

Species-specific variation in cuttlebone $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ for three species of Mediterranean cuttlefish

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Received: 2 April 2013 / Accepted: 7 October 2013
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Abstract Stable carbon ($\delta^{13}\text{C}$) and oxygen ($\delta^{18}\text{O}$) isotopes in cuttlebones of three species of Mediterranean cuttlefish (*Sepia elegans*, *S. officinalis*, and *S. orbignyana*) with different life histories were contrasted. Cuttlebone $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ were quantified at both the core and edge (representing early life and recent deposition, respectively) for all three species sampled from the southern Adriatic Sea in 2010 ($n = 28$). For *S. officinalis*, cuttlebone $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values were both lower relative to *S. elegans* and *S. orbignyana* at the core by approximately 1.0–2.0 and 3.0 ‰, respectively. Differences between core and edge in cuttlebone $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ were also observed for *S. officinalis* with observed values at the cuttlebone edge (recent) exceeding core (early life) values by 2.5 ‰ for $\delta^{13}\text{C}$ and 1.4 ‰ for $\delta^{18}\text{O}$. Differences in isotopic composition across *S. officinalis* cuttlebones are possibly reflective of ontogenetic migrations from nearshore nurseries (lower seawater $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values) to offshore overwintering habitats (higher seawater $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values). Overall, results

from this study suggest that cuttlebone $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ hold promise as natural tags for determining the degree of spatial connectivity between nearshore and offshore environments used by cuttlefish.

Introduction

Marine organisms often utilize both nearshore and offshore environments to complete their life cycle (Gillanders et al. 2003), and determining the degree of spatial connectivity among life stages is important to our understanding of population dynamics (Cowen et al. 2000; Beck et al. 2001). In response, a variety of natural tags (e.g., trace elements, stable isotopes) have been used to assess movement between nearshore and offshore environments (Gillanders 2005) and determine the origin of individuals from different nurseries (Thorrold et al. 2001; Rooker et al. 2010). Despite the increasing application of chemical tags in otoliths for assessing movement and habitat use in marine fishes (Elsdon et al. 2008), significant life-history gaps exist for many other marine organisms with carbonate structures (e.g., coleoid cephalopod statoliths, stylets, and cuttlebones) that may be suitable for assessing similar questions regarding nearshore–offshore habitat shifts (Semmens et al. 2007; Zumholz et al. 2007; Pecl et al. 2011).

Cuttlefishes (family Sepiidae) are important components of marine food webs throughout their geographic range, which includes coastal waters in several regions of the world (Piatkowski et al. 2001; Neige 2003). Although cuttlefish are ecologically and economically important, relatively little is known about their movement and habitat use, particularly during the early life period (Reid et al. 2005; Semmens et al. 2007). Sepiids are characterized by the presence of an aragonitic internal shell, the cuttlebone

Communicated by C. Harrod.

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(Reid et al. 2005), and similar to other biogenic carbonates, these structures accrete material in a predictable manner and location of the septa (chambers) is associated with specific periods in the life of a cuttlefish (Ré and Narciso 1994; Bettencourt and Guerra 2001). Stable isotopic ratios of carbon and oxygen in cuttlebones are reflective of ambient seawater ratios (Bettencourt and Guerra 1999), suggesting that cuttlebones may be useful structures for identifying ontogenetic shifts that occur between chemically distinct water masses.

Here, we report on the use of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ in the cuttlebones of three species of Mediterranean cuttlefish (*Sepia elegans*, *S. officinalis*, and *S. orbignyana*) with different life histories. While all three species hatch as benthic juveniles (no planktonic stage), the life history of *S. officinalis* differs from *S. elegans* and *S. orbignyana* as it is more common on the inner shelf and makes seasonal migrations to spawn in nearshore waters (Guerra 2006). Still, there is a lack of empirical research on *S. officinalis* movement in Mediterranean waters and little to no information regarding movement patterns and habitat use of *S. elegans* and *S. orbignyana*, which are thought to prefer deeper waters near the shelf edge (Belcari 1999). The purpose of this study was to compare cuttlebone $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ among the three species of cuttlefish and investigate whether $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ can be used to delineate movement and habitat shifts of cuttlefish.

Materials and methods

Subadult cuttlefish specimens were collected in the southwestern Adriatic Sea off Mola di Bari, Italy, in October 2010 (Fig. 1). Twenty-eight cuttlefish specimens, comprised of three species (*S. elegans* = 6, *S. officinalis* = 10, and *S. orbignyana* = 12), were collected from commercial trawlers at depths ranging from 50 to 300 m. Depth of capture varied among species and was approximated by the fishermen: *S. elegans* (~100–250 m), *S. officinalis* (<75 m), and *S. orbignyana* (~100–300 m). Upon collection, mantle length was recorded to the nearest 0.1 cm for each specimen, and the cuttlebone was extracted, cleaned with distilled water, and measured in length to the nearest 0.1 cm (Table 1).

Cuttlebone material was isolated using an approach modified from Bettencourt and Guerra (1999), in which the cuttlebone was separated into segments from posterior to anterior, with each segment representing progressive life stages. In the current study, two 1-cm sections were isolated from each cuttlebone to examine different life stages, one at the ‘core’ (posterior origin) representing deposition during early life or nursery period and one at the ‘edge’ (anterior margin) representing recent deposition (Fig. 2). For both core and edge sections, material

was carefully removed from the surface of the cuttlebone downward until the hypostracum was reached. Material was isolated from each cuttlebone with a scalpel and then powdered with a mortar and pestle. A significant portion of material was missing from a single *S. officinalis* (core section) and two *S. orbignyana* cuttlebones (edge sections); thus, these sections were excluded from analyses. Cuttlebone $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ were quantified on an automated carbonate preparation device coupled to an isotopic ratio mass

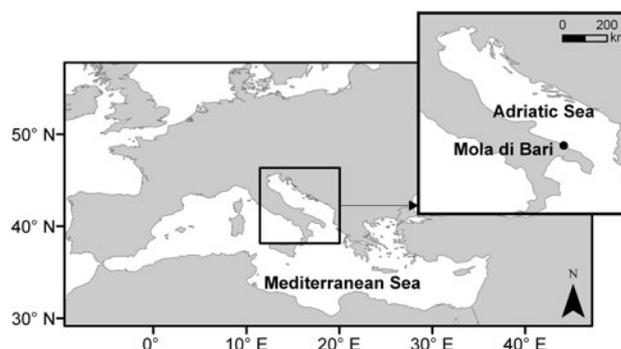


Fig. 1 Map showing location (Mola di Bari, Italy) on the southwestern Adriatic coast where cuttlefish specimens (*S. elegans*, *S. officinalis*, and *S. orbignyana*) were collected

Table 1 Collection information for three species of cuttlefish (*S. elegans*, *S. officinalis*, and *S. orbignyana*) collected from the southern Adriatic Sea

| Species | N | ML \pm SD (cm) | CL \pm SD (cm) | Depth (m) |
|--------------------------|----|------------------|------------------|-----------|
| <i>Sepia elegans</i> | 6 | 4.32 \pm 0.98 | 4.18 \pm 0.99 | 100–220 |
| <i>Sepia officinalis</i> | 10 | 7.52 \pm 0.59 | 7.31 \pm 0.53 | 50–70 |
| <i>Sepia orbignyana</i> | 12 | 5.31 \pm 1.76 | 4.99 \pm 1.73 | 120–280 |

Mean \pm SD mantle length (ML), mean \pm SD cuttlebone length (CL), and depth range of collected specimens are given for each species

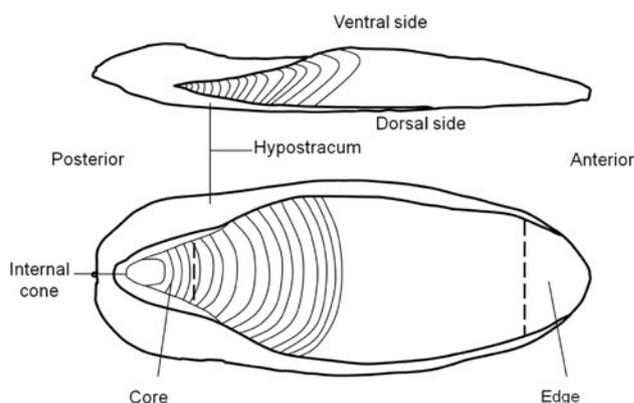


Fig. 2 Schematic diagram of a cuttlebone (based on *S. officinalis*). Dashed lines represent 1-cm sections corresponding to the core and edge sampled for stable isotopic analysis

spectrometer maintained at the Environmental Isotope Laboratory, Department of Geosciences, University of Arizona. The isotopic ratio measurements were calibrated based on repeated measurements of National Bureau of Standards (NBS), NBS-19 and NBS-18, and precision was ± 0.11 ‰ (standard deviation, SD) for $\delta^{18}\text{O}$ and ± 0.08 ‰ (SD) for $\delta^{13}\text{C}$ (Wells et al. 2012). Cuttlebone $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ reported here are based on isotopic ratios of $^{13}/^{12}\text{C}$ and $^{18}/^{16}\text{O}$ relative to the Pee Dee belemnite (PDB) scale after comparison to an in-house standard calibrated to PDB.

Multivariate analysis of variance (MANOVA) was used to test for species-specific differences in cuttlebone $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ at two life stages: (1) early life (core) and (2) recent (edge). Pillai's trace was chosen as the test statistic as it is most robust to violations of homogeneity of covariance (Wilkinson et al. 1996). Analysis of variance (ANOVA) tests were also performed to test for species-specific differences in cuttlebone $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$, and Tukey's honestly significant difference (HSD) test was used to make pairwise comparisons among species at each life stage. Ontogenetic differences in cuttlebone $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ were examined as the mean difference between core and edge pairs using paired t tests. Quadratic discriminant function analysis (QDFA) was used to classify cuttlebone $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ at each life stage. Significance for all tests was based on an alpha value of 0.05.

Results

Cuttlebone $\delta^{13}\text{C}_{\text{core}}$ and $\delta^{18}\text{O}_{\text{core}}$ (early life deposition) varied significantly among the three species (MANOVA, $P < 0.01$), and univariate contrasts indicated that both $\delta^{13}\text{C}_{\text{core}}$ and $\delta^{18}\text{O}_{\text{core}}$ differed among the three species examined (ANOVA, $P < 0.01$). Cuttlebone $\delta^{18}\text{O}_{\text{core}}$ values (mean value \pm SD) for *S. officinalis* (0.1 ± 0.2 ‰) were significantly lower than values observed for *S. elegans* (3.1 ± 0.2 ‰) and *S. orbignyana* (3.1 ± 0.2 ‰) by

approximately 3 ‰ (Tukey's HSD, $P < 0.01$; Fig. 3). Cuttlebone $\delta^{13}\text{C}_{\text{core}}$ values of *S. orbignyana* (-1.8 ± 0.5 ‰) were significantly higher than those observed for *S. elegans* (-2.6 ± 0.4 ‰) and *S. officinalis* (-4.0 ± 0.6 ‰), while $\delta^{13}\text{C}_{\text{core}}$ values of *S. elegans* were high relative to *S. officinalis* (Tukey's HSD, $P < 0.01$; Fig. 3). Overall cross-validated classification success from QDFA based on $\delta^{13}\text{C}_{\text{core}}$ and $\delta^{18}\text{O}_{\text{core}}$ was 89 %, and classification success was higher for *S. officinalis* (100 %) than for *S. elegans* (83 %) or *S. orbignyana* (83 %).

Cuttlebone $\delta^{13}\text{C}_{\text{edge}}$ and $\delta^{18}\text{O}_{\text{edge}}$ (recent deposition) were also distinct among the three species (MANOVA, $P < 0.01$), and a species-specific effect was detected for both $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ (ANOVA, $P < 0.01$). Cuttlebone $\delta^{18}\text{O}_{\text{edge}}$ values of *S. officinalis* (1.6 ± 0.3 ‰) were significantly higher relative to values observed for *S. elegans* (3.0 ± 0.4 ‰) and *S. orbignyana* (3.0 ± 0.1 ‰) (Tukey's HSD, $P < 0.01$), but no differences were found between the latter two species (Tukey's HSD, $P > 0.05$). Similarly, cuttlebone $\delta^{13}\text{C}_{\text{edge}}$ values of *S. officinalis* (-1.6 ± 0.5 ‰) were significantly lower (1 ‰ or more) relative to the two other species (Tukey's HSD, $P < 0.05$). Cuttlebone $\delta^{13}\text{C}_{\text{edge}}$ of *S. orbignyana* (-0.2 ± 0.5 ‰) and *S. elegans* (-0.5 ± 1.6 ‰) was similar (Tukey's HSD, $P > 0.05$). Overall cross-validated classification success from QDFA based on $\delta^{13}\text{C}_{\text{edge}}$ and $\delta^{18}\text{O}_{\text{edge}}$ was 88 %, and classification success by species for recent deposition was again 100 % for *S. officinalis*, with values being lower for both *S. orbignyana* (90 %) and *S. elegans* (67 %).

Differences in cuttlebone $\delta^{13}\text{C}$ and/or $\delta^{18}\text{O}$ were detected between core and edge samples of all three species, with the cuttlebone $\delta^{13}\text{C}_{\text{edge}}$ values higher than $\delta^{13}\text{C}_{\text{core}}$ for all three species (paired t test, $P < 0.01$; Fig. 4). Differences between cuttlebone $\delta^{13}\text{C}_{\text{core}}$ and $\delta^{13}\text{C}_{\text{edge}}$ values were greater (mean difference \pm SD) for *S. officinalis* (2.5 ± 0.4 ‰) than for either *S. elegans* (2.2 ± 1.3 ‰) or *S. orbignyana* (1.5 ± 0.8 ‰). Variation in cuttlebone $\delta^{18}\text{O}$ between core and edge samples was also detected for

Fig. 3 Cuttlebone $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ (‰ relative to Pee Dee belemnite) for core and edge samples of three species of cuttlefish: *S. elegans*, *S. officinalis*, and *S. orbignyana*. Confidence ellipses (1 SD around the mean) are shown for each species

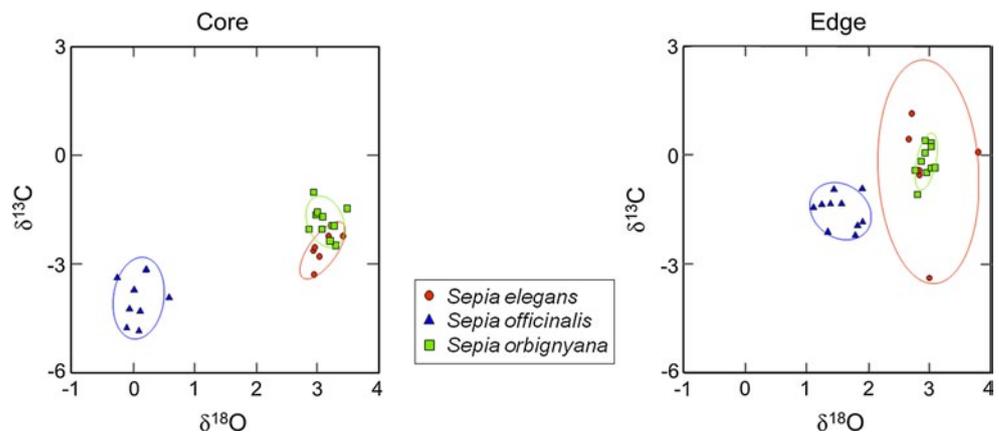
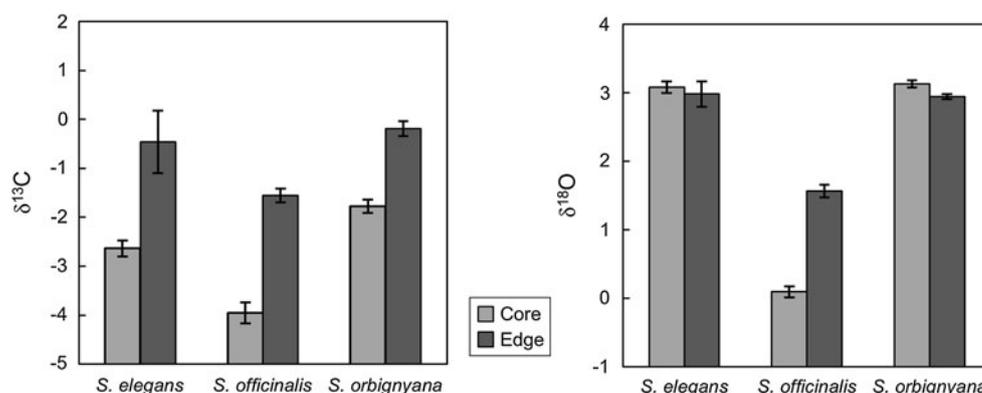


Fig. 4 Comparisons of core and edge mean cuttlebone $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ (‰ relative to Pee Dee belemnite) for each of three species of cuttlefish: *S. elegans*, *S. officinalis*, and *S. orbignyana*. Error bars are ± 1 standard error of the mean



S. officinalis and *S. orbignyana* (paired *t* test, $P < 0.01$), with $\delta^{18}\text{O}_{\text{edge}}$ values of *S. officinalis* significantly higher than $\delta^{18}\text{O}_{\text{core}}$ values (mean difference = 1.4 ± 0.4 ‰), while the opposite trend (-0.2 ± 0.1 ‰) was observed for *S. orbignyana* (Fig. 4). No significant difference in $\delta^{18}\text{O}$ between core and edge material was detected for *S. elegans* (paired *t* test, $P > 0.05$).

Discussion

Few studies have examined the use of cuttlebone $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ as natural tags for cuttlefish, preventing direct comparisons with other studies in the Mediterranean Sea; however, isotopic values from this study were comparable to cuttlebone $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values reported in adjacent waters. In the present study, $\delta^{18}\text{O}$ values were much lower in *S. officinalis* (range 0.3–1.9 ‰) than in *S. elegans* (2.7–3.8 ‰) and *S. orbignyana* (2.8–3.5 ‰). Similarly, $\delta^{13}\text{C}$ values from *S. officinalis* cuttlebones (range -4.8 to -0.9 ‰) were consistently lower than those from either *S. elegans* (-3.3 to 0 ‰) or *S. orbignyana* (-2.5 to 0 ‰). Because this is the first isotopic analysis of cuttlebones for *S. elegans* and *S. orbignyana*, regional comparisons were limited to *S. officinalis*. Cuttlebone $\delta^{18}\text{O}$ values for *S. officinalis* collected off the northwestern Iberian Peninsula (range -0.2 to 2.1 ‰) by Bettencourt and Guerra (1999) were relatively similar to our findings, while a life-history transect of $\delta^{18}\text{O}$ (from core to edge of cuttlebone) of a single *S. officinalis* from the North Sea ranged from -1.3 to 3.0 ‰ (Rexfort and Mutterlose 2006). For $\delta^{13}\text{C}$, cuttlebone values from the North Sea (Rexfort and Mutterlose 2006) and this study both generally fell within a range of -4.5 to -1.0 ‰, while values from the Iberian Peninsula (Bettencourt and Guerra 1999) were slightly higher (range -3.0 to 1.0 ‰). Observed regional variation in the isotopic composition of *S. officinalis* cuttlebones between the current study and previous studies from outside the Mediterranean is likely reflective of regional differences in $\delta^{13}\text{C}$

and $\delta^{18}\text{O}$ values of seawater or prey (DeLaygue et al. 2000; LeGrande and Schmidt 2006; Graham et al. 2010).

Cuttlebone $\delta^{13}\text{C}_{\text{core}}$ and $\delta^{18}\text{O}_{\text{core}}$ values for *S. officinalis* were lower than values observed for both *S. elegans* and *S. orbignyana*, and distinct differences between *S. officinalis* and the two other species appear linked to their early life habitat. *S. officinalis* spawn primarily in nearshore waters and juveniles of this species inhabit coastal lagoons and bays (Blanc et al. 1998; Reid et al. 2005; Guerra 2006), while spawning and nursery areas of *S. elegans* and *S. orbignyana* are thought to occur farther offshore (Reid et al. 2005). In this region of the Adriatic Sea, nearshore and offshore water masses differ physicochemically, with nearshore water often characterized by higher temperature and lower salinity (Bignami et al. 2007; Turchetto et al. 2007; Marini et al. 2008). Given that $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values of both seawater and biogenic carbonates are typically more depleted in the heavier isotope as temperature increases (Bettencourt and Guerra 1999; LeGrande and Schmidt 2006) and/or salinity decreases (DeLaygue et al. 2000; Rooker et al. 2010), cuttlefish inhabiting nearshore nurseries would be expected to have lower cuttlebone $\delta^{13}\text{C}_{\text{core}}$ and $\delta^{18}\text{O}_{\text{core}}$ values. Moreover, observed differences in cuttlebone $\delta^{13}\text{C}_{\text{core}}$ values between *S. officinalis* and the other two species (1–2 ‰ lower in *S. officinalis*) from this study are consistent with previously documented differences in benthic foraminifera $\delta^{13}\text{C}$ values between nearshore and offshore areas (1–2 ‰ lower in nearshore samples) in the southern Adriatic Sea (Grauel and Bernasconi 2010). Our finding of lower cuttlebone $\delta^{13}\text{C}_{\text{core}}$ and $\delta^{18}\text{O}_{\text{core}}$ values for *S. officinalis* relative to both *S. elegans* and *S. orbignyana* is in accord with the basic concept that this species occupies nearshore nurseries. Conversely, higher cuttlebone $\delta^{13}\text{C}_{\text{core}}$ and $\delta^{18}\text{O}_{\text{core}}$ values observed for *S. elegans* and *S. orbignyana* suggest that these species likely inhabit offshore nurseries that are minimally influenced by coastal processes (i.e., freshwater inflow).

Cuttlebone $\delta^{13}\text{C}_{\text{edge}}$ and $\delta^{18}\text{O}_{\text{edge}}$ were representative of recent deposition, and differences between core and

edge samples were used to investigate ontogenetic shifts in habitat. Both $\delta^{13}\text{C}_{\text{edge}}$ and $\delta^{18}\text{O}_{\text{edge}}$ in the cuttlebones of *S. officinalis* were high relative to the respective core values for each isotope. Changes in cuttlebone composition over time might be expected for *S. officinalis* as it is widely thought to make cross-shelf migrations from coastal nurseries in autumn (August to October) to overwinter in deeper water offshore (Blanc et al. 1998; Reid et al. 2005; Guerra 2006). Given the aforementioned nearshore–offshore gradient in temperature and salinity (Grauel and Bernasconi 2010), we would expect an increase in both $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ from the cuttlebone core to edge as *S. officinalis* move from nearshore nurseries to offshore overwintering areas. Because *S. officinalis* specimens used in our study were captured in offshore waters, it appears that the observed difference between the core and edge is largely due to changes in physicochemical conditions between the two areas; though, other sources cannot be completely excluded (Hoie et al. 2004). Higher $\delta^{13}\text{C}_{\text{edge}}$ relative to $\delta^{13}\text{C}_{\text{core}}$ was also observed in cuttlebones of *S. elegans* and *S. orbignyana*; however, it appears unlikely that these differences were due to ontogenetic movement because similar shifts were not observed for $\delta^{18}\text{O}$, which is deposited independent of metabolic and kinetic effects in biogenic carbonates and therefore considered a more reliable indicator of physicochemical water mass properties (Bettencourt and Guerra 1999; Hoie et al. 2003). Increases in cuttlebone $\delta^{13}\text{C}$ from core to edge for cuttlefish reared in the laboratory suggest that enrichment of the heavier carbon isotope may also be linked to changes in metabolic processes, ontogenetic shifts in diet, and ontogenetically controlled biofractionation (Bettencourt and Guerra 1999; Rexfort and Mutterlose 2006; Neves et al. 2009). While differences in isotopic signatures at the base of the food web may be reflected at higher trophic levels, the direct effect of a shift in producers (either due to habitat shifts or ontogenetic shifts in diet) is likely to be minimal, given that the majority of carbon in aragonitic structures would be expected to come from seawater (Campana 1999; Rooker et al. 2010).

Findings from this study suggest that $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ in cuttlebones represent promising natural tags for tracking cross-shelf movements of cuttlefish between nearshore and offshore water masses. Similar to other biogenic hard parts, the microstructure of the cuttlebone provides relative age/time information that can be combined with $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ data to develop chronologies of spatial occurrences by cuttlefish. Given the ecological value of cuttlefish throughout the Mediterranean region, cuttlebone chemistry is potentially a useful tool to improve our understanding of migration patterns and connectivity among juvenile and adult habitats.

Acknowledgments We would like to thank D. Dettman for assistance in the laboratory, as well as two anonymous reviewers for comments that improved the manuscript.

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