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journal homepage: www.elsevier.com/locate/jembeAsynchrony between dietary and nutritional shifts during the ontogeny of green turtles (*Chelonia mydas*) in the MediterraneanL. Cardona^{a,*}, P. Campos^a, Y. Levy^b, A. Demetropoulos^c, D. Margaritoulis^d^a IRBIO and Department of Animal Biology, Faculty of Biology, University of Barcelona, Avda. Diagonal 645, E-08028 Barcelona, Spain^b Israel Sea Turtle Rescue Center, Israel National Nature and Parks Authority, Mevot Yam, Mikhmoret 40297, Israel^c Cyprus Wildlife Society, P.O. Box 24281, Nicosia 1703, Cyprus^d ARCHELON, the Sea Turtle Protection Society of Greece, Solomou 57, GR-10432 Athens, Greece

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ABSTRACT

Young green turtles (*Chelonia mydas*) spend their early lives as oceanic omnivores, which consume primarily animal prey. Once they settle into neritic habitats (recruitment), they appear to shift rapidly into an herbivorous diet in tropical regions. However, the ontogeny of the dietary shift and the relevance of animal prey in the diet of neritic green turtles are poorly understood in subtropical and warm temperate regions. Stable isotopes of carbon and nitrogen in the carapace scutes of 22 green turtles from the eastern Mediterranean, ranging from 28 to 83 cm in curved carapace length (CCL_{min}), were analysed to test the hypothesis of a rapid nutritional shift following recruitment. Seagrasses prevailed in the stomach contents of all the green turtles that were larger than 30 cm CCL_{min}, but the concentration of stable isotopes in the carapace scutes revealed that turtles shorter than 40 cm CCL_{min} derived a negligible amount of assimilated nutrients from seagrasses. The concentration of stable isotopes in the carapace scutes also suggested that the contribution of seagrasses to the nutrients assimilated by green turtles increased steadily with turtle size and that some, but not all, of the turtles larger than 62 cm CCL_{min} were fully herbivorous. The overall evidence (gut contents analysis and stable isotope analysis) indicates that green turtles in the Mediterranean shift to a seagrass-based diet immediately after recruitment but turtle growth continues to rely on animal-derived nutrients for several years after recruitment. This asynchrony between the dietary and nutritional shifts is thought to be caused by the temperature sensitivity of bacterial fermentation and the low temperatures experienced by green turtles in the Mediterranean, which may result in a poor assimilation of the plant-derived nutrients for most of their neritic juvenile life.

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1. Introduction

The green turtle *Chelonia mydas* (L.) is the only sea turtle considered to be herbivorous throughout most of its life (Bjorndal, 1997) and is known to play a key role in the dynamics of seagrass meadows at least in some tropical regions (Moran and Bjorndal, 2005). Actually, the massive decline in number of green turtles in the greater Caribbean since the western colonization has been proposed to be responsible of the degradation of the essentially ungrazed seagrass meadows of today (Bjorndal and Jackson, 2003), although coastal development and declining water quality are also involved (Waycott et al., 2009). The same link might exist between green turtle decimation and seagrass decline elsewhere, but any extrapolation is hindered by the paucity of detailed information about the feeding habits of green turtles in most regions.

Traditional understanding assumes that green turtles are oceanic in their early lives but typically turn to neritic habitats when they reach a carapace length of 25–44 cm (Bjorndal and Bolten, 1988; Limpus et al., 1994; Reich et al., 2007; Arthur et al., 2008; Boyle and Limpus, 2008) and an age of 3–10 years (Zug and Glor, 1999; Zug et al., 2001; Balazs and Chaloupka, 2004; Chaloupka et al., 2004; Reich et al., 2007). It has been reported that such a change in habitat, defined hereafter as recruitment, is accompanied in the greater Caribbean and Australia by a dietary shift, where neustonic invertebrates are replaced by macrophytes as dominant items in the diet (Bjorndal, 1997; Reich et al., 2007; Arthur et al., 2008). However, the timing of the ontogenic dietary shift and the degree of omnivory may be different in other regions, as indicated by stable isotope analyses (Godley et al. 1998; Hatase et al. 2006; Cardona et al. 2009), satellite telemetry (Hatase et al. 2006), underwater video recording (Heithaus et al., 2002), and even gut content analyses (Limpus et al. 1994; Seminoff et al. 2002; Ferreira et al. 2006; Amorocho and Reina 2007). The reasons for such variability are unknown.

The Mediterranean Sea supports one of the smallest green turtle populations in the world, with only a few hundred females nesting there annually (Kasperek et al., 2001; Broderick et al., 2002; Carpenter, 2006;

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Rees et al., 2008; but see Demetropoulos and Hadjichristophorou, 2008). The foraging grounds of the species in the region are restricted to the eastern basin (Demetropoulos and Hadjichristophorou, 1995; Hays et al., 2002; Margaritoulis and Teneketzis, 2003; Teneketzis et al., 2006), where the only other vertebrate herbivores currently present are fishes. The diet of the native parrotfish *Sparisoma cretense* (L.) and those of the two rabbitfishes in the genus *Siganus* that invaded the eastern Mediterranean Sea from the Red Sea include very limited amounts of seagrasses (Azzurro et al., 2007) and hence only the native salemma *Sarpa salpa* (L.) and green turtles consume seagrasses regularly (Demetropoulos and Hadjichristophorou, 1995; Hays et al., 2002; Margaritoulis and Teneketzis, 2003; Teneketzis et al., 2006; Azzurro et al., 2007). Salemas are known to play a role in the dynamics of the meadows of the seagrass *Posidonia oceanica* (L.) Delille (Pinna et al., 2009), but nothing is known about the role of green turtles in the dynamics of Mediterranean seagrass meadows.

Gut content analyses conducted in the Mediterranean Sea are consistent with an early dietary shift and herbivory after recruitment to neritic habitats, as seagrasses are the most abundant dietary items in the gut contents of green turtles larger than 30 cm curved carapace length (hereafter CCLmin; Bolten, 1999) from Cyprus and Greece (Demetropoulos and Hadjichristophorou, 1995; Hays et al., 2002; Margaritoulis and Teneketzis, 2003; Teneketzis et al., 2006). Accordingly, stable isotope analyses have revealed a trophic level lower than that of the carnivorous loggerhead sea turtle *Caretta caretta*, even though the trophic level inferred from the relative abundance of stable isotopes of nitrogen (expressed as $\delta^{15}\text{N}$) is higher than that expected for an herbivore (Godley et al., 1998). As a consequence, Godley et al. (1998) suggested that green turtles in the Mediterranean Sea would not be pure herbivores, but opportunistic omnivores, although the ontogeny of the dietary change of green turtles in the Mediterranean Sea remained unresolved.

Analyzing the changes in the concentrations of stable isotopes across the keratin layers of the carapace scutes has proven to be a powerful tool to reconstruct the dietary ontogeny of green turtles (Reich et al., 2007; Cardona et al., 2009). This is possible because the isotopic signal of keratinous tissue does not change once it is produced (Hobson and Clark 1992; Hobson et al., 1996; Roth and Hobson 2000; Ayliffe et al., 2004). Therefore, the isotopic signal of each layer is thought to reflect the composition of the diet that was consumed when it was formed (Reich et al., 2007), with the most recent layer being the more internal and the oldest layer being the most external in the posterior margin of the scute (Kobayashi, 2001). Although the exact rate at which keratin is accreted and sloughed in green turtles is unknown, Reich et al. (2007) reported that young green turtles recruited one year ago still retained in the outermost carapace layer the stable isotope signal typical of oceanic turtles (approximately 50 μm thick), whereas they already exhibited the signal typical of neritic herbivorous turtles in the innermost carapace layer (approximately 50 μm thick). Furthermore, Reich et al. (2008) reported an average residence time of less than two months for the stable isotope signal of carapace scutes of young loggerhead sea turtles. As a consequence, layers of carapace scutes approximately 50 μm thick are expected to integrate the isotopic signal of the diet of a few months, at least in young turtles from tropical regions.

The present study analyses carbon and nitrogen stable isotopes across the layers of the carapace scutes of green turtles in the Mediterranean Sea to determine the nutritional and dietary shifts during the ontogeny of green turtles and assess their nutritional dependence on seagrasses at different ontogenic stages.

2. Materials and methods

2.1. Study site and sample collection

Samples were collected from 2006 to 2008 in southern Greece, Cyprus, and Israel. Extensive meadows of the seagrass *P. oceanica*

develop in moderately exposed locations off of southern Greece and Cyprus, whereas beds of the seagrass *Cymodocea nodosa* Ucria (Ascherson) are found primarily in shallow, sheltered bays (Lipkin et al., 2003). The only seagrass off Israel is *C. nodosa* (Lipkin et al., 2003). The brown macroalgae *Cystoseira cf humilis* Kützinger prevails in the infralittoral rocks off the coasts of southern Greece and Cyprus (Ramos-Esplá et al., 2007), whereas the green macroalgae *Codium vermilara* Olivi (Delle Chiaje) is the dominant macroalgae in the submerged horizontal platforms and rocky outcrops off Israel.

To identify prey isotopic signatures, the following potential food items were also sampled: seagrasses (*C. nodosa* and *P. oceanica*) and macroalgae (*C. cf humilis* and *C. vermilara*). The sample size was 5 for each species and region. The epiphyte-free basal area of the blades was analysed for seagrasses (as green turtles selectively avoid epiphytised older parts (Bjorndal 1980; Mortimer 1981; Lanyon et al., 1989), and epiphyte-free fragments were analysed for macroalgae. All samples were preserved salt-dried in the field, rinsed, and then frozen at -20°C in the laboratory.

The curved carapace length (CCLmin) of 22 dead, stranded green turtles from these three areas was measured, and from the carapace of each one, a costal scute was removed and stored dry. All the turtles from Greece and Cyprus had been incidentally caught with gillnets and trammelnets, except turtle #G1 (Table 1). Nothing is known about the cause of mortality of the turtles from Israel. Once in the laboratory, scutes were superficially brushed, and four samples (approximately 50 μm in thickness) were collected across the posterior margin of the scute (Reich et al., 2007; Cardona et al., 2009). Samples were collected by scraping the scute with a scalpel successively in the same area to remove four underlying layers (Cardona et al., 2009). The thickness of each of the removed layers was measured with a Baxlo[®] 4000/F thickness gauge (accuracy = 3 μm). Furthermore, the carapace scutes of 5 pelagic loggerhead sea turtles *Caretta caretta* (L.), which were shorter than 40 cm CCLmin and were incidentally captured by drifting longliners targeting large oceanic fish in the eastern Mediterranean, were analysed and used as a benchmark for the diet of a pelagic carnivore (Reich et al.,

Table 1

Carapace length (CCLmin) and isotopic values of the four carapace layers of the analysed green turtles (out: outermost layer; int1 and int2: intermediate layers; inn: innermost layer).

Turtle ID	CCLmin (cm)	$\delta^{13}\text{C}$ (‰)				$\delta^{15}\text{N}$ (‰)			
		out	int1	int2	inn	out	int1	int2	inn
<i>Greece</i>									
#G1	28.5	-18.0	-18.1	-18.3	-18.5	6.6	6.5	5.3	5.2
#G2	42.5	-14.7	-14.5	-14.5	-14.1	6.6	6.5	5.9	7.0
#G3	43.5	-14.7	-14.7	-13.9	-13.7	6.2	6.1	6.2	6.1
#G4	53.0	-19.0	-18.7	-18.5	-19.0	4.2	4.7	4.7	4.2
#G5	59.5	-13.9	-13.7	-13.7	-13.6	9.7	9.5	8.7	8.3
<i>Cyprus</i>									
#C1	30.0	-18.3	-18.1	-18.1	-18.2	5.6	5.7	5.2	5.3
#C2	31.5	-18.1	-18.2	-18.1	-17.9	6.9	6.5	5.3	5.5
#C3	34.5	-16.7	-16.2	-17.7	-17.4	5.4	5.3	5.5	5.9
#C4	38.0	-17.6	-18.0	-17.8	-18.1	5.7	5.2	5.5	7.0
#C5	62.0	-14.7	-15.3	-14.8	-15.1	3.9	4.2	5.9	5.7
#C6	63.0	-17.3	-17.3	-16.9	-17.8	6.7	6.7	6.1	6.5
#C7	79.0	-14.1	-12.3	-13.8	-13.3	6.1	4.9	6.2	6.0
<i>Israel</i>									
#I1	28.0	-17.3	-17.9	-17.5	-18.3	6.4	5.4	5.0	6.5
#I2	34.0	-17.3	-17.4	-17.8	-16.7	5.9	5.8	6.4	7.2
#I3	41.5	-15.8	-13.5	-15.9	-15.4	12.8	12.2	13.4	13.3
#I4	41.5	-20.0	-17.6	-17.4	-19.0	9.9	9.7	10.6	10.7
#I5	64.5	-14.8	-15.3	-13.5	-13.2	9.5	9.3	10.1	9.9
#I6	65.6	-17.3	-17.9	-17.9	-16.6	9.7	6.0	10.1	9.9
#I7	67.5	-18.7	-18.5	-15.8	-15.4	10.7	10.4	11.0	11.0
#I8	76.0	-11.8	-11.0	-12.5	-12.2	7.8	7.6	9.4	8.9
#I9	76.5	-17.3	-17.5	-13.2	-13.1	9.2	9.1	10.5	10.4
#I10	83.0	-9.6	-9.9	-11.0	-11.9	4.8	4.7	5.7	5.2

2007; Revelles et al., 2007a,2007b; Casale et al., 2008). Dorsal, white muscle from the zooplanktophagous fish *Spicara smaris* (L.) captured off southern Greece, Cyprus and Israel ($n = 5$ from each region) were also analyzed to elucidate possible anomalies in the pelagic–benthic carbon continuum.

2.2. Analysis of stable isotopes

Samples were dried at 60 °C, ground to a fine powder, and had their lipids extracted with a chloroform/methanol (2:1) solution. All the samples were weighed into tin cups, combusted at 1000 °C, and analysed in a continuous flow isotope ratio mass spectrometer at the Serveis Científicotècnics de la Universitat de Barcelona. Stable isotope abundances were expressed in δ notation according to the following expressions:

$$\delta^{13}\text{C} = \left(\left[\frac{R_{\text{sample}}}{R_{\text{standard}}} \right] - 1 \right) \times 10^3$$

$$\delta^{15}\text{N} = \left(\left[\frac{R_{\text{sample}}}{R_{\text{standard}}} \right] - 1 \right) \times 10^3$$

where R_{sample} and R_{standard} are the corresponding ratios of $^{13}\text{C}/^{12}\text{C}$, $^{34}\text{S}/^{32}\text{S}$, or $^{15}\text{N}/^{14}\text{N}$. The standards used for ^{13}C and ^{15}N determination were Vienna Pee Dee Belemnite (VPDB) and atmospheric nitrogen (air), respectively.

2.3. Data analysis

The IsoSource mixing model developed by Phillips and Gregg (2003) was used to assess the probability that the concentration of stable isotopes, observed in the innermost layer of the carapace scutes from the sampled turtles, could arise from a fully herbivorous diet. This method examines all possible combinations of each source contribution in small increments (1% in this study). Combinations that sum to the observed mixture of isotopic signatures within a small tolerance ($\pm 0.1\text{‰}$ in this study) are considered to be feasible solutions, from which the frequency and range of potential source contributions can be determined (Phillips and Gregg 2003). IsoSource was run for each individual turtle. Before the data were entered, the average bivariate isotopic signature of each plant in the region, in which the turtle was stranded dead, was corrected with the fractionation factors reported by Reich et al. (2008) for loggerhead sea turtle carapace scutes; i.e., 1.77‰ for $\delta^{13}\text{C}$ and -0.64‰ for $\delta^{15}\text{N}$.

Unless otherwise stated, data are shown as mean \pm SD. All statistical analyses were conducted using SPSS 15 software.

3. Results

Macroalgae were consistently depleted of ^{13}C when compared with seagrasses in the three regions and the seagrass *P. oceanica* was always more depleted of ^{13}C than the seagrass *C. nodosa* wherever they coexisted (Fig. 1). Furthermore, pelagic loggerhead sea turtles (length = 32.0 ± 7.1 cm CCLmin) were highly depleted of ^{13}C ($\delta^{13}\text{C}$: $-18.2 \pm 0.4\text{‰}$) when compared with seagrasses but not with macroalgae. The same was true for the zooplanktophagous fish *S. smaris*, whose $\delta^{13}\text{C}$ values were extremely similar to those of the pelagic loggerhead sea turtles ($\delta^{13}\text{C}$ *S. smaris* Cyprus: $-18.5 \pm 0.1\text{‰}$; $\delta^{13}\text{C}$ *S. smaris* Israel: $-18.6 \pm 0.7\text{‰}$; $\delta^{13}\text{C}$ *S. smaris* southern Greece: $-18.6 \pm 0.2\text{‰}$). Such an isotopic landscape indicates that the $\delta^{13}\text{C}$ of the carapace scutes of green turtles should increase, when they shift from oceanic to neritic habitats, only if this change is accompanied by a dietary shift to seagrasses or seagrass associated animals but not to macroalgae.

In agreement with those predictions, the $\delta^{13}\text{C}$ of the innermost layer of the carapace scutes of green turtles that were shorter than 40 cm CCLmin was close to that of pelagic loggerhead sea turtles and increased steadily with turtle size (Fig. 2). This correlation was statistically significant in Cyprus ($r^2 = 0.686$, $p = 0.021$, $n = 7$) and Israel

($r^2 = 0.691$, $p = 0.003$, $n = 10$), but not in southern Greece ($r^2 = 0.115$, $p = 0.515$, $n = 5$). Furthermore, the $\delta^{13}\text{C}$ of the innermost layer of the carapace scutes of the largest green turtles from each region was close to that expected for an herbivore relying primarily on seagrasses (Fig. 2), using the prey to predator fractionation factors reported by Reich et al (2008).

Changes in the $\delta^{13}\text{C}$ across the carapace scutes of green turtles were consistent with a shift from a pelagic to a seagrass based diet only for turtles #17 (CCLmin = 67.5 cm) and #119 (CCLmin = 76.5 cm). The variations in the $\delta^{13}\text{C}$ values across carapace layers for the other turtles were too small to be consistent with such a dietary shift (Table 1). Furthermore, the coefficient of variation of the $\delta^{13}\text{C}$ across the carapace scutes was small in green turtles that were shorter than 40 cm CCLmin, and it increased steadily with carapace length (Fig. 4), although the pattern varied among regions (ANCOVA: $F_{\text{model}} = 9.526$, $df = 3$, $r^2_{\text{corrected}} = 0.549$, $p = 0.001$; $F_{\text{region}} = 5.880$, $df = 2$, $p = 0.011$; $F_{\text{CCLmin}} = 8.479$, $df = 1$, $p = 0.009$). As a consequence, larger turtles shifted their diets more frequently than smaller ones.

The macrophytes from southern Greece did not differ in average $\delta^{15}\text{N}$, but statistically significant differences were found among macrophytes from Cyprus and Israel (Fig. 1). The variability was remarkable among the macrophytes from Cyprus, where the difference between the most ^{15}N -enriched (the macroalgae *Cystoseira cf humilis*) and most ^{15}N -depleted species (the seagrass *P. oceanica*) was 7.5‰ . A similar difference was also found between the $\delta^{15}\text{N}$ of macroalgae and seagrasses from southern Greece and their counterparts from Israel, thus revealing high levels of regional variability in the $\delta^{15}\text{N}$ baseline. Furthermore, the $\delta^{15}\text{N}$ for pelagic loggerhead sea turtles ($\delta^{15}\text{N}$: $6.0 \pm 0.5\text{‰}$) was higher than that of macrophytes in Greece only, thus indicating that there are differences in the $\delta^{15}\text{N}$ baseline for pelagic and benthic food webs. As a consequence, interpreting the changes in $\delta^{15}\text{N}$ for each carapace scute level was challenging because slight changes in the trophic level can be obscured by the high variability from macrophytes. This is well exemplified by the absence of a statistically significant correlation between the $\delta^{15}\text{N}$ and the $\delta^{13}\text{C}$ values ($r = 0.243$; $p = 0.276$; $n = 22$).

Nevertheless, green turtles appear to have 'oceanic' signatures even when sampled from coastal areas, because the $\delta^{15}\text{N}$ from the innermost layer of the carapace scutes of the green turtles that were shorter than 40 cm CCLmin was close to that of pelagic loggerhead sea turtles, as expected. Conversely, the $\delta^{15}\text{N}$ of the larger green turtles was highly variable (range: $5.2\text{--}13.3\text{‰}$) and was uncorrelated with turtle size (CCLmin) (southern Greece: $r = -0.431$, $p = 0.468$, $n = 5$; Cyprus: $r = 0.226$, $p = 0.626$, $n = 7$; Israel: $r = -0.023$, $p = 0.928$; $n = 10$). Furthermore, the $\delta^{15}\text{N}$ of the innermost layer of the carapace scutes of most of the green turtles from southern Greece and Israel was much higher than what was expected for an herbivore (Fig. 3), assuming the prey to predator fractionation factors reported by Reich et al (2008) are correct. This revealed high levels of omnivory for immature green turtles, at least off the coasts of Greece and Israel. The coefficient of variation of the $\delta^{15}\text{N}$ across carapace layers was unrelated to turtle size (Fig. 4) or stranding region (ANCOVA: $F_{\text{model}} = 0.379$, $df = 3, 2, 1$, $p = 0.769$).

When benthic macrophytes were considered the only potential prey, IsoSource failed to provide any solution to the diet of 19 sampled green turtles, thus revealing that none of them was a pure herbivore. IsoSource found a solution for the diet of three turtles from Cyprus (C6 and C7) and Israel (I10) measuring 62 cm, 79 cm and 83 cm CCLmin, but not for every turtle within that range, thus confirming that even some large turtles were not pure herbivores.

4. Discussion

Although the use of stable isotopes as diet tracers is a powerful technique, interpreting the results is not always straightforward because the method is reliable only when large differences exist between the isotopic signals of the considered sources and when the

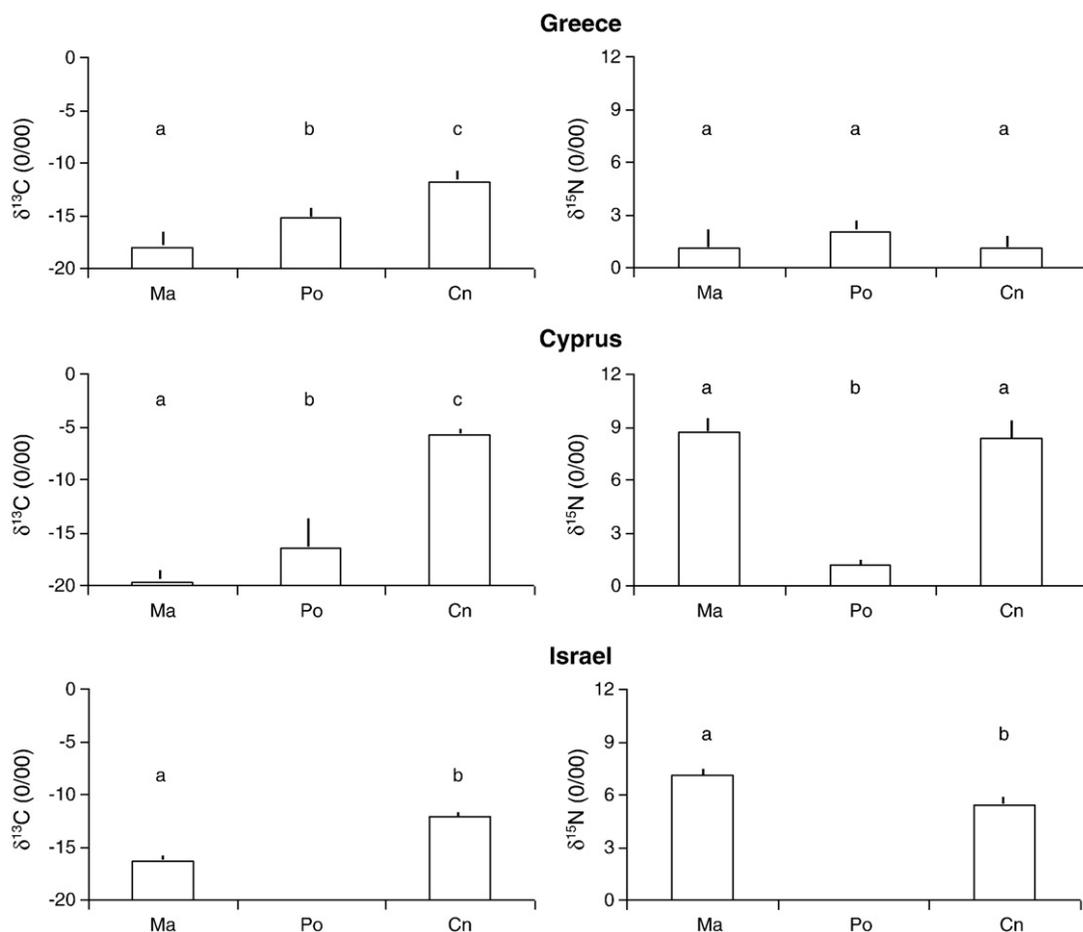


Fig. 1. Isotopic values of macrophytes from the eastern Mediterranean (Ma: the macroalgae *Cystoseira cf. humilis* from Greece and Cyprus and *Codium vermilara* from Israel; Po: the seagrass *Posidonia oceanica*, and Cn: the seagrass *Cymodocea nodosa*). Macrophyte species from each region with different letters differ in their mean values according to ANOVA and a Tukey *post hoc* test ($\delta^{13}\text{C}$ Greece: $F = 37.026$, $df = 2, 12$, $p < 0.01$; $\delta^{13}\text{C}$ Cyprus: $F = 50.691$, $df = 2, 12$, $p < 0.001$; $\delta^{15}\text{N}$ Greece: $F = 0.858$, $df = 2, 12$, $p = 0.449$; $\delta^{15}\text{N}$ Cyprus: $F = 44.440$, $df = 2, 12$, $p < 0.001$) or Student's *t* test ($\delta^{13}\text{C}$ Israel: $t = 13.841$, $df = 8$, $p < 0.001$; $\delta^{15}\text{N}$ Israel: $t = -5.940$, $df = 8$, $p < 0.001$). Sample size: $n = 5$ for each species and region.

isotopic signal varies consistently across habitats and trophic levels. However, this is not always true and the local isotopic landscape should be carefully analyzed before stable isotopes could be used as tracers.

The $\delta^{15}\text{N}$ is often used as a proxy of the trophic level because primary producers are expected to have similar $\delta^{15}\text{N}$ values, much lower than those of animals. Although this is true in some ecosystems and regions (e.g. Cardona et al., 2007), exceptions are common (e.g. Cardona et al., 2009; Drago et al., 2009). The present results reveal a high variability in $\delta^{15}\text{N}$ both among macrophyte species from the same region and also among regions within the eastern Mediterranean, with differences often larger than the average increase expected per trophic level (Minagawa and Wada, 1984; Caut et al., 2009). As a consequence, variability in the $\delta^{15}\text{N}$ across the carapace layers of individual turtles and among individual turtles may reflect not only changes in trophic level but also shifts among foraging grounds, although satellite tracking has revealed extended residence in small areas both for adult neritic females in the Mediterranean (Broderick et al., 2007) and young neritic green turtles shorter than 55 cm CCL elsewhere (Godley et al., 2003; Hart and Fujisaki, 2010). The $\delta^{15}\text{N}$ of some Mediterranean primary producers is known to change also seasonally (Vizzini and Mazzola, 2003), hence adding another possible confounding factor.

Fortunately, the $\delta^{13}\text{C}$ of macrophytes from the eastern Mediterranean varied consistently among species across regions and seagrasses were always more enriched in ^{13}C than pelagic species (loggerhead sea turtles and zooplanktophagous fish), which allowed us to interpret any enrichment in ^{13}C of the carapace scutes of green turtles as evidence of

an increased consumption of seagrasses or associated animal prey (Cardona et al., 2007).

Another consideration in the use of stable isotopes is that the fractionating factor may vary with age, feeding regime and species (Fantle et al., 1999; van der Klift and Ponsard 2003; Gaye-Siessegger et al., 2004). We had to use the fractionating factors reported for loggerhead sea turtles in an earlier stage of development (Reich et al., 2008) because there are no published data on the fractionating factors for the carapace scutes of green turtles (Seminoff et al., 2006). Published data on the fractionation factors for other tissues suggest that loggerhead sea turtles may have a larger fractionation factor for carbon and a lower fractionation factor for nitrogen than green turtles (Seminoff et al., 2006; Reich et al., 2008), although those differences might be because of differences in the size and developmental stage of the experimental animals and not because of species identity. Therefore, the outputs of the mixing models presented here should only be taken as an indication of the relative contributions of various food sources, although the results clearly demonstrate that only a few of the turtles that were larger than 60 cm CCLmin had isotopic signals consistent with a primarily herbivorous diet.

A third problem with the use of dead stranded animals is that illness and starvation prior to death may have impacted greatly the concentration of stable isotopes in the animals analysed (Hobson et al., 1993). However, only one out of 12 turtles whose death cause was known had not been incidentally caught by fishermen, thus suggesting that the isotopic signals of the animals analysed were good proxies of their actual diets.

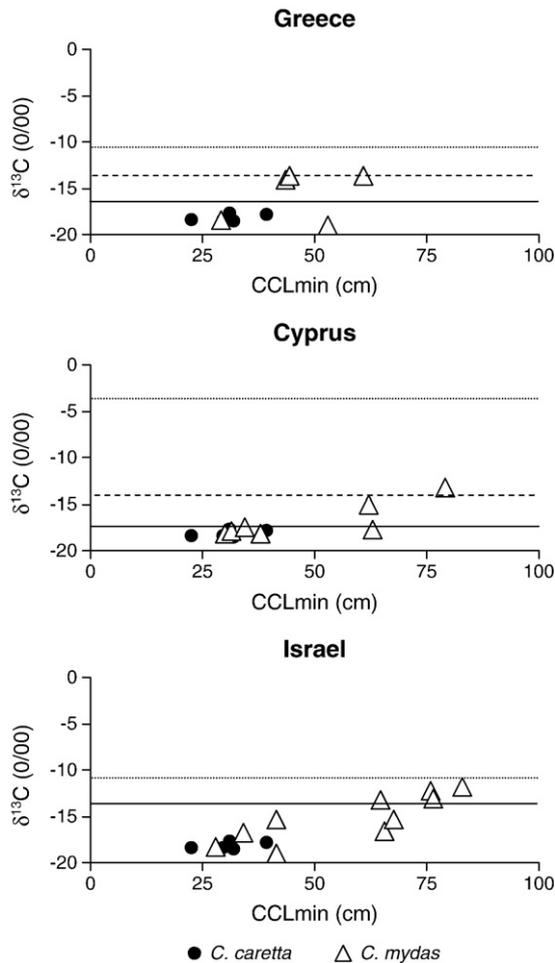


Fig. 2. Relationship between turtle size (CCLmin) and the $\delta^{13}\text{C}$ of the innermost carapace layer. Horizontal lines show the expected value of the $\delta^{13}\text{C}$ for an herbivore consuming only macroalgae (—), the seagrass *P. oceanica* (---) or the seagrass *C. nodosa* (.....), assuming a prey to predator fractionation of 1.77‰ for $\delta^{13}\text{C}$ (Reich et al. 2008).

Despite these limitations, we found that the ontogeny of the dietary shift of green turtles in the Mediterranean Sea, as recorded in the concentration of stable isotopes in carapace scutes, is intermediate between the fast change reported for the green turtles in the Greater Caribbean (Reich et al., 2007) and eastern Australia (Arthur et al., 2008) and the much slower and more complex process observed off northwestern Africa, where green turtles are best classified as omnivores rather than herbivores throughout most of their neritic juvenile lives and may resume an animal-based diet after grazing on seagrasses (Cardona et al., 2009). The evidence presented here reveals that most of the nutrients assimilated by green turtles that are shorter than 40 cm CCLmin in the Mediterranean Sea are not derived from seagrasses and that the contribution of seagrasses to the assimilated nutrients steadily increases as the turtles grow, but there is no sudden change in the concentration of stable isotopes following recruitment. Furthermore, only some green turtles, ranging from 60 to 83 cm CCLmin, might have a diet based primarily on seagrasses. The age-length relationship of green turtles in the Mediterranean Sea is unknown, but they reproduce for the first time when they are 75 cm CCLmin (Broderick et al., 2002). If the growth rate is similar to that reported for other areas (Zug and Glor 1999; Zug et al., 2001; Balazs and Chaloupka 2004; Chaloupka et al., 2004) this means that green turtles spend at least several years in this omnivorous stage.

Thus, the overall evidence indicates that green turtles in the Mediterranean Sea start grazing seagrasses as soon as recruitment

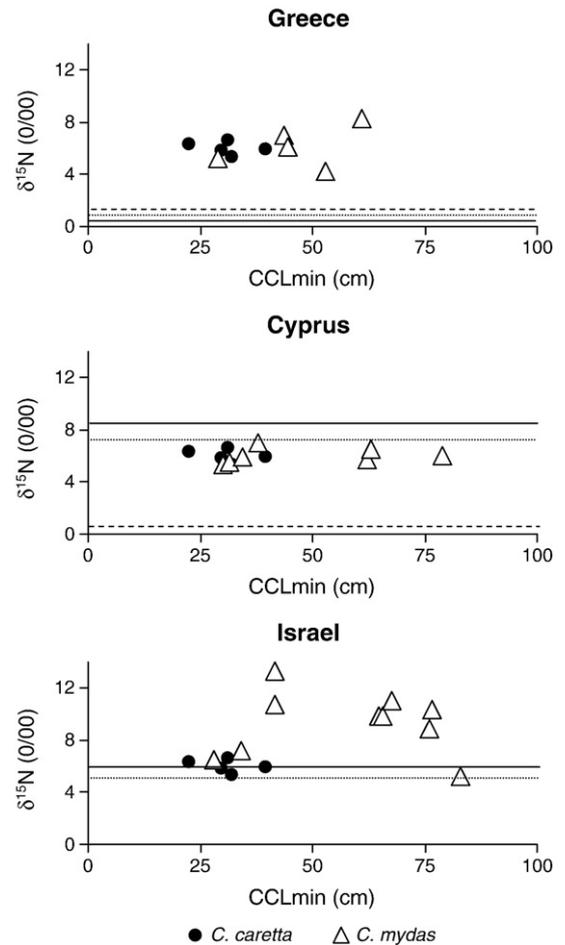


Fig. 3. Relationship between turtle size (CCLmin) and the $\delta^{15}\text{N}$ of the innermost carapace layer. Horizontal lines show the expected value of the $\delta^{15}\text{N}$ for an herbivore consuming only macroalgae (—), the seagrass *P. oceanica* (---) or the seagrass *C. nodosa* (.....), assuming a prey to predator fractionation of -0.64‰ for $\delta^{15}\text{N}$ (Reich et al. 2008).

occurs (Hays et al., 2002; Margaritoulis and Teneketzis, 2003; Teneketzis et al., 2006), yet they continue to derive most of their nutrients from animal prey until they are at least 60 cm CCLmin (Godley et al., 1998; this study). The infrequent occurrence of animal prey in the stomach contents of green turtles in the Mediterranean Sea (Demetropoulos and Hadjichristophorou, 1995; Hays et al., 2002; Teneketzis et al., 2006) indicates that animal prey is available only intermittently, but even in this situation animal prey may influence the isotopic values of green turtles. This is because animal tissues consist mainly of protein, whereas food derived from plants provides consumers with mainly carbohydrates and just a few proteins, and as a consequence, the isotopic values of omnivores will mostly reflect the ratio between animal and plant derived proteins in the diet and not the ratio between animal and plant derived biomass in the diet (Evans-White et al., 2001).

This is also true for green turtles, as the digestibility of animal material is much higher than that of plant material (Hadjichristophorou and Grove, 1983; Amorocho and Reina, 2007). Furthermore, the digestibility of plant materials in green turtles shorter than 60 cm CCLmin is positively correlated with temperature (Bjorndal, 1980) and hence is expected to be low for most of the year in regions that experience water temperatures lower than $20\text{ }^{\circ}\text{C}$ for several months annually. This is the case in most of the eastern Mediterranean Sea (Klein and Roether, 2004), Mauritania (Dedah, 1993) and southern Japan (Liu and Chai, 2009), where green turtles often do not exhibit the isotopic signal of a herbivore (Hatase et al., 2006; Cardona et al., 2009; this study). Conversely, where green turtles experience water

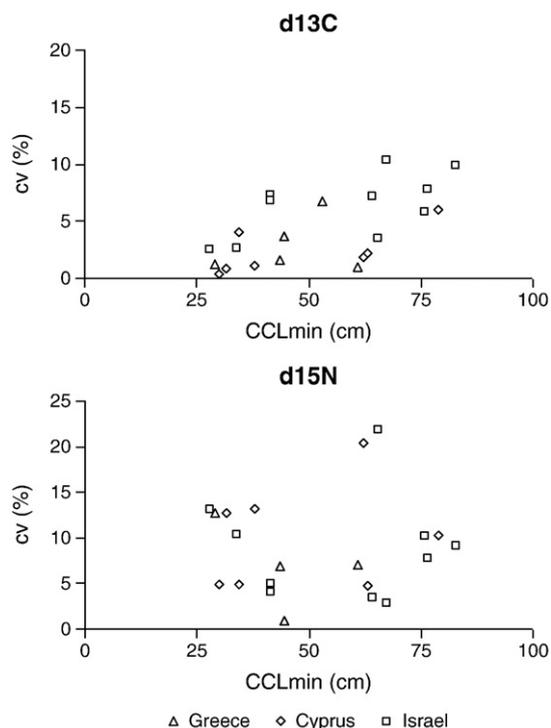


Fig. 4. Relationship between turtle size (CCLmin) and the variability of the concentration of stable isotopes across carapace layers, expressed as the coefficient of variability.

temperatures higher than 20 °C year round (Bjorndal, 1980; Brand et al., 1999), they exhibit the isotopic signal of a herbivore quickly after recruitment (Reich et al., 2007; Arthur et al., 2000). Another possible consequence of low winter temperatures is winter dormancy (Hochscheid et al., 2005), which will result in little feeding for several months. As a consequence the composition of the scutes probably reflects only warm season feeding and the annual growth rate of the scutes is probably lower than in tropical regions.

A final comment about the possible ecological role of green turtles in Mediterranean seagrass meadows is needed. The available evidence indicates that *C. nodosa* is the most important seagrass in the diet of green turtles in the Mediterranean Sea (Demetropoulos and Hadjichristophorou, 1995; Margaritoulis and Teneketzis, 2003; Teneketzis et al., 2006), although some studies have not identified the species of seagrasses found in the gut of these turtles (Hays et al., 2002), and subadult green turtles are also known to consume small amounts of *P. oceanica* (Demetropoulos, unpublished data). This preference for *C. nodosa* over *P. oceanica* is consistent with the higher nutritional value of the former species (Hemminga and Duarte, 2000) and the high concentration of phenolic compounds in the latter (Agostini et al., 1998). Habitat use data are consistent with a preference for *C. nodosa*, as green turtles foraging in the Mediterranean Sea spend most of their time at depths shallower than 10 m (Godley et al., 2002; Hays et al., 2002; Broderick et al., 2007) where *C. nodosa* prevails (Lipkin et al., 2003).

If this interpretation is correct, the meadows of *C. nodosa* are critical habitats for the conservation of green turtles in the Mediterranean Sea. Conversely, the meadows of *P. oceanica* are a marginal habitat for the species and green turtles are unlikely to play any relevant role there, although further research is needed regarding the feeding habits of adult green turtles off Libya, where important foraging grounds exist (Godley et al., 2002; Broderick et al., 2007). Concern over seagrass conservation in the Mediterranean has focused primarily on *P. oceanica* because of its extremely slow resilience (Procaccini et al., 2003), but the largest beds of *C. nodosa* in the eastern Mediterranean are located in sheltered bays and are, therefore, highly vulnerable to pollution and harbour development

(Lipkin et al., 2003). These meadows should be protected if the extinction of green turtles in the Mediterranean Sea is to be avoided. [SS]

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