



A global review of green turtle diet: sea surface temperature as a potential driver of omnivory levels

Nicole Esteban¹ · Jeanne A. Mortimer^{2,3} · Holly J. Stokes¹ · Jacques-Olivier Laloë⁴ · Richard K. F. Unsworth¹ · Graeme C. Hays⁴

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Abstract

To better understand dietary requirements, trophic shifts, and trophic interactions of the threatened green turtle (*Chelonia mydas*), we conducted a comprehensive global review and literature tabulation (177 studies) reporting diets of individuals > 25 cm carapace length. We analysed those studies involving natural sites and healthy animals that reported relative proportions of all diet components (67 studies, 89 datasets at 75 sites, 13 geographic sub-regions, 3 oceans). We compared diets by sub-region and foraging site relative to four diet components, i.e., seagrass, macroalgae, terrestrial plants (including mangroves) and animal matter. To assess sea surface temperature (SST) as an environmental driver, values were extracted from satellite data (single year) and site-specific observations (study durations) and examined relative to diet composition. Satellite data indicated that at warmer sites with temperatures > 25 °C (≥ 6 months annually), diet was predominantly herbivorous (mean = 92.97%; SE = 9.85; $n = 69$ datasets). At higher latitude sites and in cold-water currents with SST < 20 °C (≥ 6 months annually), dietary animal matter featured prominently (mean = 51.47%; SE = 4.84; $n = 20$ datasets). Site-specific observations indicated that SST had a small but significant effect on contributions of animal matter ($r^2 = 0.17$, $P = < 0.001$) and seagrass ($r^2 = 0.24$, $P = < 0.001$) but not macroalgae and terrestrial plants. Our study presents the first quantitative evidence at a global scale that temperature may be an important driver of omnivory, providing a new perspective on variations in green turtle diet, especially in light of global warming and climate change.

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✉ Nicole Esteban
n.esteban@swansea.ac.uk

¹ Department of Biosciences, Swansea University, Swansea, Wales SA2 8PP, UK

² Department of Biology, University of Florida, Gainesville, FL 32611, USA

³ P.O. Box 1443, Victoria, Mahé, Republic of Seychelles

⁴ Centre for Integrative Ecology, Deakin University, Geelong, VIC, Australia

Introduction

Dietary studies are vital to understanding the ecological role of organisms and their trophic interactions (Duffy et al. 2007), which for large marine vertebrates are often not well understood (Matich et al. 2011). Moreover, a better understanding of dietary requirements may help resource managers respond to shifts in trophic interactions between taxa (Brodeur et al. 2017) and, for sea turtles, more effectively prioritize conservation zones and policies for foraging grounds (Hamann et al. 2010; Rees et al. 2016).

Due to numerous anthropogenic threats and population declines, the green turtle (*Chelonia mydas*) was previously listed as globally Endangered on the IUCN Red List (Seminoff 2004). Successful conservation strategies, such as protection of nesting turtles and nesting and foraging habitats, have led to long-term population recovery at many sites (Chaloupka et al. 2008; Mazaris et al. 2017; Silva et al. 2017; Mortimer et al. 2020), resulting in IUCN downlisting of various green turtle subpopulations (e.g., Broderick and Patricio 2019). While sea turtles are particularly vulnerable

at their breeding grounds which are easily accessible to humans, they spend most of their lives at their foraging grounds (Hays et al. 2014). Green turtles can migrate vast distances across international borders between breeding and feeding grounds (Hays and Hawkes 2018; Hays et al. 2020) and maintain tight fidelity to their foraging grounds over successive migrations (Shimada et al. 2020). These complex life history strategies highlight the need to improve understanding of green turtle foraging behaviour in different regions and habitats (Klein et al. 2017).

Turtle diet composition can be assessed by a variety of techniques (Jones and Seminoff 2013). Traditional methods include direct observation using snorkel or SCUBA (Reisser et al. 2013), the analysis of gut contents from dead turtles (Mortimer 1981) and oesophageal lavage and faecal examination (Seminoff et al. 2002), while indirect biochemical approaches include stable isotope analysis (SIA) (Pearson et al. 2017). Modern technologies, such as remote videography (Letessier et al. 2014), animal-borne cameras (Heithaus et al. 2002), autonomous underwater vehicles (Dodge et al. 2018) as well as satellite tracking from nesting beach and subsequent in situ validation of diet at foraging locations (Esteban et al. 2018), have also been used to document the activities of turtles at their foraging habitats.

The green turtle has been associated with seagrass meadows beginning with early observations in the Indian Ocean (Frazier 1971; Hirth et al. 1973) and long-term studies in the Caribbean (e.g., Bjorndal 1980; Mortimer 1981; Vander Zanden et al. 2013) that reported a herbivorous diet dominated by seagrasses. This seagrass diet is thought to have the wider functional role of supporting seagrass ecosystem resilience (Christianen et al. 2019). Post-hatchling green turtles are believed to spend their first 3–10 years, depending on the ocean basin (Reich et al. 2007; Arthur et al. 2008), in open ocean pelagic habitat and then typically recruit to neritic habitats where their diets tend to shift from omnivorous to primarily herbivorous (see Jones and Seminoff 2013; Howell et al. 2016; Vélez-Rubio et al. 2016; Burgett et al. 2018). Recruitment size (based on curved carapace length (CCL)) varies across populations from 20–25 cm in the western Atlantic (Bjorndal and Bolten 1988) to 30–35 cm in the Indo-Pacific (Limpus et al. 1994) and 30–45 cm in the southwestern Pacific (Arthur et al. 2008) and north central Pacific (Parker et al. 2011).

Seagrasses dominate the diet of green turtles at a range of sites across the Mediterranean (Margaritoulis and Teneketzis 2003; Cardona et al. 2010; Karaa et al. 2012), Indian Ocean (Hasbún et al. 2000; Whiting et al. 2007; Stokes et al. 2019) and Pacific Ocean (Limpus and Reed 1985; Arthur et al. 2009; Prior et al. 2016). At foraging sites where seagrass is absent or sparse, green turtle diet is supplemented or dominated by macroalgae, for example, in Japan (Shimada et al. 2014), Queensland, Australia (Garnett et al. 1985; Prior

et al. 2016), Cocos-Keeling Islands (Whiting et al. 2014), Mexico (López-Mendilaharsu et al. 2005), Turkey (Özdilek et al. 2015), and Uruguay (Darré Castell et al. 2005). Terrestrial plant material, especially mangrove leaves and propagules, can also feature prominently in green turtle diets at some sites (Arthur et al. 2009; Nagaoka et al. 2012). Although green turtles are primarily herbivorous, reports of a wide ranging diet of seagrass, marine algae and invertebrates (Jones and Seminoff 2013) include purposely ingested animal matter, such as gelatinous macrozooplankton (e.g., scyphozoan jellyfish and salps), sponges, molluscs and fish (Mortimer 1981; Bjorndal 1997; Burkholder et al. 2011; Fukuoka et al. 2019; Piovano et al. 2020).

Studies in the eastern Pacific (Etnoyer et al. 2006), the Mediterranean (Cardona et al. 2010) and in the southwestern Atlantic (Santos et al. 2015) have suggested a relationship between green turtle omnivory levels and sea surface temperature (SST). Nevertheless, regional variations in diet, and the possible role of SST as a driver of these variations have not been examined at a global scale. Here, we investigate the diet of green turtles greater than 25 cm CCL (i.e. beyond the presumed 3–10 year-long post-hatchling pelagic stage) in various parts of the world. Specifically, we (1) reviewed literature to assess variation and patterns in the diets of immature and adult green turtles from foraging sites around the globe; (2) analysed the relationship between SST and diet globally to assess SST as a potential driver of omnivory; and (3) examined other possible drivers of green turtle diet that we encountered in the literature. The results of our study will provide a better understanding of diet variation across oceans and help guide green turtle conservation management especially in the context of global warming.

Materials and methods

Global review of green turtle diet

We conducted a literature search in April 2020 for papers of ‘All document types’ and ‘All languages’ on Web of Science using the search terms: ALL=(green turtle* OR *Chelonia mydas*) AND ALL=(diet* OR forag*) and Google Scholar using the search terms: TOPIC(‘green turtle*’ OR ‘*Chelonia mydas*’) AND (‘diet*’ OR ‘forag*’). Literature citations in the most recent and comprehensive articles located were then checked for studies of green turtle diet; in many cases, these involved grey literature that might have been missed by Web of Science or Google Scholar searches. We worked our way back through historical literature in this manner until no more studies reporting diet could be found.

To produce our global review of green turtle diet, we excluded studies of green turtles with carapace length < 25 cm CCL (e.g., Boyle and Limpus 2008) on the

assumption that they represented the 3–10-year-old post-hatchling pelagic life stage. We also excluded diet studies if they did not report the relative proportion of all dietary components (e.g. Russell and Balazs 2009) or were from a large-scale pelagic fishery with unknown foraging location (e.g., Parker et al. 2011; Wedemeyer-Strombel et al. 2015). Studies of turtles that were diseased or stranded were excluded due to potential bias in diet as were those of unknown foraging location (e.g., Riosmena-Rodriguez et al. 2011; Souza 2019). We excluded diet studies of captive or artificially fed turtles (e.g., Monzón-Argüello et al. 2018), along with data describing the diets of gravid female green turtles which can differ significantly from those of males, non-breeding females and immature turtles even at shared foraging habitat (Stokes et al. 2019). Where multiple studies from the same site utilised the same dataset, the most detailed study was included (e.g., Arthur et al. 2009; not Arthur et al. 2006). Excluded studies were compiled and reasons for their exclusion provided (Online Resource 1 Table S2).

Where there was no significant difference in diet between multiple sites in one study, data were presented for a centrally located site (e.g., Arthur and Balazs 2008; Stokes et al. 2019). Many of the studies we reviewed did not distinguish size classes, and did not report diet data for immature and adult individuals separately, especially when both occurred together at a benthic foraging site (e.g., Forbes 1996; Read and Limpus 2002; Prior et al. 2016). We, therefore, pooled our findings on the diet for both immature (> 25 cm CCL) and adult breeding turtles.

In our global review, we recorded the methodologies employed by each study, i.e., gut content analysis, oesophageal lavage, SIA, etc., and tabulated the proportions of individual diet items encountered. We converted results from animal-borne camera studies to diet proportion by dividing the number of bites or feeding events for a diet item (e.g. seagrass) by the total number of bites or feeding events for all diet items. We assigned each type of diet item to one of six categories. The four key nutritional categories were: seagrass, macroalgae, terrestrial plants (e.g., fruits and leaves of mangroves *Avicennia marina*, *A. schaueriana*, *A. germinans*, *Rhizophora mangle* and saltmarsh *Spartina alterniflora*; leaves of *Ficus* spp, *Hibiscus* spp, *Ochroma* spp), and animal matter. The fifth and sixth categories were anthropogenic debris (e.g., plastic fibre) and ‘other’. The category ‘other’ was not always defined in studies but, where defined, included substrate (sand, shell, stone), very digested material, unidentifiable material and natural debris (e.g., bird feathers, wood fragments, etc.). We overlaid green turtle diet composition as defined by the six categories onto a world map shapefile (Made with Natural Earth) using QGIS v3.0, including the available global seagrass distribution (UNEP-WCMC and Short 2018) for reference.

We organized the global diet studies into geographic sub-regions (Online Resource 1 Tables S1–2) based on maps produced by Wallace et al. (2010) to define the global distribution of regional management units (RMUs) of green turtles. An RMU comprises a breeding unit of turtles above the level of the nesting populations but below the level of species within a sub-region, and the RMU maps roughly indicate the distribution of animals belonging to an RMU breeding unit. For our purposes, the geographic boundaries defined by these RMU maps (excluding some areas of overlap) provided objective criteria with which to organize and then compare global studies of turtle diet by sub-region, including all diet data collected for both adults and immature turtles within each sub-region. Our 13 sub-regions corresponded with the following 13 map-defined RMUs (Wallace et al. 2010): Pacific North Central, Pacific East, Atlantic North West, Atlantic South West, Atlantic East, Mediterranean, Indian South West, Indian North West, Indian North East, Indian South East, Pacific South West, Pacific South Central, and Pacific North West. Figure 1a provides a map of the 13 sub-regions and their abbreviations.

Relationship between green turtle diet and SST

We assessed the relationship between green turtle diet and SST at two spatial resolutions. First, we used a global scale satellite-sourced SST dataset to present a visual overview. We then used in situ surface observations of SST from the International Comprehensive Ocean–Atmosphere Data Set (ICOADS) to obtain higher-resolution coastal SST data for each foraging site for fine-scale analysis.

Global SST overview

To produce a visual global overlay map of SST at each of the study sites included in this study, global day–night monthly SST averages, during a single year, derived from the AVHRR Pathfinder (Version 5, 4 km) SST cloud screened dataset (Phillips et al. 2012) were downloaded and projected on ArcMap version 10.5.1. Although accuracy and precision of satellite-sourced SST at the coastline is lower than SST measurements made in situ (Brewin et al. 2018), this dataset was used for the global overview as it provides the longest, accurate and highest-resolution SST climate data record for analysis of global SST (NCAR 2014). The dataset was not available for the entire time series. We selected the year 1993 for two reasons: it represents the midpoint of the sampling period for the diet studies (1971–2016); and it lacked El Niño and La Niña events (NOAA 2020). Quarterly periods (Jan–Mar, Apr–Jun, Jul–Sep, Oct–Dec) were selected to represent seasonal variation in temperature at different sites.

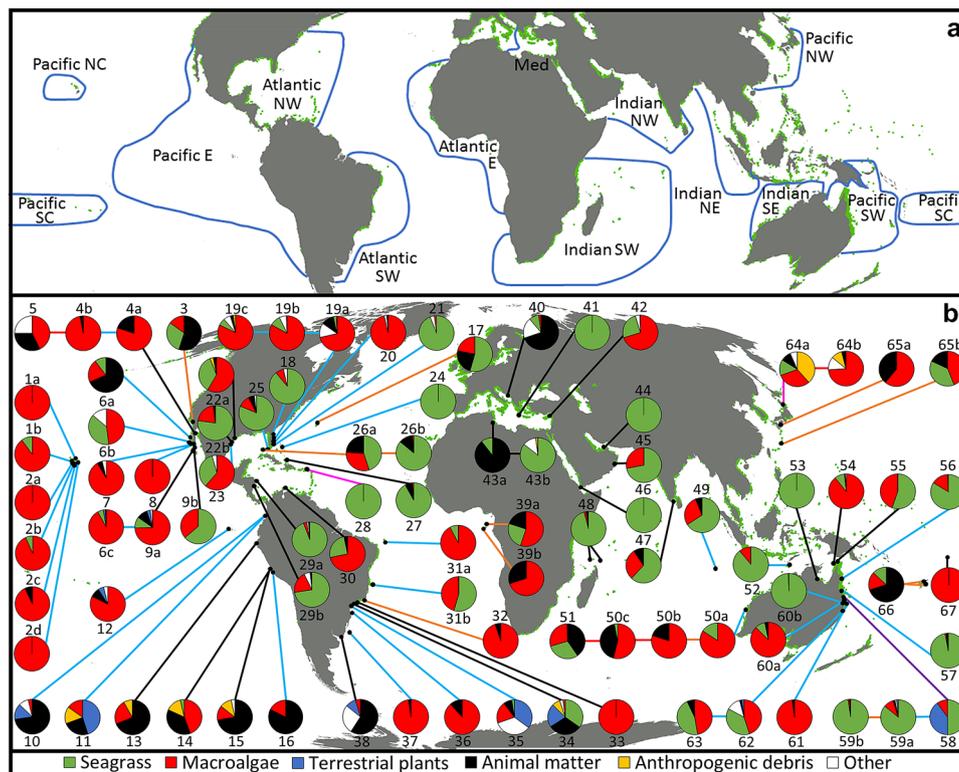


Fig. 1 Comparison of green turtle diet composition across the globe. **a** 13 geographic sub-regions, based on maps of the *Chelonia mydas* RMUs (adapted from Wallace et al. 2010), were used to compare diet composition. Moving from west to east these include: Pacific North Central (Pacific NC), Pacific East (Pacific E), Atlantic North West (Atlantic NW), Atlantic South West (Atlantic SW), Atlantic East (Atlantic E), Mediterranean (Med), Indian South West (Indian SW), Indian North West (Indian NW), Indian North East (Indian NE), Indian South East (Indian SE), Pacific South West (Pacific SW), Pacific North West (Pacific NW), Pacific South Central (Pacific SC). **b** The proportions of contribution made by each of six categories of diet items recorded in 89 datasets at 75 sites are shown by segments of the pie charts. The term ‘Other’ is not always defined and includes

substrate, very digested material, and natural debris (e.g., feathers). Methods used to study diet are represented by coloured lines—i.e., gut content analysis (black), oesophageal lavage (blue), SIA (orange), mouth content (purple), faecal examination (pink) and animal-borne camera (red) studies. Green dots indicate known seagrass observation data points (Source: UNEP-WCMC and Short, 2018, see Online Resource 1 Fig. S1–S4 for fine-scale maps). Numbers indicate source literature (see Online Resource 1 Table S1 for study site, analytical method, diet group and results), and break-down by sub-region as follows: Pacific NC (1–2), Pacific E (3–16), Atlantic NW (17–30), Atlantic SW (31–38), Atlantic E (39), Med (40–43), Indian NW (44–47), Indian SW (48), Indian NE (49), Indian SE (50–52), Pacific SW (53–63), Pacific NW (64–65), and Pacific SC (66–67)

Foraging site SST

We extracted in situ observations of SST data for the 1° by 1° pixel around each foraging site from ICOADS (NCAR 2015). We obtained data from the Enhanced ICOADS Monthly Summary Release 3.0 at the 1-degree spatial resolution for the 12 months, from January to December that coincided with the sampling period of each respective study, e.g., if sampling took place in 2005 and 2006, then SST data were included from January 2005 through December 2006. There are fewer sites included in the analysis of SST at foraging sites than in the global SST overview. This is because we avoided potential bias due to under-sampling by excluding those seven datasets with < 10 SST observations per month. Some of these datasets were for the same site and three sites were excluded from further analysis because

SST data were unavailable, i.e., South Caribbean Nicaragua, Torres Strait Australia, and Tokelau. Multiple diet composition datasets existed across several sampling periods at some sites, e.g., Bahia de los Angeles, Mexico and Shark Bay, Australia, and are included in the analysis. We calculated the mean annual SST, the maximum annual SST and the minimum annual SST for each site.

Data analysis

The average contribution of each of the six major dietary components of green turtle diet (seagrass, macroalgae, terrestrial plants, animal matter, other, and anthropogenic debris) was compared using a Kruskal–Wallis rank-sum test. To compare diet across sub-regions, a Dunn’s (1964) test was used to calculate multiple comparison *p*-values

adjusted with the Benjamini and Hochberg (1995) method. For the foraging site SST analysis, dietary component data were arcsine-square-root-transformed. Linear regression was used to explore the relationship between diet content data and SST at foraging sites. Figures are presented showing untransformed (Figs. 1–3) or back-transformed data (Fig. 4; Online Resource Fig. S5) for ease of interpretation. Statistical analyses were performed using R (R Core Team 2017). Mean \pm SE values are presented unless otherwise indicated. The significance level of all statistical tests was set at $\alpha < 0.05$.

Results

Global review of green turtle diet

Of the 177 articles examined, 67 articles with 89 datasets describing diet composition of green turtles at 75 sites around the world met the criteria for inclusion in our review (Fig. 1; Online Resource Table S1). An additional 110 diet studies were excluded from further analysis for the following reasons: unspecified diet composition ($n=40$) or foraging location ($n=7$); sampling of stranded dead/diseased individuals ($n=28$), captive turtles with artificially fed diet ($n=11$), or nesting females ($n=3$); focus on ingestion of anthropogenic debris ($n=17$); turtles below minimum carapace size ($n=2$); or duplicate dataset ($n=2$). See Online Resource 1 Table S2 for study details and exclusion reasons.

The datasets in studies that met our criteria spanned 13 sub-regions in 3 oceans and 1 sea: Pacific N Central (Hawaii) ($n=6$), Pacific E (off North, Central and South America) ($n=18$), Atlantic NW (off North and Central America, including Caribbean) ($n=19$), Atlantic SW (off South America) ($n=9$), Atlantic E (São Tomé Island) ($n=2$), Mediterranean ($n=5$), Indian NW (Arabian Peninsula and India) ($n=4$), Indian SW (Seychelles) ($n=1$), Indian NE (Cocos-Keeling) ($n=1$), Indian SE (Western Australia) ($n=5$), Pacific SW (Eastern Australia) ($n=13$), Pacific NW (Japan) ($n=4$) and Pacific S Central (Fiji and Tokelau) ($n=2$). The relative prominence of the following four key nutritional categories was reported across sites and is considered in our analysis: seagrass, macroalgae, terrestrial plants, and animal matter. The amount of anthropogenic debris in the diet also varies between sites. Nevertheless, some patterns emerge (Figs. 1 and 2). An expanded version of Fig. 1 (Online Resource 1 Figs. S1–4) shows details of regional seagrass distribution as well as contribution of the six categories of diet items.

Seagrass dominant. Seagrass contribution to diet is greatest in the following sub-regions: Indian SW (mean = 95.0%; $n=1$; Stokes et al. 2019), Indian NW (mean = 83.3%; SE = 9.6; $n=4$; e.g., Hasbún et al. 2000),

Indian NE (mean = 65.1%; $n=1$; Whiting et al. 2014), Pacific SW (mean = 59.3%; SE = 10.4; $n=13$; e.g., Fuentes et al. 2006; Prior et al. 2016), Atlantic NW (mean = 57.5%; SE = 8.2; $n=19$; e.g., Mortimer 1981; Stringell et al. 2016) and Mediterranean (mean = 46.0%; SE = 19.4; $n=5$; e.g., Karaa et al. 2012). All studies that recorded no seagrass (or virtually none) in the diet are from regions with limited documented seagrass distribution (e.g., Pacific E and Atlantic SW) (Fig. 1; Online Resource 1 Figs. S1–S4).

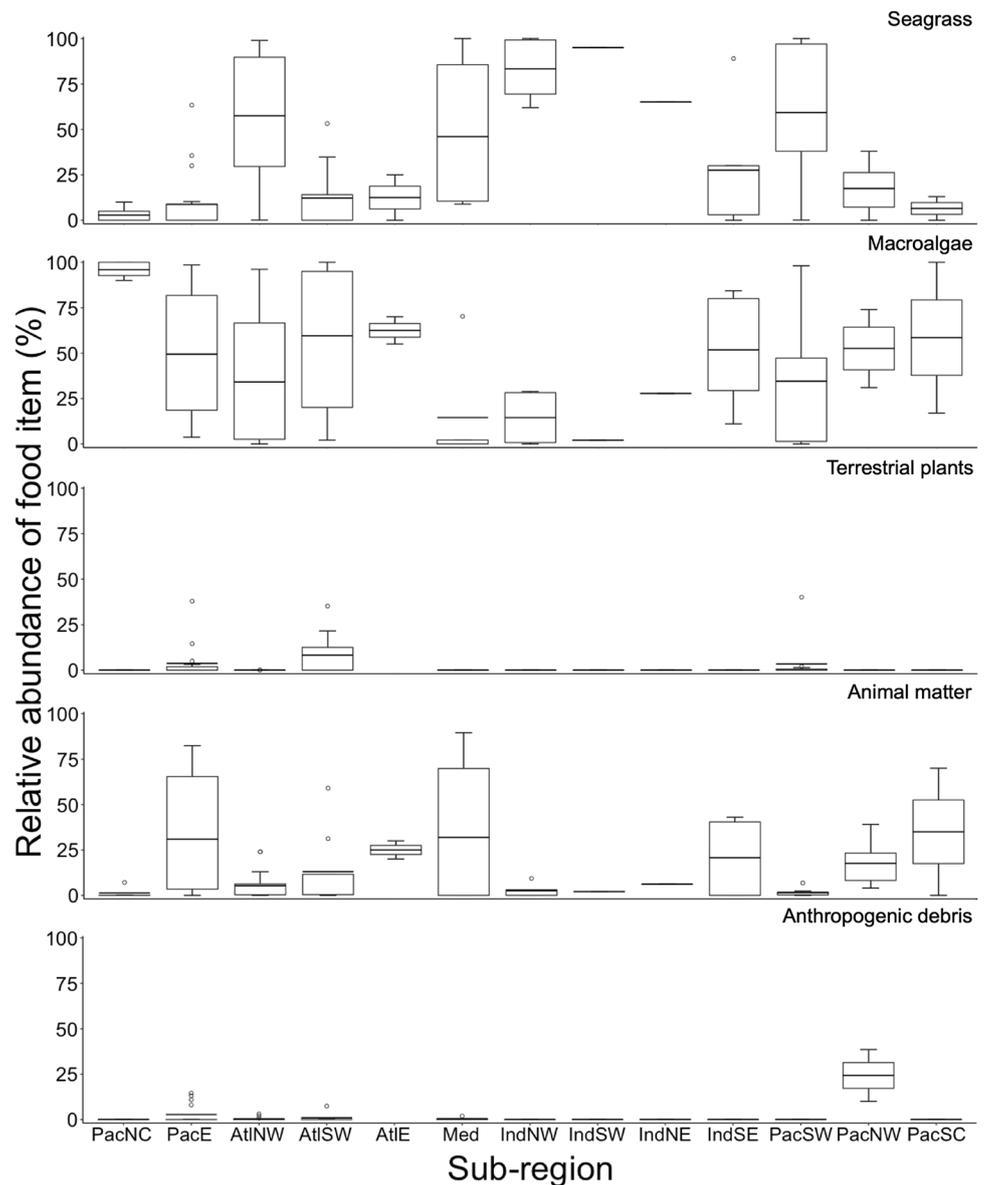
Macroalgae dominant. Macroalga is consumed most abundantly in the following sub-regions: Pacific N Central (mean = 96.0%; SE = 1.9; $n=6$; e.g., Arthur and Balazs 2008; Balazs et al. 1987), Atlantic E (mean = 62.5; SE = 7.5; $n=2$; e.g., Hancock et al. 2018), Atlantic SW (mean = 59.5%; SE = 13.9; $n=9$) especially tropical areas (e.g., Reisser et al. 2013), Pacific S Central (mean = 58.5; SE = 41.5; $n=2$; e.g., Piovano et al. 2020; Balazs 1983), Pacific NW (mean = 52.5%; SE = 9.4; $n=4$), Indian SE (mean = 51.7%; SE = 14.2; $n=5$; e.g., Shimada et al. 2014; Fukuoka et al. 2016), Pacific E (mean = 49.4%; SE = 7.7; $n=18$; e.g. Seminoff et al. 2002; Arthur and Balazs 2008; Carrión-Cortez et al. 2010; Quiñones et al. 2010), and Atlantic NW (mean = 34.1%, SE = 7.7; $n=19$) especially high in temperate areas (e.g., Holloway-Adkins and Hansiak 2017).

Seagrass and Macroalgae. Nearly equal proportions of both seagrass and macroalgae have been recorded in diets in the following sub-regions: Pacific E (López-Mendilaharsu et al. 2005), Atlantic NW in the Gulf of Mexico (Howell et al. 2016), Indian SE at Cocos (Keeling) islands (Whiting et al. 2014), and Pacific SW at Torres Strait (Andre et al. 2005).

Terrestrial plants. Terrestrial plant contribution is highest in the following sub-regions: Atlantic SW (mean = 8.3%; SE = 4.7; $n=9$) especially at estuarine sites, e.g., from 10% in Argentina (González Carman et al. 2014) to 35% in Brazil (Nagaoka et al. 2012); Pacific E (mean = 3.7%; SE = 2.3; $n=18$) especially at estuarine sites (e.g., 38% in Colombia, Sampson et al. 2018), and where mangrove fruits and leaves featured (e.g., 5% in the Galapagos Islands, Carrión-Cortez et al. 2010; 3.2% in Mexico, López-Mendilaharsu et al. 2005); and Pacific SW (mean = 3.5%; SE = 3.0; $n=13$) where mangrove cotyledons, leaves and fruit formed 40% of the diet in Shoalwater Bay, Queensland Australia (Limpus and Limpus 2000).

Animal matter. Animal matter featured to some degree in all sub-regions, especially the following: Pacific S Central pelagic sites (mean = 35%; SE = 35; $n=2$; e.g., Piovano et al. 2020); Pacific E neritic sites (mean = 30.9%; SE = 7.2; $n=18$; e.g., Amorocho and Reina 2007; Jiménez et al. 2017; Quiñones et al. 2010; Paredes 2015); Mediterranean neritic sites (mean = 31.9%; SE = 19.7; $n=5$; e.g., Lazar et al. 2010; Karaa et al. 2012); Indian SE neritic sites (mean = 20.7%;

Fig. 2 Comparison of the relative abundance of food items in green turtle diet across the globe: seagrass, macroalgae, terrestrial plants, animal matter and anthropogenic debris. The diet item percentages were collated from 89 datasets at 75 sites across 13 sub-regions for sea turtles (see Online Resource Table S1 for study site, analytical method, diet group results, source literature). Bold horizontal lines indicate mean, boxes delineate the upper and lower quartiles and whiskers define the data's range. Outliers are plotted as separate points



SE=9.3; $n=5$; e.g., Burkholder et al. 2011; Thomson et al. 2018); and at Atlantic E upwelling sites (mean = 25%; SE = 5; $n=2$; e.g., Hancock et al. 2018).

A comparison of the proportion of seagrass consumed by green turtles between sub-regions showed significant and major differences (Kruskal–Wallis test, $H_{12} = 45.17$, $p < 0.001$). Multiple comparisons showed a significant difference between green turtle diet recorded in the Atlantic NW and Atlantic SW ($p = 0.02$), Atlantic SW and Indian NW ($p = 0.03$), Atlantic NW and Pacific E ($p = 0.002$), Indian NW and Pacific E ($p = 0.008$), Atlantic NW and Pacific N Central ($p = 0.01$), Indian NW and Pacific N Central ($p = 0.01$), Atlantic SW and Pacific SW ($p = 0.02$), Pacific E and Pacific SW ($p = 0.002$), Pacific N Central and Pacific SW ($p = 0.01$). The amount of anthropogenic materials

present varied amongst sites but was most abundant in the Pacific Ocean (Pacific E and Pacific NW) (Fig. 1; Fig. 2; Online Resource 1 Table S1).

Relationship between green turtle diet and SST

Global SST overview

A global comparison of principal diet components (plant-dominated diet vs omnivorous diet) with seasonal SST provides an indication of the relative importance of SST on diet at different sites (Fig. 3). Our findings suggest that at cooler sites where SST is < 20 °C for ≥ 6 months each year, animal matter in the diet is always $> 20\%$ (range = 20.3–89.5%; mean = $51.48 \pm 4.84\%$; $n = 14$ sites; $n = 20$ datasets). These

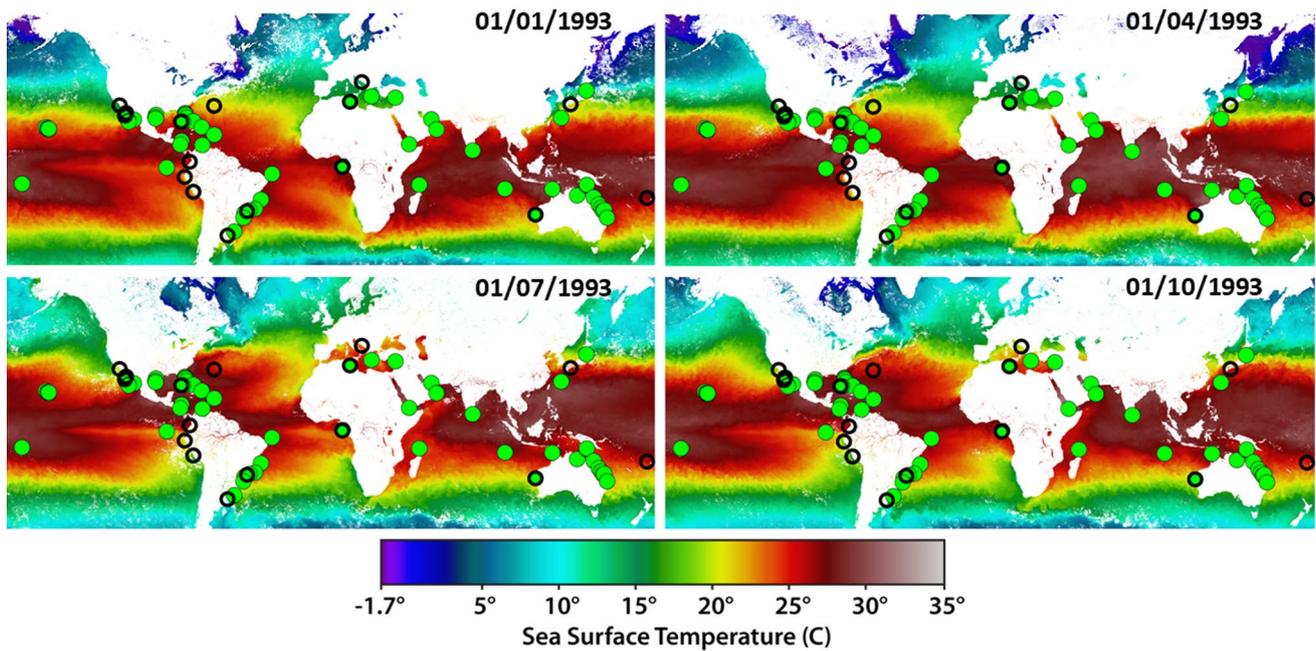
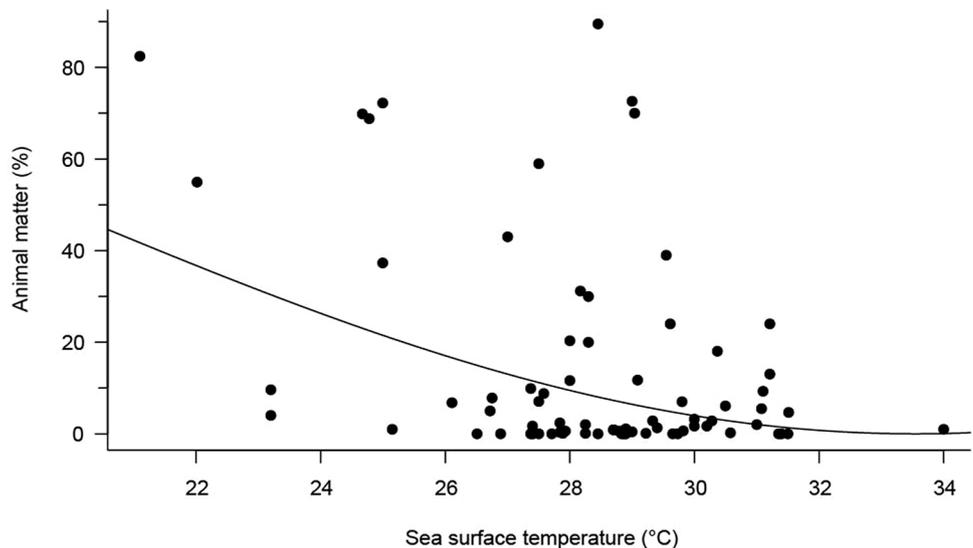


Fig. 3 The importance of plant or animal content in green turtle diet is related to sea surface temperature (SST). Generally, at higher latitudes and in cold-water currents where SST is <20 °C for at least two seasons, animal matter in the diet is >20% (black circles; mean=51.47%; SE=4.84; n=14 sites); whereas at warmer sites where SST >25 °C for at least two seasons, green turtle diet is

dominated by seagrass, macroalgae and mangroves (green circles; mean=92.97%; SE=9.85; n=57 sites). Both plant and animal matter are important components at a small number of sites (green circles outlined by black, n=4 sites). SST temperatures from the year 1993 are at the midpoint of the study time series (1971–2016; Online Resource Table S1). SST (AVHRR) data source: Phillips et al. 2012

Fig. 4 Sea surface temperature (SST) has a small effect on green turtle diet at foraging grounds: a lower proportion of animal matter is present in the diet of turtles at sites with higher SST ($r^2=0.16$, $t=-3.7$, $F_{1,72}=13.32$, $P<0.001$). SST is shown as maximum annual temperature recorded during the sampling year(s) of 82 datasets from 72 sites in the Atlantic, Indian and Pacific Oceans and Mediterranean Sea. SST (ICADS) data source: NCAR 2015



areas are at higher latitudes (e.g., California USA, Argentina and Croatia), close to cold-water currents or upwellings (e.g., Colombia and Peru) or in areas of overlapping climate zones (e.g., Brazil). Generally, at warmer sites where SST ≥25 °C for 9–12 months, green turtle diet is almost always ≤20% animal matter and is dominated by plant

matter (mean = 92.97 ± 1.19%; range = 45.5–100%; n = 57 sites; n = 69 datasets).

A few sites around the world are exceptions to the trend of decreasing animal matter with increasing SST. Contradicting diet preference (see Online Resource Table S1) existed at four sites, each in a different sub-region (Atlantic NW, Atlantic E, Mediterranean and Indian SE). These four sites

(i.e., Dry Tortugas Florida USA, São Tomé Island, Gulf of Gabes Tunisia, and Shark Bay Western Australia) are represented by green circles with a black outline (the green circle indicates a plant-dominated diet and black outline indicates > 20% animal matter) (Fig. 3). Among sites with high SST and expected plant-dominated diet, one notable exception, indicated by a black ring, is Fiji (Pacific S Central) where diet is dominated by 71% animal matter (Piovano et al. 2020). Two exceptions to an expected omnivorous diet at sites with low SST values are the Sanriku coast of Japan (Pacific NW) and Galapagos Ecuador (Pacific E), both indicated by green circles (Fig. 3).

Foraging site SST

Analysis of fine-scale SST data from 72 foraging sites shows a similar pattern to that provided by the global SST overview, with a small but significant ($p < 0.001$) relationship between SST and the proportion of animal matter in the diet ($n = 82$ datasets). The contribution of animal matter in the diet tended to increase at cooler temperatures (Fig. 4; Online Resource 1 Fig. S5) and the resulting relationship between the percent animal matter and maximum SST was small but significant ($r^2 = 0.16$, $t = -3.7$, $F_{1,72} = 13.32$, $p < 0.001$). Conversely, the contribution of seagrass to the diet tended to increase with warmer temperatures (Online Resource 1 Fig. S5). Maximum sea surface temperatures had a small but significant relationship to percent seagrass in the diet ($r^2 = 0.22$, $t = 4.5$, $F_{1,72} = 20.6$, $p < 0.001$). We also found a small effect of mean SST on percent animal matter and seagrass in the diet, and a small effect of minimum SST on percent seagrass in the diet ($p < 0.05$ in all cases; see Online Resource 1 Fig. S5). There was no effect of SST on contribution of either macroalgae or terrestrial plants (notably mangrove) to the diet (Online Resource 1 Fig. S5).

Discussion

Considerable variability in green turtle diet exists around the world, across oceans and within foraging grounds. Our review has captured much of the literature to tease apart spatial variation in green turtle diet and our analysis shows SST to be a driver of omnivory. At most foraging sites included in this study, as expected, green turtles were primarily herbivorous with three categories of plant material featuring in the diet: seagrass predominating at sites where it was abundant; macroalgae where seagrass is relatively sparse or absent; and terrestrial plant material (especially mangrove leaves and propagules, but also other terrestrial species) particularly in estuarine areas. Omnivory also featured at some sites.

Green turtle foraging strategies range from nearly total herbivory at some neritic sites (Stokes et al. 2019) to oceanic

omnivory (Turner Tomaszewicz et al. 2018), and at some sites a high degree of omnivory even after settling at neritic habitats through adulthood (Vélez-Rubio et al. 2016). Some green turtles may shuttle between neritic and oceanic environments, as in Fiji (Piovano et al. 2020). This is in contrast to the previously documented and often assumed one-way ontogenetic habitat transition (di Benedetto et al. 2017). Drivers of green turtle diet discussed in the literature include SST, characteristics of the gut biome, prey availability, size classes of turtles and impacts of anthropogenic activities.

SST as a driver of variation in green turtle diet

Our global overview and foraging site-specific analyses showed a relationship between warmer temperatures and a seagrass diet, and lower temperatures and a diet comprising large amounts of animal matter, especially macrozooplankton. We conclude that green turtle omnivory may be partly driven by water temperature, and we present the first quantitative evidence that temperature may be an important driver of diet in green turtles at a global scale, especially where the diet includes gelatinous macrozooplankton (in particular, jellyfish and salps). Gelatinous macrozooplankton featured most prominently at oceanic and extreme-latitude sites in the Pacific and Atlantic, ranging from 40% in the Pacific NW (Fukuoka et al. 2016); 30–73% in the oceanic Pacific NC (Parker et al. 2011; Wedemeyer-Strombel et al. 2015); 38–72% along the Pacific E coastline (Seminoff et al. 2006; Amorocho and Reina 2007; Quiñones et al. 2010; Lemons et al. 2011; Jiménez et al. 2017); and 40–59% in the Atlantic SW (Bugoni et al. 2003; González Carman et al. 2014). A feature shared by all these sites appears to be much cooler water temperatures (< 20 °C) during all or part of the year. Previous studies (e.g., Etnoyer et al. 2006; Cardona et al. 2010; Santos et al. 2015) have shown that green turtle omnivory levels are influenced by SST, but ours is the first study to quantify this relationship on a global scale and highlight differences in green turtle diets in different regions.

Two patterns of geographic distribution of a gelatinous macrozooplankton diet associated with cooler water temperatures are apparent. One appears to correlate with higher latitudes and cooler temperatures (e.g., Pacific E, Pacific SC, Pacific NW, southern Atlantic SW, northern Atlantic NW, and Shark Bay Australia in Indian SE). The second may be mediated by global patterns of the major warm and cold oceanic currents. Warm ocean currents tend to flow away from the equatorial region on the western side of ocean basins, and cold ocean currents flow towards the equator on the eastern side of ocean basins. It follows that cool currents may account for the patterns of high macrozooplankton consumption that appear to be associated with the California Current (off California and Baja California), the Peru Current (off Ecuador, Peru and Columbia), and the Benguela Current

(off Mauritania). Water temperature is known to affect the abundance and distribution of food resources in the oceans (O'Connor et al. 2007). At cooler sites, where estimated levels of carnivory are typically > 20%, there is high contribution of gelatinous macro-zooplankton. While latitudinal patterns of gelatinous plankton abundance are not well known, there is some evidence that their abundance may increase at higher latitudes. For example, the leatherback turtle (*Dermochelys coriacea*), which feeds almost exclusively on gelatinous plankton, breeds on tropical beaches but often migrates to forage at high latitudes (e.g. Fossette et al. 2014). A recent review of taxa feeding on gelatinous plankton, showed many examples of pelagic predators from higher latitudes (Hays et al. 2018), including coho salmon (*Oncorhynchus kisutch*), larval/juvenile sablefish (*Anoplopoma fimbria*) and Cassin's Auklet (*Ptychoramphus aleuticus*) in waters off Vancouver Island in the northern Pacific E (Mackas et al. 2007). While there was a significant relationship between SST and the percent of animal matter in the diet, there was still considerable variability in this relationship, suggesting that other factors, in addition to SST, likely also drive the diet at individual sites. Given that we found relatively few diet studies at sites with cooler temperatures (10–20 °C, e.g., Brazil), the role of SST may become clearer once more diet studies are conducted at such cooler sites.

Besides gelatinous plankton, there are other animal-based sources of diet that can be grazed from the benthos. For example, neritic habitats in Fiji (Pacific SC) support a green turtle diet dominated by herbivorous (e.g., sea urchin *Triploneustes gratilla*) and carnivorous (e.g., cone shell *Conus ebreus*) invertebrates as well as fish (Piovano et al. 2020). Larger turtles of post-recruitment size and sizes typical of the benthic habitat have been observed in oceanic habitats (Turner Tomaszewicz et al. 2018); and it is possible that turtles employ shifts in foraging behaviour during multiple transitions between the neritic and oceanic habitats of Fiji (Piovano et al. 2020).

Because we used SST data at a relatively coarse spatial scale, our study would not have identified variations or anomalies in water temperature at the level of the relatively small home ranges that foraging green turtles typically occupy (Christiansen et al. 2017). Likewise, the relationship between green turtle diet and mean SST value derived from the multi-decadal study period is unlikely to capture changes in SST values throughout that time period, nor shifts in green turtle diets on the scale reported by Bell et al. (2019). SST data at a finer spatial and temporal scale, particularly from the shallow nearshore habitats where green turtles typically forage, might shed further light on the role of SST in driving diet.

At some foraging sites, temperature does not always predict diet composition. In Japan, low SST values would predict an omnivorous diet, as it does at Shikoku, Japan, where

39% animal matter is reported in the diet (Shimada et al. 2014). But, at an even higher latitude with cooler temperatures on the Sanriku Coast of Japan, the diet comprised only 4–9.6% animal matter in similarly sized turtles (Fukuoka et al. 2016).

Although not the focus of our review, many other environmental effects and limits influence the distribution of food species, such as water depth, substrate type, water clarity, and abundance of other predators that feed on prey consumed by green turtles. Temperature is not always a good predictor of diet, but other variables, such as oceanographic features (Cox et al. 2018) and availability of food items, could be (e.g., Goldbogen et al. 2015). Improving our understanding of how food availability at foraging sites drives foraging behaviour remains a critical question (Hays et al. 2016).

Some other drivers of variation in green turtle diet

Our review suggests that, in addition to SST, other drivers may influence green turtle foraging strategies across and within regions. These drivers may include a combination of factors, such as gut microflora, the influence of habitat on spatial and seasonal prey availability, and the size class of turtles. Moreover, there may be synergism between drivers.

Gut microflora

The relationship between water temperature and diet composition may be driven to some extent by physiological factors. If the gut microflora that enables turtles to digest plant material does not function efficiently at lower temperatures, turtles may opt to feed on relatively more animal material (Amarocho and Reina 2007). In the literature, spatial variation in green turtle diet has often been explained by a combination of environment (e.g., food availability, different habitats) and characteristics of the gastrointestinal microbiome which are influenced by diet (Bjorndal 1997; Price et al. 2017). For example, seagrass *Thalassia testudinum* dominates the Caribbean benthos and is the dominant food item (e.g., Stringell et al. 2016); while in the Galapagos (Carrión-Cortez et al. 2010) and at Heron Reef Australia (Forbes 1996), the benthos is dominated by macroalgae which comprise most of the diet. Recent advances in knowledge indicate, however, that regardless of diet, the microbiome in green turtles contains the same bacterial phyla although bacterial community composition changes over time in response to diet (Ahasan et al. 2017; Campos et al. 2018; Bloodgood et al. 2020).

At Shark Bay, Australia, even though seagrass habitat dominates, green turtles primarily assimilate energy from macroalgae and gelatinous macrozooplankton. Various hypotheses were proposed by Burkholder et al. (2011) to

explain this anomaly including: that macroalgae and gelatinous macroplankton are more palatable than the dominant *Amphibolis antarctica* seagrass; that an individual's diet depends on its intestinal microflora causing a preference for either seagrass or algal dominated diets; or that a high risk of predation by sharks interferes with feeding behaviour. Certainly, Shark Bay appears to be an unusual site where green turtles are highly omnivorous and individuals specialise on varying combinations of seagrasses, macroalgae and invertebrates (Thomson et al. 2018).

Prey availability

We expect food availability will ultimately influence diet composition, with sea temperature providing a proximal influence on diet through its role on prey availability. Foraging strategy (commonly described by the Optimal Foraging Theory) predicts that individuals adjust their movements according to the spatial distribution of their prey so that a more productive environment should lead to more specialised diet (MacArthur and Pianka 1966). In this way, diet composition variation and distribution has been linked to availability of food (or prey) across marine taxa, including seabirds, marine mammals and reptiles (e.g., León and Bjørndal 2002; Pinaud et al. 2005; Hays et al. 2006; Womble and Sigler 2006).

A recent review of intraspecific variation in trophic ecology of sea turtles using SIA confirms the versatility in trophic ecology that has been suggested for green turtles (Figgenger et al. 2019), emphasising the cryptic and contrasting nature of diets in adult green turtle populations. Variations in upwelling processes in the Galapagos Islands (Pacific E), affect algal composition leading to higher diversity of red algae in diet at some sites (Carrión-Cortez et al. 2010). In Hawaii (Pacific NC), differences in the relative availability of seagrass and macroalgae are apparent over short distances. For example, green turtles consumed both seagrass and macroalgae at Kāne'ōhe Bay, O'ahu but only macroalgae at other sites amongst the six main islands of Hawaii (Arthur and Balazs 2008). At São Tomé island (Atlantic E), at two foraging sites (separated by 50 km), diet composition indicated distinct isotopic niches: a diet dominated by macroalgae and animal matter at one rocky reef site (with no seagrass) and a mixed diet of seagrass, macroalgae and animal matter at a site with seagrass (Hancock et al. 2018). Besides availability of diet components, it is also important to consider their energy value via nutritional composition (e.g., protein, fat content, Neutral Detergent Fibre (NDF) that affects digestibility). Nutrition analysis for diet of green turtles has been conducted at a number of sites (e.g. Bjørndal 1979; Sampson et al. 2018) but nutritional values are not available for many dietary components (e.g.,

Thalassodendron ciliatum Trevathan-Tackett et al. 2017), and this is an important area for future research.

We were unable to properly analyse the relationship between food availability and diet composition due to lack of detailed data about both sets of variables in individual studies. Nevertheless, all studies that recorded no seagrass in the diet, such as those in the Atlantic SW (Reisser et al. 2013; Darré Castell et al. 2005) and in the southern Pacific E (Carrión-Cortez et al. 2010; Jiménez et al. 2017), were from regions characterised by sparse to non-existent seagrass habitats (UNEP-WCMC & Short 2018). The global distribution layer for seagrass based on point data (UNEP-WCMC & Short 2018) is currently the most accurate dataset available, and although a recent study has estimated seagrass extent worldwide, the authors describe numerous weaknesses in the data (McKenzie et al. 2020) limiting its utility as a quantitative data source. This means the dataset offers no metrics with which to estimate seagrass availability as a driver of amount of seagrass in green turtle diet at a local level.

Size class of turtles

Size class may be expected to play a role in determining rates of omnivory. Studies across taxa demonstrate that individuals maximise growth rates from juvenile to maturity by selecting a high protein diet. This has been demonstrated for a variety of reptiles (e.g., Durtsche 2004; Bouchard and Bjørndal 2006; Wotherspoon and Burgin 2016) which may explain why animal matter is so important for post-hatching green turtles < 25 cm CCL (Hancock et al. 2018).

The timing and the size class at which the dietary shift between late pelagic stage and neritic recruitment varies across sub-regions. For example, green turtles in the Atlantic (Bjørndal and Bolten 1988) shift to a neritic life stage at a smaller size than those in the Indo-Pacific (Limpus et al. 1994). Stable isotope studies that sample inert tissues (e.g. bone growth layers) enable assessment of foraging history and determination of the timing of ontogenetic shift, e.g., at 20–25 cm CCL in the Atlantic SW (Bjørndal et al. 2000). This method has been used to show that timing varies across sub-regions in Atlantic SW, Pacific SW, and Mediterranean (see Reich et al. 2007; Arthur et al. 2008; Cardona et al. 2010; González Carman et al. 2012; Howell et al. 2016). In Uruguay (Atlantic SW), turtles shift from omnivory (gelatinous microzooplankton) to herbivory at approximately 45 cm CCL (Vélez-Rubio et al. 2016), but along the NW coast of Africa (Atlantic E) at about 59 cm CCL (Cardona et al. 2009). No clear ontogenetic dietary shift was reported at foraging sites in either the western Pacific, Pacific E, or Atlantic E as levels of omnivory were similar for both juveniles > 25 cm CCL and adults (Lemons et al. 2011; Shimada et al. 2014; Hancock et al. 2018).

Nevertheless, intra-population variation in diet composition also exists (Burgett et al. 2018).

Animal matter decreased in importance for larger size classes in the Gulf of Gabes (Mediterranean) (Karaa et al. 2012) and in the Dry Tortugas National Park, Florida (Atlantic NW) (Roche, 2016). At a few sites, larger size classes foraging in tropical seagrass meadows may exhibit high levels of omnivory. For example, at Fiji (Pacific SC), the diet of turtles measuring 43–89 cm CCL was 71% animal matter (40% invertebrates and 31% fishes) (Piovano et al. 2020).

Unfortunately, because many diet studies included in this review did not differentiate between size classes, we were unable to further explore size class as a driver of omnivory. We encourage future diet studies to incorporate size class into their analyses, as it may help clarify timing of the ontogenetic shift from a pelagic to a benthic life stage.

Anthropogenic impacts

Our review found that the highest levels of anthropogenic debris in the diets of green turtles were in the Pacific Ocean. In the Pacific E, at Sechura Bay, Peru (Jiménez et al. 2017) and in Gorgona Park, Colombia (Sampson et al. 2018), 8% and 13.1% of diet, respectively, comprised anthropogenic debris. In the Pacific NW, green turtles foraging along the Sanriku coast of Japan ingested a range of artificial debris, including hard and soft plastics, styrofoam, fishing line/rope and rubber (Fukuoka et al. 2016). Coastal habitat degradation associated with anthropogenic development, such as that at highly urbanised sites along the east coast of Brazil in the Atlantic SW, affects the diversity of food items and can contribute to low dietary diversity in green turtles (Santos et al. 2011). Furthermore, Santos et al. (2015) report high foraging plasticity amongst green turtles in estuaries that combine an estuarine diet with pelagic foraging, perhaps in response to habitat degradation.

Relative merits and constraints of diet analysis techniques

Our review describes diet composition based on studies that used a variety of analytical methods, each characterised by benefits and disadvantages. Besides less-invasive direct observation of foraging behaviour (e.g., Schofield et al. 2006), two relatively simple and low-cost traditional quantitative methods of gut content analysis provide specific information on the composition, occurrence and quantity of species consumed (Miller et al. 2010). The analysis of a dissected gut provides an unbiased record (Gama et al. 2016) of recently ingested food from the oesophagus (e.g., Stokes et al. 2019). Oesophageal lavage from live animals is more common but only provides an indicative record of food consumed due to relatively small sample sizes produced and

selective retention of larger items by oesophageal papillae (Reisser et al. 2013). SIA has developed in the past two decades as a powerful tool to complement these traditional methods of studying diet and trophic ecology (see review by Haywood et al. 2019). Analysis of the composition of stable isotopes ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) in tissues with different residence times provides historical evidence of diet and patterns of ontogenetic shift (Arthur et al. 2008; Cardona et al. 2009; Vander Zanden et al. 2013; Vélez-Rubio et al. 2018). For example, blood serum represents food consumed recently and epidermal tissue or scutes represent the diet consumed several months previously (Reich et al. 2008). In some cases, however, SIA may over-estimate the relative volume of animal matter in the diet because a higher proportion of animal-sourced $\delta^{15}\text{N}$ may be assimilated into the tissues compared with plant-sourced $\delta^{15}\text{N}$; or it may misrepresent relative contributions of different types of plant matter (Lemons et al. 2011; Bezerra et al. 2015). Remote videography can provide insights to diet composition; however, it is difficult to calculate the relative contribution to diet from video observations of bite counts without support from other techniques (Thomson et al. 2018).

The results of diet studies can be biased by the type of sampling used. Broadly, gut contents represent ingestion and SIA values measure assimilation. Bite counts/events from video footage may not provide an accurate measure of amounts ingested. Animal matter may be overestimated by SIA and video analysis. At Bahia de los Angeles, Mexico, depending on sampling technique, animal matter was found to comprise 3% (oesophageal lavage), 20% (gut content) and 32% (video) (Seminoff et al. 2002; 2006). Similarly, at Shark Bay, Australia, animal matter was measured at 0% (oesophageal lavage), 20% (SIA), and 40–43% (video) (Burkholder et al. 2011; Thomson et al. 2018). It would be interesting to conduct simultaneous studies using multiple methods at other sites to confirm whether such relative differences are consistent.

In contrast to traditional gut sampling, SIA analyses have teased apart some of the cryptic components of green turtle diet. In the Caribbean, Vander Zanden et al. (2013) reported that while green turtles in Costa Rica might appear to have a more omnivorous diet (due to presence of higher $\delta^{15}\text{N}$ values) than foraging aggregations in neighbouring Nicaragua, in fact, differences in stable isotope composition were attributable to regional variation in primary production and nutrient cycling rather than differences in patterns of prey consumption (Vander Zanden et al. 2013). Another limitation of SIA is that all prey items must be sampled within the same time frame that the sampled tissues are synthesised (Haywood et al. 2019). It follows that stable isotope studies that only sample potential prey items previously identified in gut or lavage samples taken at a foraging site risk excluding important prey items. For example, in Bermuda, samples

of seagrass, macroalgae and certain potential prey animals were analysed to determine stable isotope ratios (Burgett et al. 2018). But, because the diet studies had not identified mangroves in their lavage samples, stable isotopes of mangroves were not assessed even though it is possible that mangroves which occurred in the area actually featured in the diet. Sampson et al. (2018) reported they were unable to run the MixSIAR model for green turtles due to exclusion of key prey items that were not considered potential prey from previous lavage studies.

Climate change considerations

Our study concludes that SST has a small but significant effect on levels of omnivory, and so a warming climate is likely to modify the prey available to green turtles. There is some evidence that recent changes in forage availability are associated with changes in water temperature, particularly in shallow waters where summertime superheating can lead to major loss of temperature-sensitive seagrasses (Campbell et al. 2006). For example, a major die-off of colder-water seagrass species occurred in response to a marine heatwave that impacted the important green turtle foraging area in Shark Bay, Western Australia (Arias-Ortiz et al. 2018).

Future changes in local conditions (e.g. SST, sea level, salinity or water current regime) may modify ecosystem structure and biodiversity (Thomson and Heithaus 2014). An overall reduction in seagrass habitat globally has been predicted during the next decade due to a combination of anthropogenic threats (Unsworth et al. 2019). Climate change might alter patterns of oceanic currents, gyres and eddies (Toggweiler and Russell 2008) and thereby affect water temperature and the availability and distribution of sea turtle food resources. Moreover, habitats are rarely static through time and can undergo long-term natural cycles of loss and recovery (Rasheed and Unsworth 2011) influencing their capacity to support grazing turtles.

Our review indicates that green turtle diets are variable, and this flexibility may enable adaptation to changing resources after environmental perturbations, such as marine heatwaves (Arias-Ortiz et al. 2018). Turtles may adapt to seasonal changes in food availability by modifying their diets (González Carman et al. 2012). Green turtles can alter their foraging behaviour as evidenced by consumption of invasive seagrass species that spread into key foraging habitats (e.g., Becking et al. 2014; Whitman et al. 2019). Turtles might also expand their foraging home ranges, as they have with serial residency in Shark Bay, Western Australia (Thomson et al. 2018), or they may shuttle between foraging sites (Piovano et al. 2019) or even adapt to new foraging sites, as demonstrated by a loggerhead turtle that re-located to a new site after flooding and a tropical cyclone

destroyed > 1000 km² benthic habitat in its home range (Shimada et al. 2020).

Flexibility in green turtle diet is evident across regions. Temporary diet switching between seagrass and macroalgae has been recorded by individual green turtles (Fuentes et al. 2006) and longer-term diet shifts in response to invasive algae have been observed in turtle aggregations (Russell and Balazs 2015; Christianen et al. 2019). Likewise, green turtles have adapted their diet to changing environments through seasonal variation in diet (Piovano et al. 2020) and switching between reef and estuarine habitats (Machovsky-Capuska et al. 2020). At the extremes of their geographic distribution, the foraging plasticity of green turtles is demonstrated by an omnivorous diet and pelagic foraging (Santos et al. 2015). Green turtles are highly adaptive, but whether turtles will be able to sufficiently shift their diet in response to warming SST remains a concern for this threatened species. In conclusion, ours is the first study to document the full extent of variation in green turtle diet in different regions throughout the world, and to quantify this relationship on a global scale. We were also able to demonstrate a correlation between water temperature and diet composition, which has important implications in the face of climate change.

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Author contributions NE, JAM and GCH conceived the study. HJS, JAM and NE conducted the diet literature review, NE carried out the SST global analysis. JOL collated and analysed the SST dataset. NE, JAM and GCH led the writing of the manuscript with contributions from all authors.

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Data availability All diet data are presented in Online Resource 1 (Tables S1 and S2). Online data are acknowledged at appropriate points of the Methods and Reference sections.

Compliance with ethical standards

Conflicts of interest No conflicts of interest or competing interests to declare.

Code availability (software application or custom code) Not applicable.

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