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ORIGINAL PAPER

# Foraging ecology of green turtles (*Chelonia mydas*) in Peru: relationships with ontogeny and environmental variability

**Javier Quiñones**[1] · **Evelyn Paredes-Coral**[2] · **Jeffrey A. Seminoff**[3]

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## Abstract

Feeding strategies in sea turtles are among the most important aspects of their life history, influencing demographic parameters such as growth, age-at-maturity, and reproductive migrations. However, studying sea turtle diet is often challenging and knowledge about foraging ecology is lacking for most populations worldwide. We studied green turtles (*Chelonia mydas*) at two disparate sites in Peru: La Aguada (~ 14°S), an area with upwelling conditions, and Virrila Estuary (~ 5°S) with year-round warm conditions. We conducted (1) in-water capture to assess population size structure and (2) esophageal lavages to recover diet components from turtles at both sites. Diet composition and feeding strategy were evaluated using several analytical approaches, and environmental influence on diet was assessed in relation to the Peruvian Oscillation Index. Our results indicate substantially different life stages and diets at the two study sites. Green turtles at La Aguada were mostly juveniles consuming animal matter, whereas turtles at Virrila Estuary were mainly sub-adults with a diet dominated by vegetal matter. Our results suggest a life-history-based habitat use model for green turtles in the southeastern Pacific Ocean. We propose that juvenile green turtles initially recruit to more southern neritic habitats of Peru, feed on high-caloric animal matter, then as individuals grow, they transition northwards to feed on lower-caloric, but abundant, vegetal matter. Our data provide a framework for ontogenic-based developmental migrations by green turtles in this portion of the southeastern Pacific Ocean, helping policymakers on the need to implement management strategies.

**Keywords** *Chelonia mydas agassizii* · Black turtle · Trophic ecology · La Aguada · Virrila Estuary · Omnivorous diet

## Introduction

Feeding strategies in sea turtles are among the most important aspects of their life history, as nutrition strongly influences demographic parameters such as somatic growth, age-at-maturity, and the timing of reproductive migrations (Bjorndal 1997; Bolten 2003; Jones and Seminoff 2013). Moreover, diet preferences in sea turtles are a key factor for their conservation, because knowledge about the types and locations of their primary prey resources can pinpoint areas for habitat protection (Bjorndal 1999). However, studying sea turtle diet and nutrition is often challenging due to logistical constraints, and basic knowledge about foraging ecology is lacking for most populations worldwide.

The green turtle (*Chelonia mydas*) occurs in tropical and temperate habitats around the world and has been widely studied. Upon departing nesting beaches, post-hatchlings enter the oceanic zone where they remain for several or more years, while foraging on an array of invertebrates (Reich et al. 2007; Turner Tomaszewicz et al. 2018). As juveniles, green turtles recruit to neritic areas and establish residence in coastal foraging grounds, where some individuals may transition among disparate neritic habitats as they grow (Bolten 2003), yet this is not a general rule. For example, in temperate waters of the southwest Atlantic, juvenile green turtles are not strictly herbivores or neritic, as they may shift from coastal and estuarine waters during cold seasons to

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Javier Quiñones
javierantonioquinones@gmail.com;
jquinones@imarpe.gob.pe

[1] Oficina de Investigaciones en Depredadores Superiores, Instituto del Mar del Perú, Esq. Gamarra y Gral. Valle S/N, Chucuito, Callao, Peru

[2] Marine Biology Research Group, Ghent University, Campus Sterre S8 Krijgslaan 281, B-9000 Ghent, Belgium

[3] NOAA-Southwest Fisheries Science Center, 8901 La Jolla Shores Drive, La Jolla, CA 92037, USA

open waters in warmer seasons (Gonzalez-Carman et al. 2012). Historical paradigms suggest that green turtles in neritic habitats are obligate herbivores, consuming a diet dominated by seagrasses and/or marine algae. Indeed, early studies of green turtles in the Caribbean documented their near-exclusive reliance on turtlegrass (*Thalassia testudinum*; Bjorndal 1980), and many populations worldwide are known for their dependence on marine algae (Bjorndal 1997; Hirth 1997; Jones and Seminoff 2013). However, in recent years, it has become clear that green turtles' diets are much more diverse than previously described, and the species consumes large amounts of animal matter in several global regions (Amorocho and Reina 2007; Cardona et al. 2009; Esteban et al. 2020).

The dietary diversity of green turtles draws intrigue as to how and why individuals are largely herbivorous at some sites but omnivorous at others. The mechanisms driving this disparity may be related to a facultative response by green turtles to differing prey availabilities across sites (e.g., Santos et al. 2015; Gillis et al. 2018), to energetic changes relating to ontogeny (Werner Gilliam 1984; Bolten 2003), and/or to ontogenic changes in the gut microbiota (Morais et al. 2014). For example, the aforementioned preponderance of turtlegrass in Caribbean green turtle diet is not surprising considering this marine angiosperm's once ubiquitous distribution (Larkum et al. 2006). Diet may also be influenced by a turtle's physiological capacity to digest food in the context of local temperature regimes (Esteban et al. 2020). Considering that the digestive efficiency for seagrasses in green turtles declines with lower water temperature (Bjorndal 1980), seagrass and other vegetal prey may be expected to feature less prominently in the diets of green turtles living in cooler-water foraging areas (Santos et al. 2015). In addition, intrinsic factors such as lifestage-specific nutritional requirements may shape an individual's dietary patterns.

In the Eastern Pacific (EP), green turtles (also known locally as black turtles [*Chelonia mydas agassizii*]) inhabit shallow neritic waters from southern California USA (~ 32°N) to northern Chile (~ 27°S). Like elsewhere, EP green turtles show substantial variability in diet and trophic status at local and regional scales (Seminoff et al. 2021). Along the coast of Peru, green turtles at northern sites like Sechura Bay (~ 05°30'S) consume mostly red algae, squid eggs, and coastal fishes (Santillán 2008; Jiménez et al. 2017), whereas individuals farther south, near Pisco (~ 14°S), often target sea anemones and scyphozoan jellies (Paredes 2015; Quiñones et al. 2010). These differences likely owe to the dynamic oceanography and substantial spatiotemporal variability in physical and biological characteristics in this region (e.g., Fiedler 2002; Pennington et al. 2006). There are two well-defined biogeographic regions along the Peruvian coast: the Panamaic Province (Eastern Tropical Pacific), a warm-water pool influenced by the Ecuador-Peru Coastal Current, and the Peruvian Province (Southeast Pacific) a temperate marine environment shaped by the upwelling Humboldt Current (Spalding et al. 2007; Chaigneau et al. 2013). Bridging these two regions is a transitional zone with a northern limit at ~ 04°S that fluxes latitudinally due to influences of the El Niño Southern Oscillation (ENSO) (Vegas-Velez et al. 1980; Paredes et al. 1998; Sullivan et al. 1999). The presence of the two biogeographic provinces along the Peruvian coast, coupled with a distinct transitional zone, provides an ideal setting to examine physical and biological oceanographic influences on green turtle demography and trophic status. However, despite some knowledge about spatio-temporal differences in resource use, it is unclear how environmental variability and individual lifestage influence green turtle foraging ecology in these areas.

To explore these themes, we studied green turtle demography and diet at two coastal neritic foraging grounds in Peru, La Aguada (Paracas Bay) in the Peruvian Province and Virrila Estuary (Sechura Bay) in the transitional zone, separated by 1200 km. We used in-water capture, body measurements, esophageal lavage, and a variety of analytical approaches to: (1) define the lifestages and demographic structure at these sites, (2) characterize diet (and diet variability) among green turtles at both locations, and (3) examine changes in diet at seasonal and annual scales in relation to environmental conditions. Also, we propose a life-history-based habitat use model for green turtles in the southeastern Pacific Ocean. These data will serve as a baseline with which to compare the results of future green turtle diet studies, and will add greater understanding about the extrinsic factors that influence green turtle diet.

## Methods

### Study areas

We studied green turtles at La Aguada (13°50' S; 76°15' W) from 2010 to 2017, and at Virrila Estuary (05°50' S; 80°50' W) from 2012 to 2018. La Aguada (Fig. 1), is a small inlet (maximum 8-m depth) located in southeastern Paracas Bay along the central-southern coast of Peru ca. 230 km south of Lima. The area is dominated by cold coastal waters of the Humboldt Current System (mean SST = 19 °C, range = 15.1–24.3 °C) yet is one of the main green turtle feeding grounds in southern portions of the EP (Marquez 1990), hereafter referred to as the southeast Pacific. La Aguada is mostly sandy-bottomed and dominated by the invasive alga *Caulerpa filiformis* (Environmental Research Management, 2013), with lesser amounts of native green (*Ulva* sp., *Enteromorpha* sp.) and red algae (*Chondracanthus* sp.) (Gil-Kodaka et al. 2002). During the austral Spring,

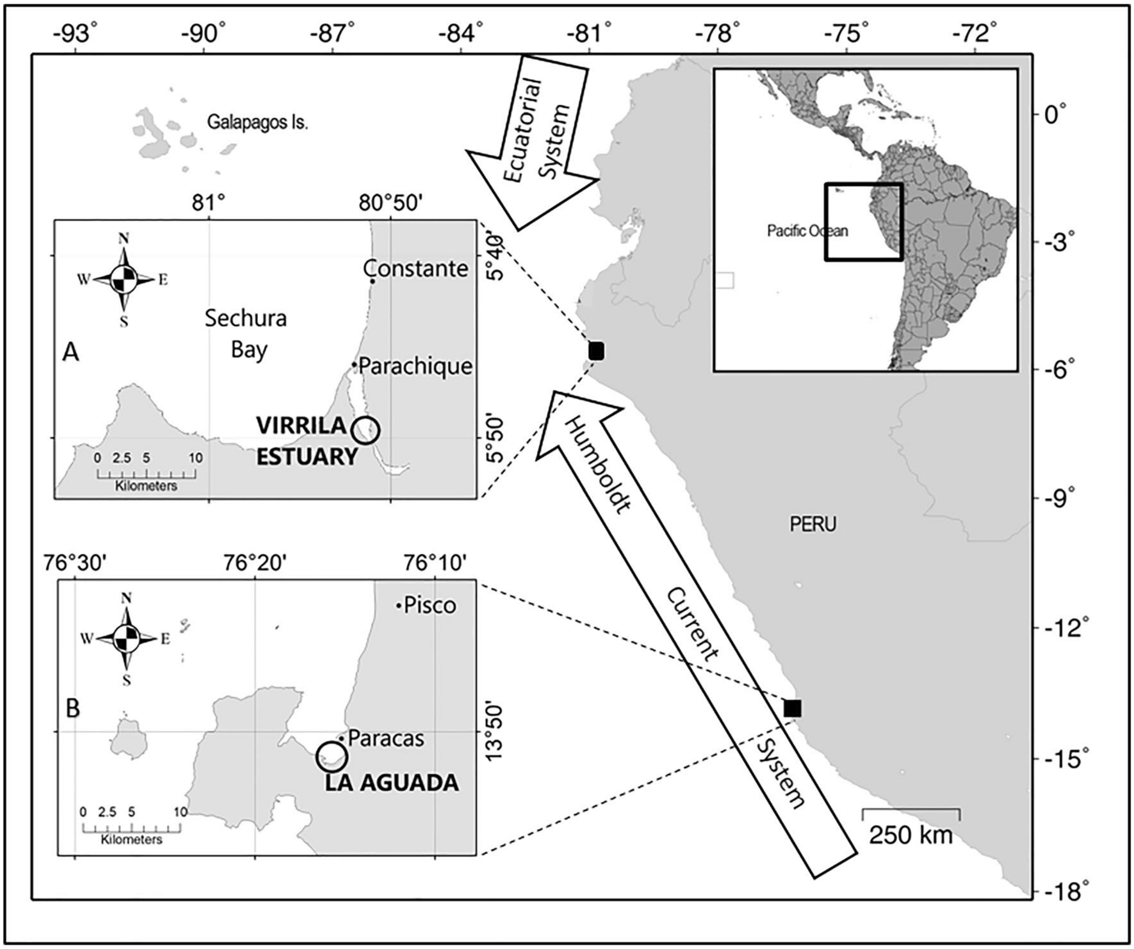

**Fig. 1** Green turtle (*Chelonia mydas*) study sites along the coast of Peru. **A** The Virrila Estuary in northern Peru, located in the transitional zone between cold waters of the Humboldt upwelling ecosystem and the warm waters of the Equatorial ecosystem; **B** La Aguada, characterized by permanent upwelling along the central coast of Peru

Summer, and Autumn, pelagic medusae of the large jelly *Chrysaora plocamia* are abundant in the area (Quiñones 2008); during Winter and Spring, there are important concentrations of sea anemones (*Paranthus* sp.) in the sandy areas (Environmental Research Management 2013; Paredes 2015). La Aguada is used by artisanal fishers targeting nearshore species such as mullet (*Mugil cephalus*), stingray (*Hypanus dipterurus*), and silverside fish (*Odontesthes regia regia*).

Virrila Estuary in Sechura Bay is on the northern coast of Peru (Fig. 1) and is in the transitional ecotone where cool, north-flowing upwelled waters converge with the warm, less-productive tropical waters originating from equatorial regions to the north (Swartzman et al. 2008; Velez Zuazo et al. 2014; Ibañez-Erquiaga et al. 2018). Mean annual SST is 24.7 °C, (range = 18–33.9 °C; maximum temperature registered during the 2017 El Niño event). Virrila is the only coastal estuary in Peru, and contains shallow waters with water depths up to 6 m. The estuary is affected by strong tidal changes, which influence green turtle movements in and out of the estuary (Paredes-Coral 2017). During the rainy season (November–May) and ENSO events, the estuary is connected to the Piura River via the Ramon, Ñapique, and La Niña lagoons (Paredes-Coral 2017). It is mostly a clay-bottomed habitat dominated by the green algae *Caulerpa filiformis* and *Ulva* sp. (94.5% cover), and also hosts the red algae *Chondracanthus chamissoi* and *Rhodymenia* sp. (5.5% cover) (IMARPE 2007). The area is used by local artisanal fishermen targeting mullet.

## Sea turtle capture and measurement

Green turtles were captured using tangle nets (mesh size = 60–65 cm stretched; length = 900 m at La Aguada, 180 m at Virrila Estuary). Upon capture, turtles were handled by trained personnel following established ethical protocols to reduce animal stress and overheating (Ehrhart and Ogren 1999). We measured curved carapace length

(CCL, ± 0.1 cm) with a flexible tape measure, and body weight (± 1 kg) with a spring balance. A body condition index (BCI = body mass/SCL$^3$) was calculated to evaluate the size versus mass relationship of each turtle (Bjorndal et al. 2000). To define life stage, individuals with CCL < 69 cm CCL were classified as juveniles, turtles with CCL from 69 to 85 cm were considered subadults, and turtles with CCL > 85 were classified as putative adults, based on mean size of nesting females—an inexact proxy for size-at-maturity—at the nearest nesting beach (Galapagos Islands, Zárate et al. 2013).

## Esophageal lavage

Green turtle diet was determined using esophageal lavage, a low-cost technique that enables the rapid retrieval of recently consumed food from the esophagus and anterior stomach regions of sea turtles without injuring the animal (Forbes and Limpus 1993). This method was applied immediately after capture on turtles with body mass > 25 kg and in good apparent health. A manual water pump was used to gently introduce clean seawater into the esophageal region to flush out food particles. We used retrieval tubes with varying outside diameters (ODs) based on the individuals' size: for turtles with CCL < 65 cm, the inflow and retrieval tubes were both 13-mm OD, and for animals with CCL ≥ 65 cm, the in-flow and retrieval tube ODs were 15 mm and 17 mm, respectively. Glycerine or cooking oil was applied to facilitate frictionless introduction of the tips of the water in-flow and sample retrieval tubes; tubes were inserted no deeper than the anterior edge of the plastron. Recovered food samples (entire contents) were placed in plastic bottles, fixed in a 10% formalin solution, and stored in a dark environment until analysis to avoid discoloration. Each diet constituent was isolated and its dry weight was determined using the gravimetric method (Hyslop 1980).

## Prey species identification

Recovered food items were identified and classified to the lowest possible taxonomic category using a stereoscopic microscope and a combination of available keys for encountered taxa. Algae species were determined according to Acleto (1986) and invertebrates were identified based on Alamo and Valdivieso (1997), Morandini and Marques (2010), and Sanamyan et al. (2004). The samples were dried at 70° C in a vacuum oven ($p = 0.05$ bar) to reach a constant weight (Paredes 2015), then weighed on an analytical balance.

## Diet composition analysis

Diet samples were sorted by prey type and analyzed using multiple techniques. First, we calculated the Frequency of Occurrence ($F_i$) of each prey item to determine which items were most-frequently consumed by green turtles:

$$F_i = (N_i / N), \tag{1}$$

where $F_i$ is the frequency of occurrence of prey type $i$, $N_i$ is the number of turtles that consumed the prey item $i$ and $N$ is the total number of individuals sampled.

Second, we calculated Prey-Specific Abundance ($P_i$) as the relative percentage an item comprises of all prey items in only those turtles in which the actual item occurs:

$$P_i = (\Sigma S_i / \Sigma S_{ti})100, \tag{2}$$

where $P_i$ is the prey-specific abundance of prey type $i$, $S_i$ is total diet contents (dry weight) comprised of prey $i$, and $S_{ti}$ is the total esophaegal contents weight of only those turtles with prey item $i$ in their lavage samples (Amundsen et al. 1996).

Third, we calculated the Index of Preponderance ($I_i$) expressed in percentage, for the major taxonomic prey groups as well as for each specific prey item, to provide a measurable basis for grading the importance of the various food groups and items encountered in lavage samples (Natarajan and Jhingran 1961). This index provides a summary of frequency of occurrence as well as the respective weight of various food items, and was calculated as:

$$Ii = \frac{F_i \times W}{\sum \left(F_i \times W\right)} \times 100, \tag{3}$$

where $Ii$ is the index of preponderance for prey species $i$, $F_i$ is the frequency of occurrence for prey type $i$ (see above), and $W$ is the weight frequency (see below) for each food item. Weight frequency was determined according to Hyslop (1980) as follows:

$$W = W_i / W_t \times 100, \tag{4}$$

where $W_i$ is the total weight of item $i$ and $W_t$ is the total weight of all the items. Calculations of $Ii$ excluded putative incidentally consumed elements such as plastic, sand, stones, and assorted marine debris.

## Feeding strategy assessment

To determine the particular feeding strategies among the sampled turtles we derived the mean abundance ($A_i$) of each prey item ($i$) as the product of $F_i \times P_i$. These values were then plotted in a 2-dimensional space ($F_i$, x-axis; $P_i$, y-axis) to yield a scatterplot known as a feeding strategy diagram (Fig. 2; Amundsen et al. 1996). For this study, the interpretation of the diagram is focused on the vertical axis, which represents the feeding strategy in terms of specialization or generalization. Predators specialize on items located at the upper part of the diagram whereas those prey items positioned in the lower portion of the plot are only occasionally consumed (i.e., generalist consumption). When expanding focus to include the horizontal axis, prey items located at the upper left of the graph are indicative of dietary specialization at the individual level, whereas items located at the upper right are reflective of dietary specialization at the population level.

### Temporal variability and environmental context of diet composition

To evaluate temporal variability of green turtle diet at seasonal scales, Index of Preponderance $(I_i)$ analyses were pooled by seasons and by prey items. In La Aguada, a mean of 20.5 ± 7.0 (range: 16–31) samples was analyzed per season between 2010 and 2017, and in the Virrila Estuary, a mean of 36.0 ± 14.6 (range: 17–51) samples was analyzed per season between 2012 and 2018. The seasons for this analysis included Summer (15 Dec to 14 Mar), Autumn (15 Mar to 14 Jun), Winter (15 June to 14 Sep), and Spring (15 Sep to 14 Dec).

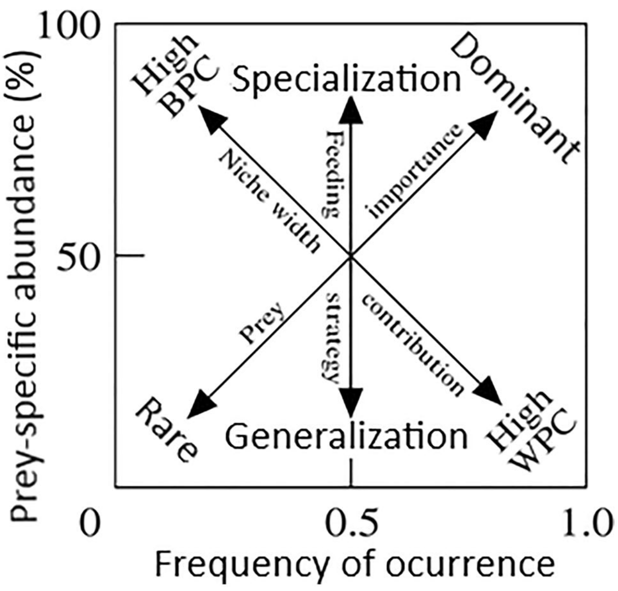

**Fig. 2** Schematic of feeding diagram to interpret green turtle feeding strategy. Prey importance is indicated by the diagonal from the lower left to the upper right corner. The vertical axis represents the feeding strategy in terms of specialization or generalization. The distribution pattern of items along the diagonal from the upper left to the lower right corner is indicative of the contributions of between- and within-phenotype components to the niche width (BPC and WPC respectively). Modified from Amundsen et al. (1996)

We measured SST in situ during each visit to La Aguada ($n=39$) and Virrila Estuary ($n=19$). In addition, we used the Peruvian Oscillation Index (POI) to provide an environmental context across years. The POI index was calculated from monthly average SST during a ~ 70-year time series (1950–2019) measured at five coastal stations along the Peruvian coast. The POI best represents the coastal SST variation in Peru and is positively correlated with other El Niño indices in the Eastern Tropical Pacific region (Purca 2005).

### Statistical analysis

Initially, we carried out a Box-Cox transformation to normalize the data. To explore the size (CCL) differences of green turtle between the two sites, a two-sample *t* test was used, the mean sizes are presented with their standard deviations, ranges and sample size. To compare SST between La Aguada and Virrila Estuary we used a Mann–Whitney *U* test, and to evaluate SST at seasonal scales we used the Kruskal–Wallis test performed for the four seasons at each site. To study the relationship between inter-annual environmental variability and green turtle diet, the Indices of Preponderance of the main prey items $(Ii)$ were pooled by years: 2010–2017 for La Aguada, and 2012–2018 for Virrila Estuary. We then used Spearman's correlation $(r_s)$ to explore the relationship between POI and occurrence of the primary diet content items during the months when turtles were sampled.

## Results

### Size classes

The mean size of turtles in La Aguada was 60.1 ± 9 cm CCL (range: 44.8–80.6 cm; $n=86$), where 81.4% were juveniles and 16% were sub-adults; no adults were encountered based on the mean nesting size from the Galapagos nesting aggregation (Zarate et al. 2013). In Virrila Estuary, the mean size of green turtles was 73.4 ± 9 cm CCL (range: 52–90.9 cm; $n=113$), with 29.2% juveniles, 61.9% sub-adults, and 8.8% adults (Fig. 3, Table 1). According to the two-sample t test, mean size of green turtles at Virrila Estuary was significantly larger than that for their counterparts in La Aguada ($p$ value < 0.05).

### Diet composition

Esophageal lavage efforts were performed on a mean of 12 green turtles each year at La Aguada (total among all

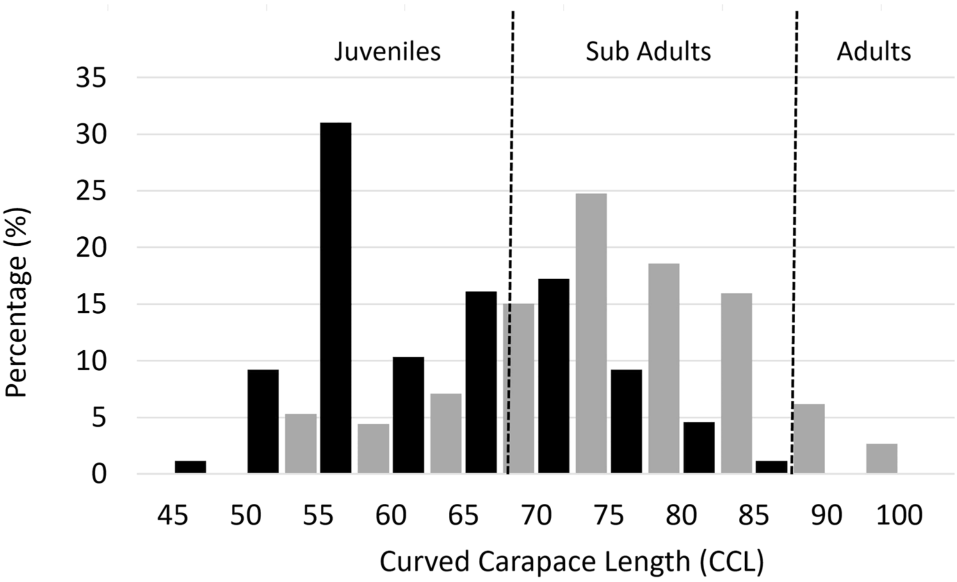

**Fig. 3** Size (CCL) distribution of green turtles captured at **A** La Aguada (black bars) (*n* = 86), and **B** Virrila Estuary (grey bars) (*n* = 113). Dotted lines denote size thresholds for juveniles (< 69 cm CCL); sub-adults (69 to 85 cm CCL) and adults (> 85 cm CCL) as per Zárate et al. (2013) for green turtles in the Galapagos Islands, the largest green turtle rookery near Peru

**Table 1** Green turtle size structure (cm CCL) and maturity class structure in La Aguada (13°50'S) from 2010 to 2017 and in the Virrila Estuary (05°50'S) from 2012 to 2018. sd = standard deviation; *n* = number of sampled individuals; % = proportion of study population for of any given maturity size class

| | La Aguada | | | Virrila Estuary | | |
|---|---|---|---|---|---|---|
| | Mean ± sd (cm) | Range (cm) | *n* (%) | Mean ± sd (cm) | Range (cm) | *n* (%) |
| Juveniles | 57.1 ± 6.5 | 44.8–69.0 | 71 (82.6) | 62.4 ± 5.5 | 52.0–68.8 | 33 (29.2) |
| Sub-adults | 74.3 ± 3.2 | 69.2–80.6 | 15 (17.4) | 76.6 ± 4.6 | 69.3–84.9 | 70 (61.9) |
| Adults | – | – | – | 87.3 ± 2.4 | 85.0–90.9 | 10 (8.9) |
| Total | 60.1 ± 8.9 | 44.8–80.6 | 86 (100) | 73.4 ± 9.1 | 52.0–90.9 | 113 (100) |

years = 86 turtles) and a mean of 16 turtles annually at Virrila Estuary (total = 113 turtles). Diet analyses showed that the diet of green turtles in La Aguada was dominated by animal matter (> 70% *Ii*), mainly represented by Cnidarians, such as the sea anemone *Paranthus* sp. (59.7% *Ii*) and the scyphozoan jelly *Chrysaora plocamia* (9.3% *Ii*). Plant matter in the diet of green turtles at La Aguada constituted ~ 30% *Ii*, mostly represented by the green alga *U. papenfussi* (25.9% *Ii*) and the red alga *Chondracanthus chamissoi* (2.3% *Ii*).

Conversely, the diet of green turtles in Virrila Estuary was dominated by plant matter (95% *Ii*), mainly represented by the green algae *U. papenfussi* (75.4% *Ii*) and *Caulerpa filiformis* (14.4% *Ii*); the seagrass *Ruppia maritima* (5% *Ii*) was also an important diet item. Animal matter was only minimally encountered in diet samples from Virrila green turtles, with the main animal prey being unidentified Bivalvia (1% *Ii*) and mullet *Mugil cephalus* (0.7% *Ii*) (Table 2). Although not quantified in terms of dietary proportion, plastic was encountered in 43% and 24% of the lavage samples from La Aguada and Virrila Estuary, respectively.

## Feeding strategy

According to their location in the feeding strategy diagram (Fig. 4; vertical axis), turtles at both locations showed a mixed feeding strategy, with variable degrees of specialization and generalization on different prey items. At La Aguada, individuals specialized in the scyphozoan jelly *Chrysaora plocamia* and the sea anemone *Paranthus* sp., whereas algae, bivalves and fish were only consumed occasionally. The green alga *U. papenfussi* was consumed by approximately half of the turtles at La Aguada, but its average dietary contribution was low (11.8% *Ai*; Fig. 4A) thus suggesting a mixed feeding strategy with individual specialization. At Virrila Estuary, our results suggest dietary specialization by most turtles towards *U. papenfussi,* although some individuals specialized on *Caulerpa filiformis.* Other items such as red algae, fish, bivalves and sea anemones were included occasionally, in small proportions, in the diet of some individuals (Fig. 4B) suggesting a mixed feeding strategy with population specialization.

**Table 2** Prey items recovered from green turtles in La Aguada (13°50'S) and in Virrila Estuary (05°50'S).

| Phylum | La Aguada $Ai$ | La Aguada % $I_i$ | Virrila Estuary $Ai$ | Virrila Estuary % $I_i$ |
|---|---|---|---|---|
| Vegetal matter | | | | |
| Chlorophyta | | | | |
| *Caulerpa filiformis* | 0.6 | 0.1 | 6.3 | 6.9 |
| *Ulva papenfussi* | 11.8 | 25.9 | 34.5 | 81.6 |
| *Chaetomorpha* sp. | 1.3 | 0.6 | | |
| Rhodophyta | | | | |
| *Chondracanthus chamissoi* | 2.0 | 2.3 | | |
| *Rhodymenia* sp. | | | 1.6 | 0.09 |
| Gigartinacea | 1.6 | 0.1 | 0.4 | 0.1 |
| Tracheophyta | | | | |
| *Ruppia maritima* | 3.1 | 0.6 | 3.1 | 5.4 |
| Animal matter | | | | |
| Cnidaria | | | | |
| *Paranthus* sp. | 19.1 | 59.7 | | |
| *Actinaria* sp. | | | 1.5 | 0.2 |
| *Chrysaora plocamia* | 12.6 | 9.3 | 0.8 | 0.2 |
| Chordata | | | | |
| *Mugil cephalus* | | | 0.8 | 0.8 |
| *Odontesthes regia regia* eggs | 0.05 | 0.03 | | |
| Mollusca | | | | |
| Bivalvia und | 1.7 | 1.1 | 4.0 | 1.1 |
| Artropoda | 0.45 | 1.02 | 1.04 | 0.04 |
| Anelida | 0.02 | 0.13 | 0.01 | 0 |
| Bryozoa | | | 0.4 | 0 |
| Echinodermata | 0.06 | 0.02 | | |
| Insecta | 0.16 | 0 | | |

$Ai$ = prey abundance, $\%I_i$ = Index of Preponderance. The Index of Preponderance gives a summary picture of the frequency of occurrence (Fi) as well as the respective weight of various food items ($W$): $\text{Ii} = (\text{Fi x W}) \times 100/\sum (\text{Fi x W})$

## Temporal variability in diet composition

There were seasonal differences in the diet of green turtles in both locations. At La Aguada, prey of animal origin dominated green turtle diet during Spring (76% *Ii*), Summer (86% *Ii*), and Winter (63% *Ii*), whereas in Autumn, diets were more balanced between animal- and plant-based prey types (37% *Ii* and 47% *Ii*, respectively) (Fig. 5A). During Spring, green turtle diets were strongly dominated by *Paranthus* sp. (73% *Ii*), followed by *U. papenfussi* (23% *Ii*) and amphipods (2% *Ii*) (Fig. 4A). In Summer, *C. plocamia* (41% *Ii*) and *Paranthus* sp. (34% *Ii*) dominated, with lesser contributions by *U. papenfussi* (11% *Ii*) and *C. chamissoi* (12% *Ii*). During Winter, the dominant prey of animal origin included *C. plocamia* (40% *Ii*) and *Paranthus* sp. (22% *Ii*), although the alga *U. papenfussi* (34% *Ii*) was also frequently encountered. In Autumn, diet was comprised of *R. maritima* (25% *Ii*), *Paranthus* sp. (24% *Ii*), *C. plocamia* (15% *Ii*), *C. chamissoi* (15% *Ii*), and *U. papenfussi* (14% *Ii*). In general, a strong preponderance of animal-based prey was found for all years for La Aguada, with *Paranthus* sp. as the dominant prey type (43–63% *Ii*) during 2010–2011 and 2014–2016.

Green turtle diet in Virrila Estuary was dominated by plant-based prey during all seasons. During Spring, *U. papenfussi* (71% *Ii*), and *C. filiformis* (22% *Ii*) dominated the diet. In Summer, green turtle diet was made up almost entirely of *U. papenfussi* (92% *Ii*). During Autumn, a wide array of taxa was recorded, with a predominance of plant-based prey (47% *Ii*) represented mainly by *R. martima*, *C. filiformis*, and *U. papenfussi*; prey of animal origin totaled 37% *Ii* and was comprised of bivalves and mullet. In Winter, *R. maritima* and *U. papenfussi* were practically the only two items registered, with 54% *Ii* and 45% *Ii*, respectively. Despite the year-round dominance of plant matter consumption, animal prey was important for green turtles during Autumn (Fig. 4B).

## Environmental context of diet composition

The mean annual SST at La Aguada was 19.0 ± 1.8 °C and was significantly lower than the mean annual SST in the Virrila Estuary (Mann–Whitney $U = 5675$, $p < 0.05$), which was 24.8 ± 3.4 °C. Within each respective site, mean SST varied significantly among seasons. At La Aguada, for example, mean Summer SST was 19.7 ± 1.2 °C whereas in Winter, it was 18.7 ± 0.9 °C. Conversely, in Virrila Estuary, temperatures were much higher, with a mean Summer SST of 26.0 ± 3.4 °C and mean Winter SST of 22.6 ± 2.4 °C Table 3.

At La Aguada, the green alga *U. papenfussi* was always an important dietary component, with the highest *Ii* values at 42% during 2016 (mean SST = 20.3 ± 0.6 °C) and 58% during 2017 (mean SST = 20.1 ± 0.5 °C), both El Niño years. In addition, the seagrass *R. maritima* was a key food item during 2015 (mean SST = 18.3 ± 0.9 °C) (Fig. 6A). At Virrila Estuary, during the El Niño events of 2015–2016 and 2017, there was a strong decrease of at least 1.5 orders of magnitude in *U. papenfussi* consumption by green turtles. Instead, *C. filiformis* was the dominant prey in 2015 (76% *Ii*), and *R. maritima* in 2016 (48% *Ii*) and 2017 (27% *Ii*). Also in 2016 and 2017, the presence of animal matter in moderate amounts was recorded, represented by Bivalvia (30% and 41% *Ii*, respectively) and the fish *M. cephalus* (9% and 2% *Ii*, respectively). In 2018, neutral conditions were restored, with the consequent recovery of *Ulva papenfussi* in green turtle diet (74% *Ii*), similar to the high values recorded during 2015–16 and 2017 El Niño years (Fig. 6B).

With respect to the influence of POI phase on green turtle diet, there was no clear relationship between POI and main prey item encounter rates in La Aguada: $r_s$ [*Paranthus*

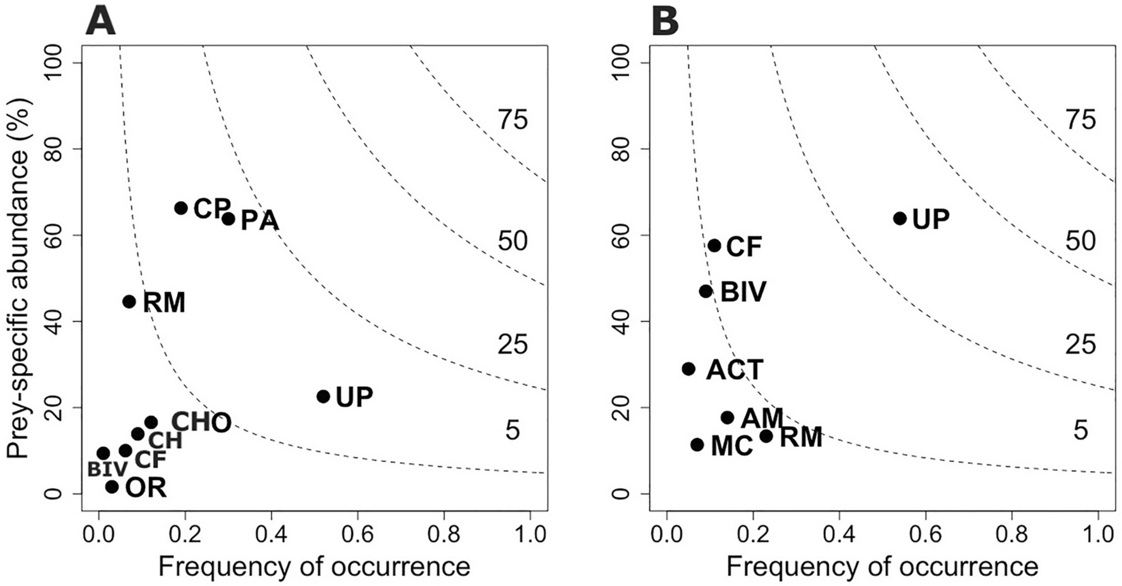

**Fig. 4** Feeding diagram of green turtles captured in **A** La Aguada and **B** Virrila Estuary showing a mixed feeding strategy. Isolines indicate different prey mean abundances (Ai). **A** Individual specialization towards the sea anemone (*Paranthus* sp., PA) and the jellyfish (*Chrysaora plocamia*, CP). **B** Population specialization towards the sea lettuce (*U. papenfussi*, UP) and individual specialization towards the green algae (*Caulerpa filiformis*, CF). Other items consumed occasionally, as a generalized feeding strategy, include the red algae (*Chondracanthus chamissoi*, CHO), red algae (*Chaetomorpha* sp., CH), silverside fish (*Odontesthes regia*, OR) and bivalves (BIV), seagrass (*Ruppia maritima*, RM), fish (*Mugil cephalus*, MC), sea anemone (*Actinaria* sp., ACT) and unidentified animal matter (AM)

sp.] = – 0.679, $p = 0.094$; $r_s$ [*C. plocamia*] = 0.3, $p = 0.624$; $r_s$ [*U. papenfussi*] = 0.657, $p = 0.156$; Fig. 6A). Whereas *Paranthus* sp. dominated green turtle diet during negative (60–63% *Ii*), neutral (35% *Ii*), and positive (43–52% *Ii*) phases of the POI, *C. plocamia* featured prominently (46–64% *Ii*) during both neutral and positive phases of the POI. In contrast, at Virrila Estuary, a strong negative relationship was found between POI and occurrence of the main prey item *U. papenfussi* ($r_s = 0.786$, $p = -0.036$; Fig. 6B). A major dominance (88–100% *Ii*) of *Ulva papenfussi* was recorded for green turtles in Virrila Estuary in 2012–2013, and was correlated with both neutral and negative POI phases.

## Discussion

This study provided a rare opportunity to compare green turtle foraging ecology at two very different habitat types in the southeastern Pacific Ocean, one within the cold Humboldt Current and the other one in a warmer transitional zone, both separated by 1200 km. In addition to in-water capture and demographic study of turtles, we conducted esophageal lavage efforts to evaluate recently ingested food by turtles assembled at each area. With the wide size range and multiple life-history stages of studied turtles, we had the opportunity to evaluate the influence of size and ontogeny on foraging ecology, which perhaps could reveal the influence of life-history on diet preference among individuals (Jones and Seminoff 2013). When coupled with information on environmental variability, our data provide a framework for ontogenic-based developmental migrations by green turtles in this portion of the southeastern Pacific Ocean.

### Spatial differences in green turtle demography

There was a strong disparity in mean body size between sites that reflects differences in the predominant lifestages for green turtles present in each area. While green turtles in La Aguada were mostly juveniles, most individuals in Virrila Estuary were sub-adults and adults. This strong size disparity between the two tested foraging aggregations suggests that the observed dietary discrepancies are influenced by the differing ontogenic stages among studied turtles.

The presence of distinct size ranges may be indicative of size- and/or lifestage-based habitat partitioning, perhaps related to the different resources at each site (i.e. extrinsic) and/or the differing nutritional requirements (i.e. intrinsic) of the life stages for green turtles assembled at each site (Cardona et al. 2009). The concept of green turtles expressing differing habitat preferences as they transition across lifestages has been described as a ‘developmental migration’ (Carr and Hirth 1962) and may provide a mechanism for the size/lifestage disparity between our two study sites. However, so far this framework has largely been applied to green

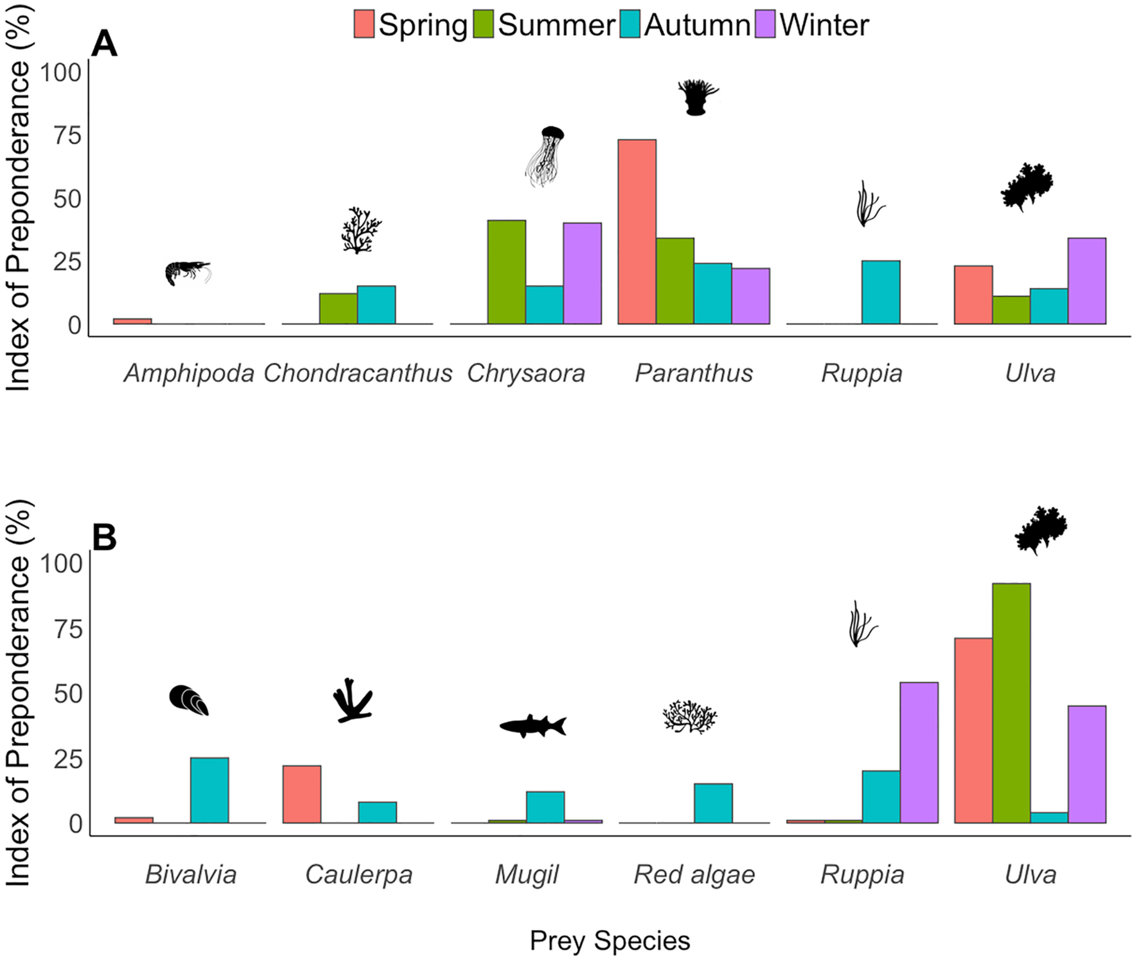

**Fig. 5** Index of Preponderance (*Ii*) for green turtles (*Chelonia mydas*) grouped by prey items for **A** La Aguada and **B** Virrila Estuary. Item silhouettes are referential

**Table 3** Sea surface temperatures (SST, °C) at the green turtle study sites of La Aguada and Virrila Estuary.

| Season / Place | La Aguada | | | Virrila Estuary | | |
|---|---|---|---|---|---|---|
| | Mean ± sd | Range | *n* | Mean ± sd | Range | *n* |
| Summer | 19.7 ± 1.2 | 16.2–21.5 | 62 | 26.0 ± 3.4 | 20.0–32.3 | 32 |
| Autumn | 20.6 ± 2.1 | 15.7–24.3 | 87 | 27.5 ± 2.1 | 24.3–30.5 | 13 |
| Winter | 18.7 ± 0.9 | 16.4–18.9 | 77 | 22.6 ± 2.4 | 18.1–27.3 | 23 |
| Spring | 17.7 ± 1.3 | 15.1–21.0 | 108 | 22.6 ± 2.9 | 17.2–27.4 | 25 |

Sample sizes vary due to differences in study effort at La Aguada (39 visits) and Virrila Estuary (19 visits)

turtles in the Caribbean region, where expansive seagrass (*Thalassia testudinum)* pastures dominate the neritic systems in the region, unlike coastal habitats of Peru where macroalgae are the dominant marine autotrophs. This study presents an initial opportunity to further explore patterns and drivers for lifestage-based habitat segregation in algae-dominated and rocky reef habitats of the southeastern Pacific Ocean.

With respect to extrinsic drivers affecting the presence of green turtles of different lifestages, we note that the two areas are substantially different in habitat type, prey availability, and dominant green turtle lifestage. For example, in La Aguada, prey supply is abundant and dominated by animal matter; we hypothesize that smaller turtles require greater energy input facilitated to high prey availability to maximize somatic growth rates and thus transition more rapidly to the subadult lifestage (e.g., Seminoff et al. 2002; Velez Zuazo et al. 2014). Conversely, in Virrila Estuary, vegetal matter dominates, and the site has a preponderance

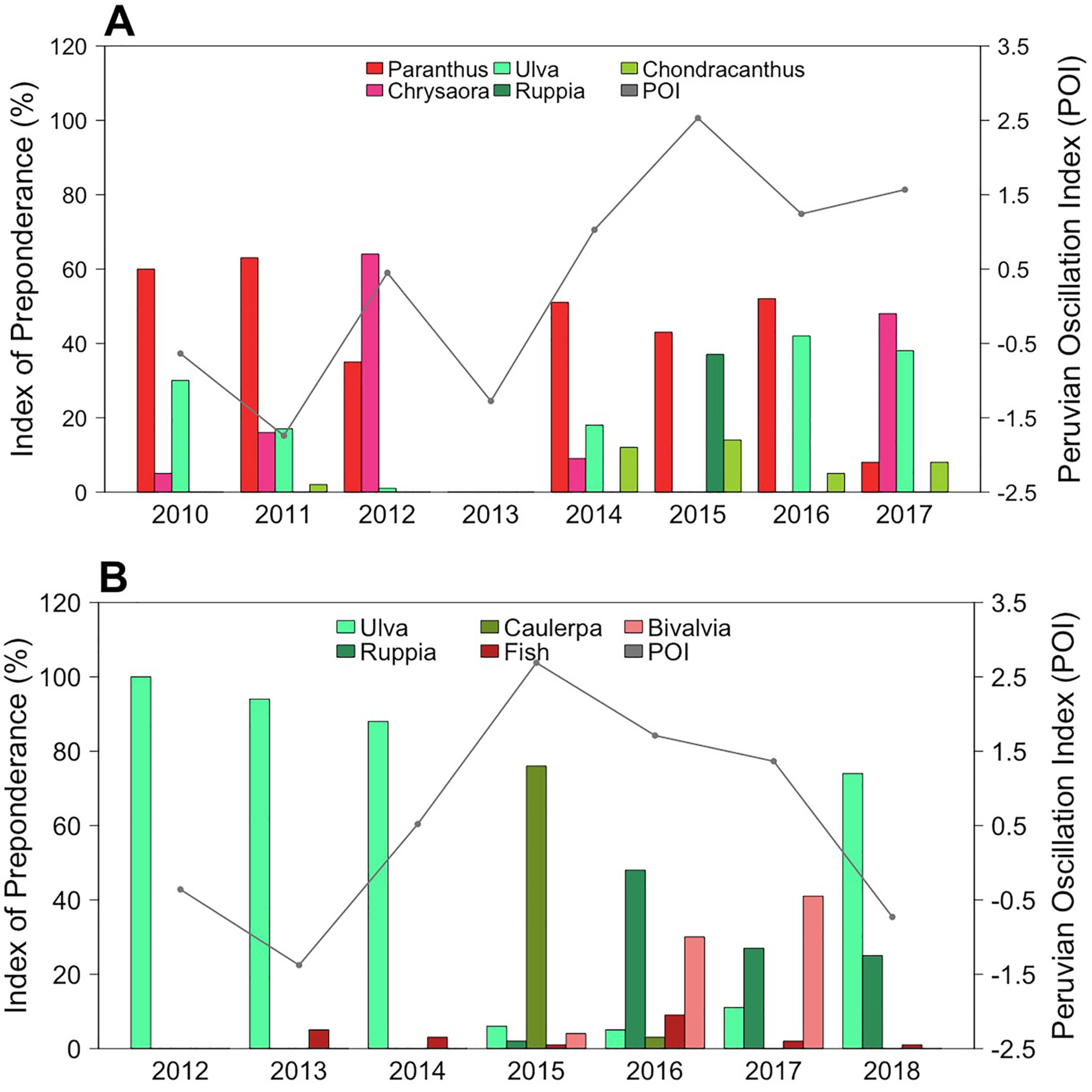

**Fig. 6** Index of Preponderance for green turtles (*Chelonia mydas*) grouped by inter-annual scales for **A** La Aguada and **B** Virrila Estuary. Green shades indicate prey from vegetal origin and reddish shades from animal origin. Grey trend lines represent the Peruvian Oscillation Index (POI). Note: Warm years or El Niño are represented by POI > +0.5; neutral years by POI < +0.5 and > − 0.5 and cold years or La Niña by POI < − 0.5

of larger subadults with some adults present. Perhaps the larger—and presumably older—green turtles at this site have had more time to acquire the gut microbiota necessary to digest plant matter. If so, this would suggest an intrinsic physiological mechanism for the disparity in diets between the two study sites (Meylan et al. 2011; Gulick et al. 2022).

As found elsewhere, large green turtles often shift to herbivory after adhering to an omnivorous diet strategy during their juvenile lifestages. Although the specific physiological and/or behavioral mechanisms driving this shift are unclear, perhaps the metabolic requirements of larger turtles is low enough such that vegetal food of relatively low caloric value can fulfill growth and reproduction energetic requirements due to prolific availability of this prey type for turtles in coastal habitats. This pattern follows the developmental habitat shifts reported previously for sea turtles, where benthic feeding areas are used by immature turtles, while larger individuals moved to other areas differing in resource availability to complete their maturation process (Meylan et al. 2011). Evaluating the prey consumed as well as the life stages present adds a novel layer for exploring the environmental drivers for these 'developmental migrations', as well as the differing foraging ecologies that may occur during such events.

## Spatial variability on diet composition

In the context of developmental migration theory, typically once green turtles recruit to neritic waters they gradually shift to an herbivorous diet dominated by benthic foods such as seagrasses and/or macroalgae (Bjorndal 1997; Esteban et al. 2020); however, this does not appear to hold true in the southeastern Pacific. For example, at the cold Humboldt Current site (La Aguada) green turtle diets appear to specialize in animal matter, such as sea anemones (*Paranthus* sp.) and jellies (*C. plocamia*), which together represent almost 70% of the total diet volume; however, the green alga *U. papenfussi* and, to a lesser extent the red alga *C. chamissoi* are also important diet items. On the other hand, green turtles at the warm ecotone site (Virrila Estuary) specialized almost exclusively on vegetal prey, especially green algae, such as *U. papenfussi* which represents more than 80% of the total diet abundance as well as *C. filiformis*, albeit to a lesser extent. These dietary shifts and the spatial segregation could benefit turtles by minimizing intraspecific competition for food among different age classes (Werner and Gilliam 1984).

The large importance of invertebrates in the diet of green turtles at La Aguada is similar to other diet studies in the southeastern Pacific. For example, at Gorgona Island in the Colombian Pacific, green turtle diet also was dominated by invertebrates, such as tunicates (Salpidae and Doliolidae) (Amorocho and Reina 2007) and in Sechura Bay of Northern Peru, *Chelonia* diet was dominated by squid eggs (*Loligo gahi*) (Jiménez et al. 2017). Furthermore, in offshore waters of Peru (03 –15°S), Kelez (2011) used stable isotope analysis to establish that crustaceans were the most consumed prey type by green turtles. Thus, it appears that green turtles at multiple foraging areas in the southeastern Pacific commonly depend on a varied diet that includes significant animal matter.

While green turtles in the EP are known for eating more invertebrates than their counterparts elsewhere the world, this study shows that at least some local populations maintain diets dominated by plant matter, as exemplified in Virrila estuary where we found high amounts of the green alga *Ulva papenfussi* in green turtle lavage samples (Fig. 4B). Green algae are also important to the diet of green turtles in other regions in the EP, including Bahía Magdalena, Mexico where green turtles depend on *Codium* sp. for more than half their diet intake (López Mendilaharsu et al. 2008), and in the Galapagos Islands, Ecuador where *Ulva* sp. comprised nearly half the diet (Carrión-Cortez et al. 2010; Table 4). Similarly, Seminoff et al. (2002) reported that green turtle diets in the central Gulf of California, Mexico were dominated by red filamentous algae (~90% volume) from the order Gracilariaceae. These findings indicate that even though green turtles in the EP are well-known for their invertebrate consumption, like many other areas worldwide the species also heavily depends on vegetal food.

Finally, with respect to our application of esophageal lavage, in our study this technique proved to be an effective method for evaluating the food consumed by turtles. Nevertheless, despite the widespread application of this practice for studying sea turtle diets (e.g., Seminoff et al. 2002; Vélez-Rubio et al. 2016; Méndez-Salgado et al. 2020), we acknowledge that the lavage technique can at times result in a biased view of what foods are consumed, both in terms of what is recovered and the short time frame of inference. Some items may have been ingested incidentally, and certain items may flush more easily from the esophagus according to their size, shape, and texture (Burkholder et al. 2011; Gonzalez Carman et al. 2014). However, we found this approach to be safe for turtles, effective for recovering dietary components, and inexpensive to implement, which was a huge advantage for our limited study budget.

## Environmental influences on diet

In La Aguada inlet, the sea anemone *Paranthus* sp. was consumed year-round during the neutral year 2012 and the El Niño years of 2015 and 2016 (all with positive POI values). However, the highest *Paranthus* sp. consumption rates (> 60% *Ii*) were encountered during 'cold' years such as 2011 and 2010 (both with negative POI values). This pattern of greater invertebrate consumption during cooler years suggests water temperature may play a role in shaping local green turtle diet intake. As reported by Spencer et al. (1998) for aquatic turtles, lower temperature resulted in a slower rate of digestion of vegetable matter. Moreover, at Gorgona Island (Colombian Pacific), the digestibility of proteins from animal matter was 85–91% compared to only 67% for vegetable matter (Amorocho and Reina 2008). Thus, it is possible that colder waters of the southeastern Pacific make it more difficult to digest plant material, which inherently has lower digestibility, thereby causing green turtles eat more invertebrates which are presumably easier to digest in colder temperatures. Indeed, mean SST in La Aguada was 19 °C, with seasonal means as low as 15° during Winter; recall that this area is very close (< 10 km) to one of the most important upwelling cores in the Humboldt Current around Pisco (Gutiérrez et al. 2011).

In addition to influences from low ambient temperature, the high consumption levels of invertebrates in La Aguada could be driven by the greater availability of these resources in the area. For example, *Paranthus* sp. is abundant in sandy bottoms during Winter and Spring (Environmental Research Management 2013; Paredes 2015). In addition, the scyphozoan jelly *C. plocamia*, a key green turtle diet item (Quiñones et al. 2010), is also highly abundant in La Aguada, with a mean biomass of (27.1 ± 27.2 kg jelly/100 m/

**Table 4** Dietary constituents of green turtles (*Chelonia mydas*) sampled throughout the Eastern Pacific Ocean as determined via the esophageal lavage technique (Forbes and Limpus 1993) and from stable isotope analysis (San Diego Bay, California)

| Study Area | Primary diet constituents | | Reference |
|---|---|---|---|
| | Vegetal matter | Animal matter | |
| San Diego Bay, California, U.S.A | Eelgrass (14–38%), Red and green algae (28%) | Mobil invertebrates (24–56%)<br>Sessile invertebrates (2–32%) | Lemons et al. 2011 |
| Bahía de los Ángeles, Baja California, Mexico (28°55’N) | Red algae (> 91%)<br>(*Gracilaria* spp.)<br>Green algae (6%) | Annelida and cnidarian (< 5%) | Seminoff et al. 2002 |
| Bahía Magdalena, Baja California Sur, Mexico (24°38’N) | Red algae (42%)<br>(*Gracilaria* spp.)<br>Green algae (> 55%)<br>(*Codium* spp.) | Porifera (< 1%) | López Mendilaharsu et al. 2008 |
| Isla Gorgona, Cauca, Colombia (02°57’N) | Mangroove fruit (13%) | Tunicates (66%)<br>Crustaceans (4%) | Amorocho et al. 2007 |
| | Mangroove fruit (39%)<br>Total algae (9%) | Invertebrates (6%) | Sampson et al. 2018 |
| Isla Isabela and Isla Santa Cruz, Galapagos Archipelago, Ecuador (0°36’S) | Red algae (33%)<br>Green algae (43%)<br>(*Ulva* sp.)<br>Mangrove fruit (5%) | Cnidarians (7%) | Carrión et al. 2010 |
| Bahía Sechura, Piura, Perú (05°40’S) | Red algae (12%)<br>(*Rhodymenia* spp.)<br>Green algae (6%) | Squid eggs (33%)<br>Coastal fish (16%)<br>Jellyfish (7.3%)<br>Gastropod eggs (5%) | Jiménez et al. 2017 |
| San Andrés, Pisco, Ica, Perú (13°45’S) | Green algae and red algae (13%) | Jellyfish (50%)<br>(*Chrysaora plocamia*)<br>Mollusks (17%) | Quiñones et al. 2010 |
| La Aguada, Paracas, Pisco, Perú (13°50’S) | Green algae (26%)<br>(*Ulva papenfussi*)<br>Red algae (2.3%)<br>(*Chondracantus* spp.) | Sea anemone (60%) (*Paranthus* spp.)<br>Jellyfish (9.3%) (*Chrysaora plocamia*) | This study |
| Virrila Estuary, Sechura, Piura, Perú (05°50’S) | Green algae<br>*Ulva papenfussi* 82%, *Caulerpa filiformis* 7%, Sea grass (5.4%) (*Ruppia marítima*) | Unidentified Bivalvia (1.1%), Teleost fishes (0.8%) (*Mugil cephalus*) | This study |

hour; range: 0.5–84.6 kg) (J. Quiñones, unpublished data), mainly during Spring, Summer, and Autumn (Quiñones 2008). Thus, it appears that there may be multiple extrinsic factors (e.g. temperature, food availability) influencing the diet of green turtles at La Aguada foraging site.

Consistent with the aforementioned potential influence of temperature on diet, in the Virrila Estuary local waters can reach 25 °C, which is relatively high compared to the La Aguada study site. At Virrila Estuary, the green alga *Ulva papenfussi* (sea lettuce), was the most consumed item overall and was frequently encountered during 2012, 2013 and 2014 (all with negative POI values), yet rarely found in diet samples during the El Niño years 2015, 2016, and 2017 (all with positive POI values). During these latter years, *U. papenfussi* was replaced in the diet of green turtles by *Caulerpa filiformis* and *Ruppia maritima*, then when POI conditions diminished in 2018, *U. papenfussi* reestablished as the most preyed-upon diet item (Fig. 6B). Conversely, in La Aguada there is not a clear relationship between POI and jelly consumption; however, the higher levels of *Paranthus* sp. consumption (> 60% *Ii*) were related to cold POI years, such as 2010 and 2011 (Fig. 6A).

It is unclear whether the decrease in *U. pappenfussi* during El Niño years was related to physiological limitations for plant matter digestion during cold periods or perhaps due to decreased availability of this resource. It is apparent that both *U. papenfussi* and *C. filiformis* are common algae that live on the clay bottoms of the estuary (IMARPE 2007), but we encourage studies to assess how this resource’s availability shifts in relation to water temperature. For instance, at seasonal scales in La Aguada, during Summer and Winter the sea jelly *Chrysaora plocamia* dominated green turtle diet, while in Spring and Autumn, the sea anemone *Paranthus* sp. was highly consumed. Such influences are also apparent in Virrila Estuary, where the green alga *U. papenfussi* was the dominant green turtle diet item during Summer and Spring, whereas the seagrass *Ruppia maritima* was more prevalent during Winter; animal matter was also present in lower amounts during Autumn (Fig. 5B). In our evaluation, a variety of environmental indices tied to temperature (ENSO, POI, SST) can be evaluated on seasonal and annual scales, allowing us to explore the role of the environment on foraging ecology. Because of the long-term nature of this study, we were able to track how diet changed with shifting conditions for both the ENSO and POI environmental phenomena.

## A green turtle life history model for Peru

Our results provide new insight on the foraging strategies of green turtles with a focus on two distinct areas along the Peruvian coast that serve as foraging habitats for the species. We suggest that post-pelagic juvenile green turtles initially recruit to neritic habitats of La Aguada, evidenced by the constant presence of epibionts of oceanic origin on the smallest turtles (Quiñones et al. 2021). Upon arrival at this more southern location, individuals feed on a wide array of high-calorie animal matter due largely to the influences of cooler waters. As individuals get larger, they then transition northward to the Virrila Estuary, where it is warmer and they depend on the widely available, presumably lower calorie vegetal prey as they grow to maturity. The diet composition and size classes at both study areas support this hypothesis. A similar scenario is found in juvenile green turtle foraging areas in the southwestern Atlantic Ocean: at the sub-tropical site of Ubatuba (~ 23°S), green turtles adhere to an omnivorous diet with large amounts of the jellyfish *Velella velella*, whereas at the tropical site of Praia Do Forte (~ 12°S), they have an exclusively herbivorous diet (Campos and Cardona 2019).

The preponderance of juvenile individuals in La Aguada provides evidence for the developmental habitat hypothesis, supporting the important role of neritic habitats for the benthic juvenile life stage (Meylan et al. 2011; Velez Zuazo et al. 2014). The common occurrence of open ocean epibionts in juvenile green turtles, such as *Conchoderma virgatum*, *Lepas anatifera*, *Planes cyaneus* and *Remora remora* confirms that these turtles recruit in La Aguada shortly after their "lost years" in oceanic waters (Quiñones et al. 2021). When these turtles reach areas further north in the Virrila Estuary or Sechura Bay (more than 1200 km to the north), they no longer have any epibiont of oceanic origin and are of much larger sizes and weights (J. Quiñones, unpublished information), most being sub-adults. Upon reaching adulthood, it is apparent that at least some green turtles remain in coastal Peru. However, the lack of adult turtles at La Aguada and their small proportion in Virrila Estuary indicate that most green turtles move to other areas in the southeastern Pacific upon maturity. We hypothesize that after they migrate as adults to their nesting and reproductive areas in the Galápagos, adult green turtles rarely return to coastal Peru and instead reside in the Galapagos Islands (Seminoff et al. 2008) or elsewhere to the north. Nevertheless, little information is available about key areas of the southeastern Pacific that host adult green turtles; thus we recommend capture efforts in yet-unstudied areas throughout the region to elucidate the preferred habitats for this life stage.

## Conservation implications

Both sites—La Aguada and Virrila Estuary—have been shown to consistently provide suitable conditions that support the year-round presence of green turtles, which are currently protected under national legislation in Peru. However, these foraging grounds are located close to multi-use areas (e.g., San Andres and Parachique artisanal docks), where economic activities such as artisanal fisheries, aquaculture, and tourism take place. Consequently, green turtles at these foraging grounds are facing considerable anthropogenic threats such as illegal fisheries, bycatch, poaching, boat strikes, and plastic pollution (Paredes-Coral 2017; Quiñones et al. 2017, 2021). We, therefore, encourage studies in these areas that determine the severity of these threats. Moreover, the environmental and behavioural drivers for plastic ingestion should be integrated in future studies to evaluate the impact of this ubiquitous marine pollutant on green turtle health (Santos et al. 2021). This study not only provides ecological information to increase the knowledge base for green turtles of a wide size range, but also informs policymakers on the need to implement management strategies and law enforcement at La Aguada and Virrila Estuary as well as along the pathways linking these important sites.

**Supplementary Information** The online version contains supplementary material available at https://doi.org/10.1007/s00227-022-04126-8.

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**Author contributions** JQ and EP conceived and designed the experiments and performed the surveys on the field; JQ and EP analyzed the data and prepared figures and tables; JQ, EP and JS wrote a first draft of the manuscript. All authors contributed equally to and approved the final version of manuscript.

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**Data availability** The datasets generated during and/or analyzed during the current study are not publicly available, because the intellectual property of all raw data belongs to the government of Peru, specifically the Instituto del Mar del Peru (IMARPE), which belongs to the Ministry of Production; but are available from the corresponding author on reasonable request.

## Declarations

**Conflict of Interests** The authors declare no competing interests.

**Ethical Approval** Research permits were provided by Servicio Nacional de Areas Naturales Protegidas (SERFOR) (National Service for Natural Protected Areas) for conducting sea turtle surveys in La Aguada (N208-2013-SERNANPRNP/ J, N105-2013- SERNANP-RNP/J, N087-2011- SERNANP-RNP/J). Research in the Virrila Estuary were permitted by SERFOR (N° 130–2016 – SERFOR/DGGSPFFS); before 2015 we worked under local permission issued by the Sechura municipality.

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