medium and large *C. fulgida* collected in Walvis Bay during September 2003.

Jellyfish are common close to the shore and strandings *en masse* have occurred for as long as the organisms have existed (Sappenfield et al. 2017). Such events are usually seasonal and reflect population- and species-specific cycles that are made obvious by winds and currents (Graham et al. 2001). *Chrysaora fulgida* are always present in Walvis Bay (Supplementary Figure S2), and, although populations include a mix of size classes, they tend to be dominated by small- and medium-sized individuals or ephyrae (Supplementary Figure S3). The results indicate that, regardless of season, the patterns in $\delta^{15}N$ are maintained (Supplementary Table S1), which suggests an intra-annual stability to the baseline that is supported by the interannual stability observed offshore (as per MacKenzie et al. 2014). It also implies that animals are routinely advected onshore to supplement the population in shallow water. Given that planulae require a hard substrate on which to settle (e.g. Arai 1997) and that such substrates are scarce offshore (Rogers and Bremner 1991), it can be speculated that these few advected individuals likely make a disproportionate contribution to the renewal of polyp and hence medusa populations.

Interpreted this way, the data also imply that the specimens of *C. africana* (mean size 254 mm diameter [SD 85]) are resident in the very shallow waters of Walvis Bay and are not subject to large-scale offshore advection. This would agree with previous observations (Ras et al. 2020).

Conclusions

The results presented here are based on almost 80 stable isotope determinations of *C. fulgida* and 12 of *C. africana*. They suggest an intriguing scenario and yield several hypotheses that can be tested in the future. Whereas we consider that the observation of decreasing $\delta^{15}N$ with increasing body size of *C. fulgida* in Walvis Bay most likely reflects the onshore advection of larger individuals from the offshore domain where the baseline $\delta^{15}N$ is lower, rather than their feeding at a lower trophic level than smaller individuals inshore, we accept that our arguments are largely speculative. As such they should be treated with some degree of caution and as working hypotheses, largely because no seston samples were collected concurrently with the jellyfish and because our understanding of temporal changes in stable isotope values is poor, especially offshore. Whereas arguments about trophic fractionation *per se* need not be invoked to explain our findings, we note with some concern that few of the more recent studies on the stable isotopes of jellyfish have utilised the findings of D'Ambra et al. (2014) (e.g. Fleming et al. 2015; Javidpour et al. 2016; Wang et al. 2020). Rather, these latter authors have chosen to interpret their data using the enrichment values of Post (2002), arguing simply that those of D'Ambra et al. (2014) were not "appropriate for this study" (Wang et al. 2020, p 696), or that their use resulted in "unfeasibl[e]" conclusions (Fleming et al. 2015, p 15). Given that enrichment values impact any clear interpretation of stable isotope analyses (Bond and Diamond 2011), more work in this area is urgently needed.

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