



Juvenile green turtles demonstrate developmental plasticity in a dynamic seascape

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Abstract

Organisms adopt life-history strategies that optimize growth, survival, and reproduction under varying environmental constraints. Understanding how these strategies vary across life stages is critical for ecological insight and ultimately effective conservation. Although the green turtle (*Chelonia mydas*) is one of the most widely studied marine turtle species, substantial gaps remain in our understanding of juvenile ecology within neritic foraging habitats, where environmental conditions—such as habitat quality, resource availability, and seasonal variability—can have lasting effects on growth, survival, and future reproductive potential. Still, no global synthesis has examined how such environmental variability shapes juvenile development. We conducted a structured global literature review with a thematic content analysis to synthesize current knowledge about juvenile green turtle foraging ecology—encompassing spatial use, diet, and foraging strategies—and associated developmental patterns. Drawing on 172 peer-reviewed studies published from 1979 to 2025; we identify key environmental drivers influencing foraging ecology and development. Our findings reveal substantial variation within and among populations, challenging traditional deterministic models of green turtle ontogeny. Juveniles function as facultative omnivores, with foraging strategies and developmental trajectories shaped by ecological context rather than fixed pathways. This variation reflects how individuals balance energy acquisition, expenditure, and habitat use under different environmental conditions, resulting in context-dependent growth responses rather than discrete or predetermined strategies. Within this context, three broad, non-exclusive growth-motivated strategies emerge: Resident Optimizers, Seasonal Responders, and Competition-Constrained Shifters, each reflecting different responses to environmental conditions and associated energetic constraints. By synthesizing global data, this review advances understanding of juvenile foraging ecology and reveals novel context-dependent, growth-motivated developmental strategies. We provide a foundation for future research and emphasize the need for flexible, regionally tailored conservation approaches that reflect the dynamic nature of juvenile green turtle development.

Keywords systematic review, foraging ecology, developmental strategies, seascape variability, ecological flexibility, growth optimization, environmental drivers

Introduction

A central tenet of life-history theory is that organisms adopt strategies that maximize fitness under environmental constraints by optimizing key processes such as growth, reproduction, and survival (Arendt 1997, Angilletta et al. 2004). In long-lived species, their growth rate during early life stages directly influences age at maturity, susceptibility to predation, and ultimately, lifetime reproductive output (Van der Have and De Jong 1996, Niewiarowski 2001). Faster juvenile growth might enhance survival by reducing time spent in high-risk developmental stages, thereby increasing the likelihood of successful reproduction later in life (Stephens

and Krebs 1986, Huey and Berrigan 2001). Environmental variability further shapes these trade-offs by constraining resource availability and altering energetic demands, thereby influencing energy acquisition, resource use, and behaviour, with consequences for development (Tamburello et al. 2015, Laiolo and Obeso 2017, Pecuchet et al. 2018). Such environmentally mediated developmental responses are widely documented across taxa (Fryxell et al. 2005, Pinaud and Weimerskirch 2007, Fusco and Minelli 2010), and may become increasingly important under projected climate change (Intergovernmental Panel on Climate Change, 2023), which is expected to intensify spatiotemporal variation in habitat quality through changes in both biotic (i.e.

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food availability) and abiotic (i.e. temperature) drivers across systems (Crozier et al. 2008, Donelson et al. 2019). For instance, spadefoot toad tadpoles (*Spea multiplicata*) (Cope 1863) exhibit trophic polyphenism associated with environmental conditions and resource availability (Ghioca-Robrecht et al. 2009), while desert pupfish (*Cyprinodon nevadensis*) (Eigenmann and Eigenmann 1889) display environmentally driven variation in body shape and behaviour across habitats (Lema 2008).

One way this developmental flexibility is expressed is through ontogenetic shifts—transitions between distinct habitats or diets across life stages that are generally considered adaptive responses to changing energetic demands and ecological trade-offs (Werner and Gilliam 1984, Sánchez-Hernández et al. 2019). Ontogenetic shifts are particularly common in marine systems, where dynamic oceanographic processes create marked spatial and temporal variation in habitat quality and resource availability (Kroeker et al. 2020, Jin and Dong 2024). In marine species with complex life cycles, individuals must therefore adjust behaviour, habitat use, and resource acquisition under contrasting ecological contexts (Snover 2008). For example, many fishes shift habitat as they grow, reflecting changes in how individuals balance access to profitable foraging habitats against predation risk and environmental variability as body size and energetic demands increase (Kimirei et al. 2013, Grol et al. 2014). Comparable transitions are also observed in marine turtles, which often move from oceanic to neritic environments as they grow, although the timing and extent of these transitions vary among species, with some remaining oceanic for prolonged periods while others recruit earlier to neritic habitats (Bolten et al. 2003, Candela et al. 2026).

Green turtles (*Chelonia mydas*) (Linnaeus 1758) provide a model species for examining how environmental variability shapes developmental trajectories. This circumglobally distributed species occupies a broad range of habitats across life stages throughout the Atlantic, Pacific, and Indian Oceans (Wallace et al. 2010, Seminoff et al. 2015). Traditionally, green turtle ontogeny has been described as a deterministic progression through three distinct early stages: a terrestrial ‘egg and hatching’ stage, an ‘oceanic early juvenile’ stage, and a ‘neritic juvenile and subadult’ stage during which individuals forage and grow until reaching sexual maturity. Once mature, turtles undertake reproductive migrations between coastal foraging areas and breeding habitats, with females briefly returning to land to nest (Fig. 1; Bolten et al. 2003, Musick and Limpus 2017).

Within this framework, ontogenetic shifts have often been interpreted as developmentally programmed transitions from omnivorous oceanic to herbivorous neritic phases (Bolten et al. 2003, Musick and Limpus 2017). However, even within this traditionally deterministic model, dispersal trajectories during the early oceanic stage are shaped by both ocean circulation patterns and active behavioural responses, exposing individuals from the same rookery to contrasting environments, potentially influencing habitat use and developmental pathways (Putman and Mansfield 2015, Phillips et al. 2025, Candela et al. 2026). Consistent with this, increasing evidence suggests that ontogenetic shifts in green turtles are highly variable both among and within populations. Recent studies have documented substantial variability in habitat use (Williard et al. 2017, Quiñones et al. 2022), diet (Esteban et al. 2020), site fidelity (Williard et al. 2017, Quiñones et al. 2022), and residency (Vélez-Rubio et al. 2018, Pillans et al. 2022), as well as persistence in oceanic habits beyond early ju-

venile stages (López-Mendilaharsu et al. 2005, Alfaro-Shigueto et al. 2011, Turner Tomaszewicz et al. 2018). Together, these findings suggest that ontogenetic shifts can vary according to environmental context and associated trade-offs, rather than being defined by fixed age or size thresholds. Ontogenetic shifts may emerge when somatic growth becomes constrained or when alternative developmental strategies confer greater energetic or ecological advantages (Bjorndal et al. 2000, 2019, Welsh and Mansfield 2022, Vanderklift et al. 2023, Phillips et al. 2025).

Despite growing evidence for variability and plasticity in juvenile development, a comprehensive synthesis of developmental strategies in juvenile green turtles across their global range remains lacking. Understanding this variability is important because juvenile stages represent a critical period for growth, survival, and future reproduction (Bjorndal et al. 1988, Seminoff et al. 2002). Although the global conservation status of green turtles has improved in recent years, with the species now listed as ‘Least Concern’ at the global scale (Wallace and Broderick 2025), populations remain exposed to ongoing anthropogenic and environmental pressures—including habitat degradation, fisheries bycatch, and climate-driven environmental shifts (Fuentes et al. 2023)—and several regional management units (RMUs) remain vulnerable or endangered (Wallace et al. 2025). Consequently, understanding how environmental variability influences juvenile developmental strategies is increasingly important, particularly given rapid anthropogenic-driven change of the marine environment. Yet, research has historically focused disproportionately on reproductive stages and nesting habitats due to their accessibility, while the ‘neritic juvenile and subadult’ stages have remained comparatively understudied (Wildermann et al. 2018, Fuentes et al. 2023). As a result, our understanding of how environmental conditions shape juvenile developmental strategies across populations remains limited.

Here, we compile, analyse, and synthesize available research on juvenile green turtles in neritic habitats, with a particular focus on how environmental drivers shape developmental strategies throughout ontogeny. By identifying common patterns and context-dependent variability, we aim to advance understanding of green turtle ecology and highlight how overlooking key life stages may lead to oversimplified and incomplete perspectives of their life history, with potential consequences for conservation and management (Canale et al. 2010, Beaman et al. 2016). More broadly, we propose that green turtles represent a powerful model for improving our general understanding of how environmental variability shapes developmental strategies in long-lived, mobile species.

Methods

Literature review

We employed a structured approach integrating a systematic literature review with thematic content analysis to synthesize current knowledge on the foraging ecology of juvenile green turtles and associated developmental strategies shaping ontogeny. The synthesis focused specifically on individuals recruited to neritic (coastal) habitats, excluding studies on post-hatchlings or captive turtles. Oceanic individuals were included when carapace measurements indicated transition beyond the early oceanic

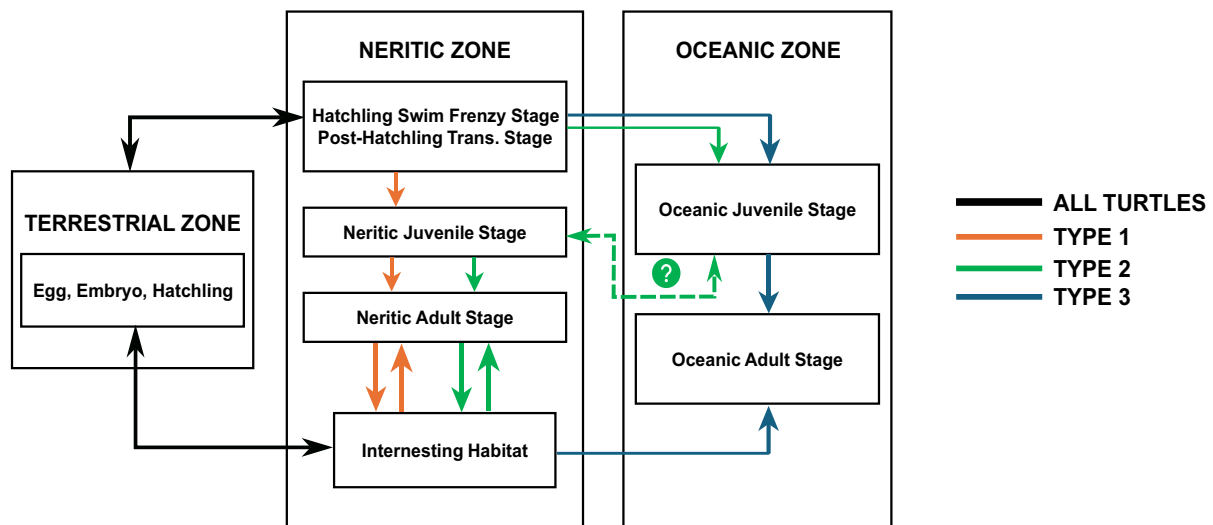


Figure 1 Generalized sea turtle life history, modified from the original schematic by Bolten et al. (2003), illustrating ontogenetic habitat shifts across terrestrial, oceanic, and neritic zones. The schematic follows Bolten's life-history framework describing three generalized developmental patterns based on habitat use and ontogenetic transition (Type 1: complete neritic development; Type 2: oceanic → neritic shift; and Type 3: complete oceanic development). In this modified version, the three life-history types are distinguished by separate pathways, with shared movement steps indicated by black arrows. Green turtles (*Chelonia mydas*) are classically defined as Type 2, characterized by an early developmental stage in the oceanic zone followed by later developmental and foraging stages in neritic habitats. A dashed double-headed arrow, marked with a question mark, highlights uncertainty around the degree of flexibility in juvenile movements between oceanic and neritic habitats within this classic framework.

stage [Curved Carapace Length (CCL): 27–71.2 cm], recognizing that recruitment to neritic habitats varies among regions and populations (Bolten et al. 2003, Seminoff et al. 2003, Musick and Limpus 2017).

An extensive literature search was conducted using Harzing's Publish or Perish full-text databases (Harzing 1997), including peer-reviewed journal articles available on Google Scholar and Scopus, with final access in January 2025. Targeted keyword combinations were used to retrieve studies related to juvenile green turtle diet in neritic environments, foraging, spatial ecology/habitat use, ontogeny, and environmental interactions in the following form: 'green turtle AND juvenile OR immature AND forag* OR neritic OR coastal OR ontogen* OR habitat use OR diet OR environment.' A preliminary search including the scientific name *Chelonia mydas* was also conducted; however, it did not yield additional relevant records and was therefore excluded from the final search string. The search returned 627 publications (500 from Google Scholar and 127 from Scopus), which underwent a multi-stage screening process to refine the dataset (Fig. 2).

The screening protocol followed a structured approach consistent with PRISMA guidelines and consisted of four sequential steps (Page et al. 2021). Step I involved duplicate removal, with 94 duplicates excluded and 533 records retained for screening (Google Scholar: $n = 487$; Scopus: $n = 46$). In Step II, titles, abstracts, and keyword sections were screened to verify inclusion of at least one predefined keywords; 291 studies were excluded, leaving 242 records. During Step III, the remaining studies were reviewed in full to confirm their relevance to juvenile green turtles in neritic environments, 101 studies were excluded because they focused on adult turtles, hatchlings, or captive individuals, unless juvenile-specific data were provided. This resulted in 141 eligible studies. Eligibility required addressing at least one of the following themes: coastal recruitment, ontogenetic development, diet, foraging behaviour, spatial use, or environmental influences

on these processes. Finally, Step IV employed backward snowballing method by reviewing reference lists of the included studies, adding 31 relevant studies not captured in the initial search (Fig. 2; Supplementary Material 1). This approach ensured a curated dataset representative of the current understanding of juvenile green turtle foraging ecology across geographic regions (Supplementary Material 1).

Database construction and thematic content analysis

Data from the selected publications were compiled into a structured database and classified under three thematic domains: Study Site Information, Turtle-Specific Data, and Foraging and Developmental Strategies Information, aligned with the analytical objectives of this review (Fig. 2).

Study Site Information included country, site and geographic coordinates (i.e. latitude and longitude), ocean basin, and physical characteristics (e.g. habitat type, tidal regime, average depth, climate classification, and sea surface temperature), when reported. Temporal aspects were recorded, including the years and months during which data collection occurred. Each study site was geographically referenced to the appropriate Green Turtle RMU, based on the framework developed by Wallace et al. (2023).

Turtle-Specific Data encompassed biological descriptors and methodological attributes. These included the life stage of sampled individuals, sample sizes, and morphometric measurements such as CCL or SCL, reported as mean, minimum, and maximum values. To ensure comparability across studies and regions, SCL measurements were converted to CCL using region-specific linear equations derived from published studies (Supplementary Material 2). Sample size was reported in all but one study, while life stage was not specified in 11 studies. If recruitment size—

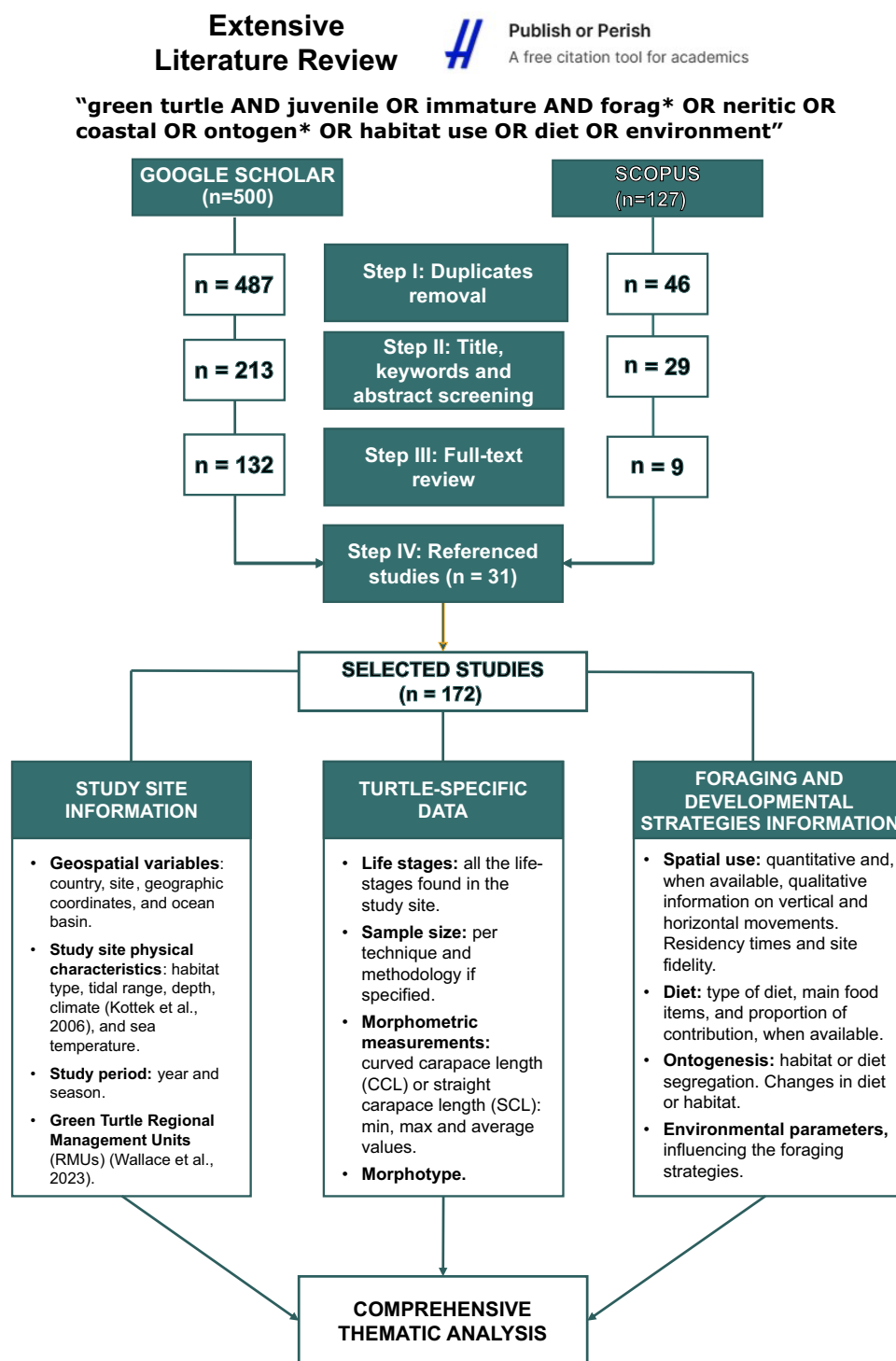


Figure 2 Schematic of the systematic literature review and data extraction framework used to synthesize knowledge on the foraging ecology and developmental strategies of juvenile green turtles in neritic habitats. The initial search, conducted using Harzing's Publish or Perish software, returned 627 records from Google Scholar ($n = 500$) and Scopus ($n = 127$), with final access in January 2025. Numbers in the screening flow indicate records retained after each step. Following duplicate removal ($n = 94$), 533 records were retained for title, abstract, and keyword screening. This screening stage excluded 291 records, leaving 242 records for full-text assessment. Full-text screening excluded a further 101 records that did not meet the inclusion criteria, including studies focused only on adults, hatchlings, captive individuals, or records without clearly defined life-stage information. Backward citation searching of included papers added 31 studies, yielding a final curated dataset of 172 studies. Extracted studies were analysed to construct a structured database categorized into three thematic areas: Study Site Information [geospatial coordinates, ocean basin, habitat type, tidal regime, depth, climate, sea surface temperature, study period, and Green Turtle RMUs (Wallace et al. 2023)]; Turtle-Specific Data (life stages, sample sizes by technique, morphometrics such as curved and straight carapace length (CCL/SCL) with conversions where required (Supplementary Material 2), morphotype]; and Foraging and Developmental Strategies, encompassing spatial use patterns, site fidelity, residency times, diet, and ontogenetic shifts in diet or habitat use, as well as the potential environmental parameters influencing this (Supplementary Material 1).

defined here as the size at which individuals first enter and begin using neritic foraging habitats (Bolten et al. 2003)—was explicitly reported in a study, then that value was used. If not specified, then we used the smallest CCL of live individuals observed at the foraging ground, excluding records from stranded or dead turtles to avoid potential bias from individuals that may not have yet transitioned from oceanic habitats (Supplementary Material 2). Morphotype information (e.g. ‘black’ and ‘yellow’ turtles in the Pacific) was recorded where available but did not provide sufficient resolution to differentiate foraging or developmental strategies (Pritchard 1971, Álvarez-Varas et al. 2021).

Foraging and Developmental Strategies Information captured ecological patterns associated with diet and spatial use. Spatial use was categorized both horizontally (e.g. home range, core areas of habitat use) and vertically (e.g. dive profiles), with preference given to quantitative metrics such as mean depth, utilization distribution or net distance movements. Where reported, we also recorded long-distance displacements undertaken by individuals (Supplementary Material 3). Across studies, core areas and home ranges were most defined as the 50% and 95% utilization distributions (UD50 and UD95), representing core and representative habitat use areas, respectively. Where these metrics were absent, qualitative descriptions of spatial use were recorded.

Diet composition was analysed at the lowest available taxonomic level, with main food items (i.e. seagrasses, macroalgae, terrestrial plants, and animal matter) (Esteban et al. 2020) used to infer diet types (Supplementary Material 4). Diet was classified as herbivorous when plant matter $\geq 94\%$ of the total composition, and as omnivorous when animal matter $> 6\%$, consistent with interpretations used in studies reporting quantitative dietary data (Brand-Gardner et al. 1999, Arthur and Balazs 2008, Nagaoaka et al. 2012, Stringell et al. 2016). For studies lacking quantitative proportions, dietary categories followed the original study interpretation or the primary food items reported. Ontogenetic variation in both spatial use and diet composition was recorded where available. Methods used for data collection (e.g. satellite and acoustic telemetry, stable isotope analysis, and gut content examination) were documented to assess comparability across studies and identify prevailing techniques. Environmental drivers influencing foraging strategies were also extracted when identified by study authors (Supplementary Material 1). Together, these parameters were used to assess how local and regional environmental conditions may shape foraging ecology and developmental strategies.

Synthesis and mapping

Following database construction, data were analysed to identify regional patterns in juvenile green turtle foraging ecology. Information on spatial use and diet was synthesized across studies to detect trends, while developmental strategies were recorded where ontogenetic transitions were described. Environmental parameters were analysed in tandem with ecological data to assess their role in shaping foraging ecology and developmental strategies. Key findings were subsequently mapped in R version 4.3.2 (R Core Team 2023) using the *sf* package (Pebesma and Bivand, 2023) for handling and visualizing spatial vector data, together with maps (Becker et al. 2018) and *rnatualearth* (Massicotte et al. 2023) to obtain global coastline and regional boundary lay-

ers. These packages enabled visualization of regional variation in foraging strategies.

Results

Our synthesis included 172 studies covering 176 unique site records. Nearly 90% were published between 2005 and 2025, reflecting growing interest in juvenile green turtle ecology, albeit with uneven geographic coverage. The Atlantic (55.8%) and Pacific (37.8%) Oceans dominated the dataset, while the Indian Ocean (5.8%) and Mediterranean Sea (2.3%) were poorly represented. Within the Atlantic, the North and Tropical Atlantic accounted for 25.6% and 17.4% of studies, respectively. In the Pacific, the North Pacific accounted for 18.0% of records, while other regions each contributed $< 10\%$. Among RMUs, the North Atlantic (RMU 11) alone accounted for 39.5% of mapped studies, whereas several regions, including the Northwest Indian (RMU 14) and parts of the Pacific (RMUs 19 and 20), were poorly represented (Fig. 3; Supplementary Material 1).

Among the 172 studies, 52.9% examined spatial use, 49.4% diet, and 22.7% ontogeny, with considerable thematic overlap (33 studies covering two topics and three addressing all three) (Fig. 3; Supplementary Material 1). Spatial use ($n = 91$) was primarily investigated using satellite and acoustic telemetry, and capture-mark-recapture (71.4%), with biologgers used less frequently. Diet studies ($n = 85$) most often relied on gut content or oesophageal lavage (52.9%), followed by stable isotope analysis (SIA, 38.8%), with comparatively fewer studies using other approaches (e.g. microbiome, eDNA). Ontogeny-focused research ($n = 39$) similarly relied on diet-based approaches, particularly SIA (43.6%) and gut content-based methods (33.3%) (Supplementary Material 1).

Across studies examining drivers of juvenile foraging and development, we identified 14 categories of environmental parameters, including four key categories: resource availability (mentioned in the majority of spatial-use and ontogeny related studies), resource distribution (mentioned mainly in spatial-use studies), resource quality (mentioned mainly in diet studies), and temperature (mentioned in all three types of studies). Habitat structure and diel patterns of foraging and resting were also mentioned regularly. However, 23.1% of studies were purely descriptive and did not explicitly link behaviour to environmental parameters.

Earliest life stage observations at neritic foraging grounds

Minimum size data from 104 study sites were consolidated to 80 locations by retaining only the smallest individual per site (Supplementary Material 2). Of these, 66.3% were in the Atlantic, 23.7% in the Pacific, and 5.0% both in the Indian Ocean and Mediterranean Sea, highlighting regional gaps in early recruitment data. Minimum size was generally higher in the Pacific, averaging 38.6 ± 5.5 cm CCL, with 78.9% of sites reporting 35.0–45.0 cm CCL. For the Atlantic Ocean, CCL averaged 29.8 ± 6.7 cm, with 62.2% of sites reporting 25.0–35.0 cm. Smaller individuals (~ 15.0 cm CCL) were reported in the north-west Gulf of Mexico (Moncada et al. 2006, Howell et al. 2016), whereas larger CCL (> 39.0 cm) were recorded at multiple Atlantic sites (Griffin et al. 2019, Metcalfe et al. 2020, Metz et al. 2020). In the Mediterranean

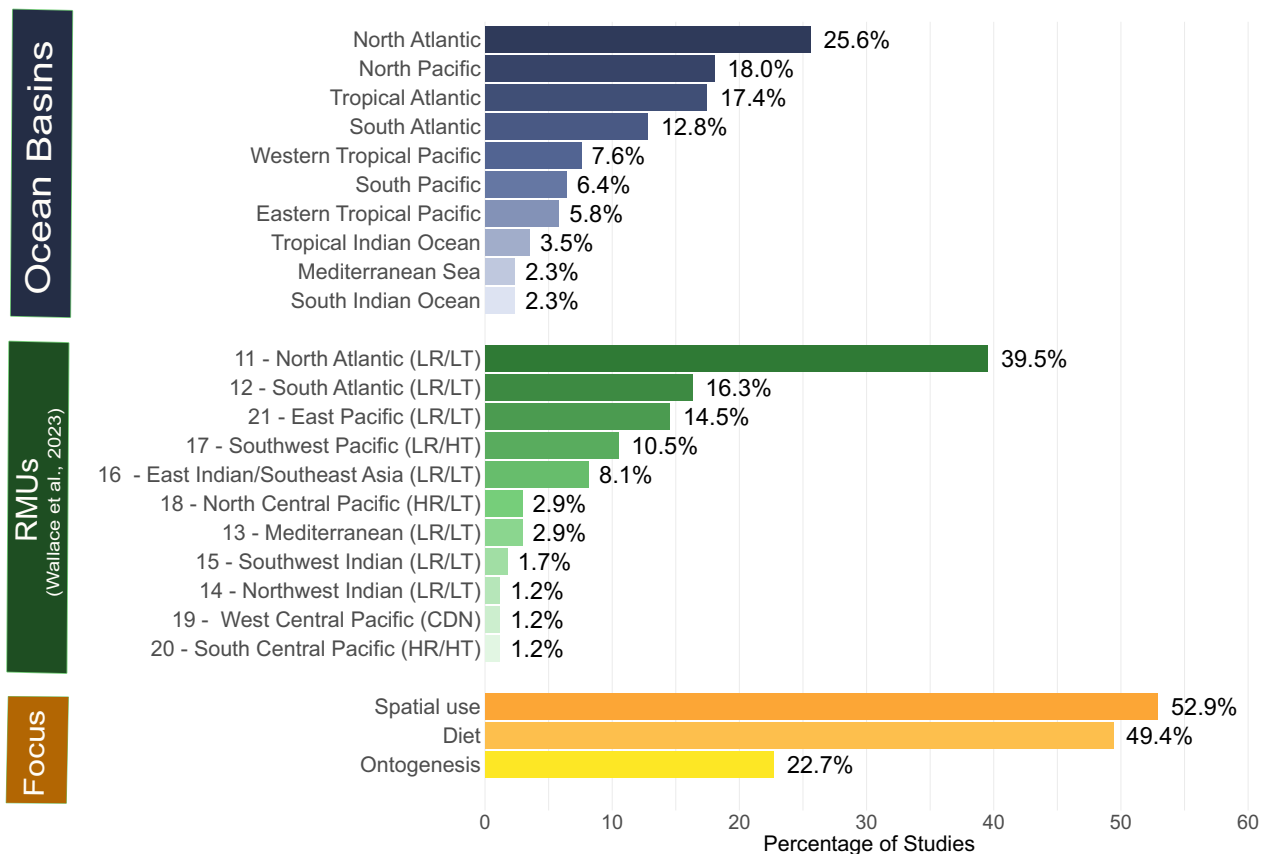


Figure 3 Proportion of studies associated with each Ocean Basin, RMU (Wallace et al. 2023), and study focus. The bars represent the percentage of the total dataset that pertains to each category. These proportions reflect how frequently studies address specific geographic regions or research themes. Because some studies cover multiple Ocean Basins or RMUs, and many address more than one research focus (e.g. both diet and spatial use), the cumulative proportions within each group may exceed or fall short of 100%. RMUs are labelled with conservation status codes based on Wallace et al. (2025), which include: LR—Low Risk, HR—High Risk, LT—Low Threat, HT—High Threat, and CDN—Critical Data Needs. These classifications indicate the relative conservation urgency for each RMU, considering biological vulnerability, threat level, and the need for further data (Supplementary Material 1).

Sea (i.e. Cyprus, Greece, and Israel), limited data suggest recruitment may occur between 25.0 and 30.0 cm CCL (Margaritoulis and Teneketzis 2003, Cardona et al. 2010). Indian Ocean records span from 18.5 cm in Dolphins' Bay, Iran (Rezaie-Atagholipour et al. 2021), to >40.0 cm in Mangrove Bay, Australia (Pillans et al. 2022) (Supplementary Material 2).

Movement patterns and residency

Juvenile green turtles exhibit substantial variability in spatial use across neritic foraging grounds, reflected in wide variation in core areas (UD50), and home ranges (UD95), both among and within sites (Supplementary Material 3). However, the spatial and temporal extent represented by these metrics varied considerably across studies. Differences in tracking methodology, study duration, and analytical approaches influenced the precision and comparability of estimates, with some studies incorporating broader-scale movements into home range calculations while others effectively excluded them. Consequently, observed variability likely reflects a combination of biological differences and methodological variation and should therefore be interpreted cautiously, particularly in cross-study comparisons.

For instance, some turtles exhibit restricted movements, with average UD50s of 0.01 km² (± 0.00 SD) in Saint Thomas, US Virgin Islands (Tropical Atlantic) (Brunson et al. 2024) and average UD95s of 0.02 km² (± 0.00 SD) in Seal Beach, USA (northeastern Pacific) (Crear et al. 2017). Conversely, much larger movements were reported in the Gulf of Mexico (northwest Atlantic), with average UD50s of 332.00 km² (± 353.60 SD) and average UD95s of 2186.80 km² (± 1151.80 SD) (Shaver et al. 2013, Metz et al. 2020). Inter-individual variability within populations is also pronounced, with UD95s ranging from 0.39 to 143.25 km² in Martinique (Tropical Atlantic) (Siegwalt et al. 2020) and 34.10 to 910.00 km² in Mauritania (southeastern Atlantic) (Mestre et al. 2025), and UD50s from 63.50 to 1056.70 km² in Texas, USA (North Atlantic) (Shaver et al. 2013). Despite these extremes, most studies report average foraging UD50s <10.00 km² and UD95s <25.00 km² (Supplementary Material 3). Across studies where both CCL and space-use metrics were reported (UD50: $n = 37$; UD95: $n = 28$), no consistent relationship was detected between those.

Localized residency and restricted space use

Smaller UD50s (<10.00 km²) and UD95s (<25.00 km²) are typically associated with localized resource availability, diel movements,

and sheltered habitats that reduce exposure to environmental stressors. In Martinique (Atlantic Ocean) and Mayotte (western Indian Ocean), turtles show strong fidelity to small seagrass patches, with movements influenced by local currents, tides, and resting-site availability (Chambault et al. 2018, 2020, Siegwalt et al. 2020). Similar patterns occur in Palm Beach, USA (northwest Atlantic), where restricted space use is linked to algae-rich patch reefs in a high-energy coastal setting (Makowski et al. 2006), and across reef and mangrove systems (i.e. Mangrove Bay, Australia, and eastern Indian Ocean) where foraging and sheltering areas overlap (Hazel et al. 2013, Crear et al. 2017, Pillans et al. 2022). However, substantial inter-individual variation persists, with some individuals occupying home ranges up to four times larger than others within the same population (Makowski et al. 2006, [Supplementary Material 3](#)).

Overwintering strategies and seasonal displacement

Large UD50s ($>26.00 \text{ Km}^2$) and UD95s ($>44.00 \text{ Km}^2$) values often reflect seasonal displacement between distinct areas, rather than persistent year-round use of the entire estimated range. During colder periods, juvenile green turtles exhibit a range of responses to declining water temperatures (typically decreasing to $10\text{--}20^\circ\text{C}$ depending on region), often accompanied by changes in resource availability and quality. Where seasonal displacement occurs, utilization distributions reflect the extent of those displacements, rather than continuous residency within single home ranges (Metz et al. 2020, [Supplementary Material 3](#)).

Overwintering responses include coastal displacement towards warmer regions, or displacements into more thermally stable waters through offshore movements into deeper oceanic habitats beyond the neritic zone. Coastal movements have been documented in the southwestern Atlantic (Argentina, Uruguay, and Brazil), Gulf of Mexico, Japan (northwestern Pacific), and North Carolina, USA (northwestern Atlantic) (Carman et al. 2012, Shaver et al. 2013, Williard et al. 2017, Vélez-Rubio et al. 2018, Fukuoka et al. 2019, Metz et al. 2020, Gama et al. 2021). Offshore overwintering has also been reported in multiple regions, including Brazil and Uruguay (southwestern Atlantic), Florida and North Carolina (northwestern Atlantic) (Carman et al. 2012, Williard et al. 2017, Welsh and Mansfield 2022). Interestingly, individuals within the same population, such as in the northwestern Atlantic (North Carolina, USA), can adopt different strategies (McClellan and Read 2009). In Banc d'Arguin, Mauritania (eastern Atlantic), turtles move from shallow coastal waters to adjacent offshore/oceanic habitats during colder months before returning to coastal areas, maintaining strong site fidelity while exhibiting large home ranges ($\text{UD95} = 163.10 \pm 230.30 \text{ km}^2$) that reflect these seasonal displacements rather than continuous use of broad foraging areas (Mestre et al. 2025).

Among turtles exhibiting seasonal displacement, some return to the same foraging sites following winter, whereas others establish new foraging areas, resulting in sequential rather than persistent home ranges and suggesting cyclic responses to seasonal environmental conditions rather than unidirectional developmental shifts (Vélez-Rubio et al. 2016, Crear et al. 2017, Williard et al. 2017, Fukuoka et al. 2019, [Supplementary Material 3](#)). However, this distinction is often difficult to resolve because tag loss and short tracking duration rarely allow multi-year observations (Carman et al. 2012, Fuentes et al. 2020, Metz et al. 2020).

Not all turtles respond to declining temperatures with large-scale movement. Some remain resident, reduce activity, and shift into deeper waters available within the coastal area (Southwood et al. 2003, Lamont et al. 2015, Hardy et al. 2023). In these cases, reduced movement may function as a third overwintering strategy (i.e. brumation), allowing turtles to persist locally despite potentially unfavourable temperatures, without long-distance displacement (Seminoff 2000, Lamont et al. 2018).

Unidirectional movements and developmental displacements

In contrast to seasonal, reversible displacement, some turtles exhibit non-seasonal, unidirectional movements that do not coincide with temperature decline and are rarely followed by a return to the original foraging area. These movements are commonly interpreted as ontogenetic transitions associated with increasing body size or shifts in habitat use, and are therefore classified here as developmental displacement (Meylan et al. 2011). However, departures from established foraging grounds have also been associated with crowding, resource depletion and declining growth rates, indicating that density-dependent constraints may contribute to their timing. In Florida and the Bahamas, for instance, departures occurred without consistent size or seasonal thresholds and were instead associated with declining resource availability and population recovery (Bjorndal et al. 2019, Meylan et al. 2022). Potentially comparable density- or resource-dependent movements have been reported in the eastern Atlantic and northwestern Pacific, although the underlying mechanisms remain less clearly resolved (Nishizawa et al. 2013, Lelong et al. 2024).

Turtles undertaking unidirectional movements were generally larger than those exhibiting seasonal displacement (mean CCL: $73.30 \pm 13.60 \text{ cm}$ vs. $46.40 \pm 13.10 \text{ cm}$; Welch's two-sample t -test: $t = 8.65$, $df = 44.36$, $P < 0.001$) ([Supplementary Material 3](#)). This size difference indicated that developmental displacement is size-structured but does not necessarily demonstrate a fixed ontogenetic threshold or distinguish intrinsic developmental effects from density-dependent constraints on growth. These movements were more frequently reported in the North and Tropical Atlantic, although this likely reflects sampling bias linked to greater research effort in those regions and the extended monitoring required to detect return movements or lack thereof (Meylan et al. 2011, Chambault et al. 2018, Siegwalt et al. 2022). Comparable long-distance movements have also been documented in the northwestern Pacific (e.g. Japan and Korea), although it remains unclear whether individuals return to their original habitats, with movements likely reflecting unresolved combinations of seasonal and developmental displacements (Shimada et al. 2014, Fukuoka et al. 2015, 2019, Jang et al. 2024).

Diet and trophic plasticity

Globally, juvenile green turtle diets were classified at the population level as either herbivorous ($n = 37$, 43.00%) or omnivorous ($n = 42$, 48.80%); however, these categories are not mutually exclusive, as 7 populations (8.20%) showed variation in diet classification across independent studies depending on methodology or sampling periods ([Supplementary Material 4](#)). For example, the Bahía Magdalena population (Mexico, eastern Pacific) was described as omnivorous (López-Mendilaharsu et al. 2005), but

also herbivorous during part of that period (López-Mendilaharsu et al. 2008). Similar discrepancies were reported at the Paranaguá Coast, Brazil (southwest Atlantic) (Guebert-Bartholo et al. 2011, Gama et al. 2016, 2021, 2024), as well as in Kane'ohe Bay, USA (central Pacific) (Seaborn et al. 2005, Arthur and Balazs 2008) and the Bermuda Platform, Bermuda (North Atlantic) (Burgett et al. 2018, Gulick et al. 2021); these discrepancies might be related to differing methodologies (e.g. Guebert-Bartholo et al. 2011, Gama et al. 2016, 2021, 2024).

Across sites, macroalgae are more frequently consumed than seagrasses, dominating 56.3% of herbivorous and 48.7% of omnivorous diets (Supplementary Material 4). Turtles show a consistent preference for Rhodophyta (red algae) across regions. For example, red algae contributed >65% at several sites (e.g. Noronha, Brazil; Kawela Bay, USA; and Wiggins Island, Australia) (Balazs et al. 1987, Seminoff et al. 2002, Prior et al. 2016, Holloway-Adkins and Dennis Hanisak 2017, Martins et al. 2020, Supplementary Material 4). This preference is consistent across regions and not restricted to macroalgae-dominated systems. For instance, in Moreton Bay, Australia (Pacific Ocean), red algae accounted for 47.30% of the diet, comparable to seagrass (45.70%), despite the latter being a dominant habitat-forming resource (Brand-Gardner et al. 1999). Chlorophyta (green algae) are rarely dominant and often increase when preferred Rhodophyta are limited (López-Mendilaharsu et al. 2008, Carrión-Cortez et al. 2010, Bastos et al. 2022), while Phaeophyta (brown algae), mostly consumed in tropical regions, contribute ≤16% of diet composition (Carrión-Cortez et al. 2010, Reisser et al. 2013, Read et al. 2024). Occasional increases in drifting *Sargassum* consumption have been attributed to seasonal shifts in availability, consistent with opportunistic foraging (Howell and Shaver 2021).

Macroalgae consumption is geographically widespread and shows no clear distributional pattern, whereas seagrass-dominated diets are regionally concentrated, particularly in the North and Tropical Atlantic and western Tropical Pacific, where they can account for >80% of dietary intake (Limpus et al. 2005, Stringell et al. 2016, Read et al. 2024, Supplementary Material 4). In these regions, turtles often preferentially consume native, higher-nutrient seagrass species such as *Thalassia testudinum* and/or *Syringodium filiforme* (Christianen et al. 2019, Cassell et al. 2024, Supplementary Material 4), although dietary flexibility is evident where these are replaced or limited, incorporating invasive species such as *Halophila stipulacea* despite its lower nutritional quality (Siegwalt et al. 2022).

Animal matter is a consistent diet component across many foraging grounds, including both the southwest and southeast Atlantic (e.g. Mauritania, Argentina, and Brazil) (Cardona et al. 2009, González Carman et al. 2014, Morais et al. 2014) and Pacific (e.g. New Caledonia, Colombia, and Peru) (Amorocho and Reina 2007, Quiñones et al. 2022, Read et al. 2024). Diets commonly include cnidarians, ctenophores, tunicates, and other slow-moving or sessile invertebrates (i.e. molluscs, crustaceans, echinoderms, or poriferans). Their contribution may often be underestimated due to limitations of gut-content analysis in detecting remains of soft-bodied prey (Seminoff et al. 2002). Occasional ingestion of vertebrate prey, such as fish, has also been reported (Parker et al. 2011, Gama et al. 2024), in some cases linked to scavenging associated with fisheries (Clyde-Brockway et al. 2022, Supplementary Material 4).

Consumption of terrestrial plant material, particularly mangrove components, is uncommon but can occur locally under constrained conditions. For example, ingestion has been documented in Cananéia, Brazil (southwest Atlantic) and Gorgona, Colombia (eastern Pacific), likely reflecting restricted access to preferred resources or local environmental conditions (Amorocho and Reina 2007, Nagaoka et al. 2012), with additional records reported across multiple regions (i.e. Argentina, Australia, and Bermuda) (Limpus et al. 2005, Carman et al. 2012, Gulick et al. 2021).

In contrast to neritic foraging grounds, some juvenile turtles forage in oceanic habitats where vegetation is unavailable. In these environments, diets are dominated by animal matter, as evidenced by gut content and stable isotope analyses (Turner Tomaszewicz et al. 2017, Fukuoka et al. 2019, Piovano et al. 2020, Seminoff et al. 2021), with some individuals described as fully carnivorous (Parker et al. 2011).

Dietary variation is evident both between and within populations. In Green Island, Australia (southwestern Pacific), e.g. some individuals specialize on macroalgae while others feed primarily on seagrass, with evidence of switching diets over time (Fuentes et al. 2006). In Shark Bay, Australia (eastern Indian Ocean), dietary specialization has been linked to predator presence, which may constrain access to preferred foraging areas (Burkholder et al. 2011). Beyond local spatial variation, seasonal shifts in diet are common in regions with strong productivity pulses. In the southwest Atlantic, turtles feed on gelatinous zooplankton in Argentinian waters during summer and move north in winter to forage on macroalgae and seagrass in Uruguay and Brazil (Carman et al. 2012, Vélez-Rubio et al. 2016, Campos and Cardona 2019). Comparable patterns occur in upwelling zones where oceanographic changes affect resource availability. For instance, in the Paranaguá Estuary, Brazil (South Atlantic), macroalgae dominate during warmer months while animal matter consumption increases in autumn and winter when these resources become more abundant (Gama et al., 2016, 2021, 2024). Similar responses have been documented in eastern Pacific regions (i.e. Colombia, Costa Rica, or northwestern Mexico), where turtles exploit short-lived resource pulses (López-Mendilaharsu et al. 2008, Sampson et al. 2018, Clyde-Brockway et al. 2022). These patterns indicate that individuals can remain resident while adjusting their diets to seasonal changes in resource availability, although those short-lived switches in diet to take advantage of ephemeral prey pulses are likely underrepresented due to methodological limitations (Burkholder et al. 2011, Esteban et al. 2020).

Size-related variation in spatial use and diet

Ontogenetic changes in habitat use and diet were widely documented across studies, although the degree of spatial and trophic segregation varied. Spatial analyses frequently showed habitat partitioning between life stages within and among foraging grounds. Smaller individuals typically occupy shallow, sheltered, and nearshore areas, whereas larger turtles are more often found in deeper or offshore habitats (Madeira et al. 2022, Welsh and Mansfield 2022, Vanderklift et al. 2023). This pattern is particularly evident in environments with strong hydrodynamic conditions or high predator presence, where shallow habitats may reduce ener-

getic expenditure and predator risk for smaller turtles (Hazel et al. 2013, Fernandes et al. 2017, Mello-Fonseca et al. 2021).

Across multiple regions, larger body size (CCL) is positively correlated with distance from shore, as reported in Mangrove Bay, Australia (eastern Indian Ocean) and Hawaii, USA (central Pacific) (Meylan et al. 2022, Vanderklift et al. 2023). Vertical segregation generally mirrors this pattern, with smaller turtles remaining in shallower waters that provide greater shelter (Carrión-Cortez et al. 2010, Nagaoka et al. 2012, Roche et al. 2021). Mean dive depths range from <1 m in estuarine systems (McClellan and Read 2009) to ~7 m in island environments like Mayotte, France (western Indian Ocean), with occasional deeper dives (>30 m) linked to thermoregulation and/or shelter (Chambault et al. 2020).

At broader spatial extents, size-structured patterns across latitude have been reported, although the underlying drivers remain unclear. In the northwestern Pacific, smaller turtles (37–43 cm CCL) occur seasonally in northern areas (e.g. Sanriku Coast, Japan), while larger individuals (50–70 cm CCL) are more frequent in southern regions (e.g. Jeju Island, Korea, South China Sea) (Shimada et al. 2014, Fukuoka et al. 2019, Jang et al. 2024). Similar gradients have been described in the southwestern Atlantic and southeastern Pacific, with smaller turtles more common at higher latitudes (e.g. Argentina, Chile, and Peru) and larger individuals in tropical regions (e.g. Brazil and Ecuador) (Velez-Zuazo et al. 2014, Álvarez-Varas et al. 2017, Campos and Cardona 2019). Nonetheless, these patterns are not consistent across all regions, and several sites—including some located in Fiji (southwestern Pacific), Malaysia (eastern Indian), Australia (southwestern Pacific), or Japan (northwestern Pacific)—support a wide range of body sizes (Hazel et al. 2009, Hamabata et al. 2015, Palaniappan and Hamid 2017, Piovano et al. 2020). Since most studies are limited to one or two sites, this makes it difficult to disentangle latitudinal effects from variation in habitat structure, prey availability, and oceanographic conditions. As a result, observed size-latitude associations likely reflect a combination of regional environmental context and size-dependent habitat use, rather than latitude or temperature alone.

Ontogenetic shifts are often more clearly detected through dietary analyses (Supplementary Material 1). Stable isotope and gut content studies commonly indicate a shift from omnivory in smaller individuals to increased herbivory with size (Arthur et al. 2008, Morais et al. 2014). However, substantial trophic overlap among size classes persists in some populations—including Shark Bay, Australia (eastern Indian Ocean), Bahía Magdalena, Mexico (western Pacific), or Sao Tome and Principe and Turks and Caicos (Atlantic Ocean)—indicating weaker ontogenetic differentiation (López-Mendilaharsu et al. 2008, Burkholder et al. 2011, Stringell et al. 2016, Hancock et al. 2018).

Discussion

Traditional views of green turtle ontogeny emphasize a relatively fixed, size-based progression through habitats and diets (Bolten et al. 2003, Arthur et al. 2008, Musick and Limpus 2017). Our synthesis challenges this paradigm and instead supports a context-dependent framework in which juveniles exhibit both intra-individual plasticity (adjusting behaviour over time), and inter-individual plasticity (distinct developmental approaches within populations) (Shimada et al. 2014, Turner Tomaszewicz et al.

2017, Campos and Cardona 2019). Juveniles function as facultative omnivores whose foraging and habitat-use decisions balance energy acquisition and expenditure to support continued growth under varying ecological conditions. Rather than following a pre-determined herbivore-dominated developmental trajectory, these responses emerge through the combined influence of ecological pressures—including temperature, the resource landscape (i.e. availability and distribution of prey), population density, and resource quality—as well as in inter-individual differences.

Temperature influences metabolic performance—including digestive capacity and energy budgets—thereby shaping growth, activity, and habitat use. In cold waters, reduced digestive efficiency limits consumption of fibrous diets such as seagrasses due to slower gut passage and enzymatic activity (Bjorndal 1980, Mendonca 1983, Innis et al. 2007), consistent with patterns observed in other herbivorous reptiles (Troyer 1982, Bjorndal 1997). Although the thermal sensitivity of microbial fermentation in green turtles remains unclear; reduced digestive throughput may favour reliance on readily digestible animal matter in cooler environments (Bjorndal 1979, Lamont and Iverson 2018, Gama et al. 2024). Seasonal cooling can also reduce foraging activity altogether (Bjorndal 1980, Mendonca 1983, Innis et al. 2007), leading to a range of responses—including metabolic dormancy, relocation to warmer areas, or movement to deeper thermally stable waters (Felger et al. 1976, Parker et al. 2011, MacDonald et al. 2012, Shaver et al. 2013, Lamont et al. 2015, Williard et al. 2017, Vélez-Rubio et al. 2018, Welsh and Mansfield 2022, Hardy et al. 2023). Together, these responses reflect context-dependent trade-offs between maintaining energy intake and reducing expenditure, with important consequences for body condition and growth (Ultsch 2006, Vélez-Rubio et al. 2018, 2026), rather than fixed movement behaviours.

The **resource landscape** shapes how and when resources can be accessed, influencing both foraging behaviour and space use. In dynamic ecosystems—such as Gorgona National Park, Colombia (eastern Pacific)—productivity pulses associated with upwelling and phytoplankton blooms promote frequent shifts in foraging areas or opportunistic use of ephemeral prey (Amorcho and Reina 2007, Cardona et al. 2010, González Carman et al. 2014, Vélez-Rubio et al. 2016, Turner Tomaszewicz et al. 2018, Fukuoka et al. 2019, Piovano et al. 2020). Turtles may rapidly adjust their diet, space use, or both in response to short-term variation in prey availability, distribution and renewal (Godley et al. 2003, Meylan et al. 2022, Mestre et al. 2025). However, such responses are likely underrepresented in the literature because short-lived dietary shifts and associated displacements are difficult to detect unless sampling coincides with transient events (Heaslip et al. 2012, Pecuchet et al. 2018). In more stable systems, turtles generally show stronger site fidelity and respond to local variation through adjustments in diet or microhabitat rather than broad spatial displacements (Prior et al. 2016, Siegwalt et al. 2022, Gama et al. 2024). Even within stable environments, local variation in prey availability may still promote flexible resource use when energetically advantageous (López-Mendilaharsu et al. 2008, Quiñones et al. 2022, Vanderklift et al. 2023).

Density-dependence further shapes developmental responses. Where resource availability declines relative to population density, competition can constrain growth and promote displacement. Although these movements may have been inter-

preted as fixed ontogenetic transitions, the absence of consistent size thresholds linked with those displacements suggests this may not be the case (Bjorndal et al. 2000, 2019). Instead, crowding and declining resource availability may affect individuals' energy allocation among maintenance and growth differently, producing flexible displacement responses to those local constraints (Bjorndal et al. 2019, Meylan et al. 2022).

Resource quality also influences prey selection and intake. Even in resource-rich areas, turtles often target prey that maximize energetic return, whereas more fibrous or chemically defended taxa are consumed less frequently (Foster and Hodgson 1998, Kasimala et al. 2015, Siegwalt et al. 2022). Where high-quality resources are scarce or seasonally unavailable, individuals may shift towards less nutritious items or increase intake to maintain energy balance (Forbes 1996, Cardona et al. 2010, Lamont and Iversen 2018, Gama et al. 2021, Siegwalt et al. 2022). Prey selection therefore reflects trade-offs among nutritional quality, digestibility and energetic return, reinforcing the role of facultative omnivory in supporting juvenile growth optimization (Stephens and Krebs 1986, Heaslip et al. 2012, Hays et al. 2018).

Collectively, these drivers suggest that 'juvenile and sub-adult phases' are better understood as a continuum of context-responsive developmental states rather than as fixed ontogenetic stages. This interpretation parallels the recent reassessment of the early juvenile 'oceanic stage' as an active and responsive dispersal phase (Williard et al. 2017, Gaspar et al. 2025, Phillips et al. 2025). We propose three broad, non-exclusive developmental strategies, observed both across and within populations, within this continuum: Resident Optimizers, Seasonal Responders, and Competition-Constrained Shifters (Fig. 4). These strategies are not defined solely by movement, but by how individuals adjust behaviour, diet, activity, and space use to optimize growth under local ecological and energetic constraints.

Resident Optimizers occupy neritic habitats where thermal conditions are favourable and relatively stable, and high-quality foraging resources remain consistently available, supporting year-round growth. These habitats are also characterized by low to moderate population density, which minimizes competitive energetic constraints and reduce the need for spatial adjustments to maintain energy intake. Individuals consequently exhibit strong site fidelity and restricted space use. Local variation in resource availability or predation risk is accommodated through fine scale shifts in diet or microhabitat use, rather than displacement to new foraging areas. This strategy has been documented across tropical and subtropical Atlantic foraging grounds (Godley et al. 2003, Lamont et al. 2015, Campos and Cardona 2019, Griffin et al. 2019, 2020, Metz et al. 2020, Meylan et al. 2022, Hardy et al. 2023, Lamont and Hart 2023, Brunson et al. 2024) but may appear disproportionately common because research has been concentrated in those stable, well-studied systems. The prevalence of this strategy may, however, diminish as populations recover and competition for resources increases (Hays et al. 2024, 2025).

Seasonal Responders occur where seasonal changes in temperature and resource availability create cyclic constraints and opportunities. Resources vary across space and time, producing seasonal changes in their availability and quality, as well as in the intensity of competition. Individuals respond through reversible movements among coastal or offshore habitats, seasonal dietary shifts or reduced activity while overwintering (brumation-

like) within the same area (Felger et al. 1976, Cardona et al. 2010, Fukuoka et al. 2019, Piovano et al. 2020, Vélez-Rubio et al. 2026). These responses allow turtles to exploit temporary resource pulses or avoid periods when low temperatures reduce digestive performance and resource availability. Rather than representing permanent habitat transitions, they reflect a close link among thermal conditions, trophic opportunities and energetic requirements. This strategy requires considerable behavioural and physiological flexibility, enabling turtles to capitalize on growth opportunities while avoiding seasonal bottlenecks.

Competition - Constrained Shifters occur where resource availability is low relative to population density, constraining energy intake and limiting growth. These constraints may be intensified by variable or suboptimal thermal conditions and declining resource quality, which further reduce energetic returns. In these systems, competition reduces access to resources, and individuals may respond by undertaking directional shifts from an initial neritic foraging ground to alternative habitats with greater per capita resource availability, without consistent ontogenetic or seasonal triggers (Nishizawa et al. 2013, Bjorndal et al. 2019, Lelong et al. 2024). Sustained grazing for instance may intensify these constraints by reducing seagrass availability or altering meadow structure (Gulick et al. 2021). Unlike the reversible movements of Seasonal Responders, these competition-driven directional shifts reflect persistent density-dependent constraints on resource access and growth.

These strategies should not be viewed as discrete categories, but rather as non-exclusive expressions of developmental flexibility that may emerge within individuals, vary within populations, or recur across regions exposed to similar ecological pressures. Individuals may adjust their behaviour within a strategy space or shift between strategies as temperature, resource conditions and population density change, particularly when existing conditions constrain growth. For example, juveniles in the southwestern Atlantic can shift between Resident Optimizers and Seasonal Responders as local conditions change (Vélez-Rubio et al. 2018, Campos and Cardona 2019, Gama et al. 2024, Vélez-Rubio et al. 2026), illustrating that developmental trajectories can vary within the same foraging ground. Thus, juvenile ontogeny may be better understood as a growth-driven process shaped by local ecological context and individual energetic trade-offs than as a predetermined sequence of habitat transitions.

This plasticity-based model aligns with life-history theory, which predicts that behavioural and physiological flexibility can enhance population-level survival and persistence under changing conditions (Arendt 1997, Stearns 1998), and may increase resilience in long-lived ectotherms by helping maintain energy balance across shifting thermal and resource environments (Angilletta et al. 2004). From a conservation perspective, this means that foraging habitats should not be evaluated solely by where turtles are recorded, but by the ecological functions those areas provide. Habitats may support year-round growth, provide seasonal refugia or temporary feeding opportunities, or facilitate transitions when local conditions become limiting. These functions may shift over time, particularly following disturbances such as marine heatwaves, or other environmental influences (Nowicki et al. 2019). Recognizing these functional differences is essential for identifying the habitats and ecological processes that sustain juvenile development under environmental change.

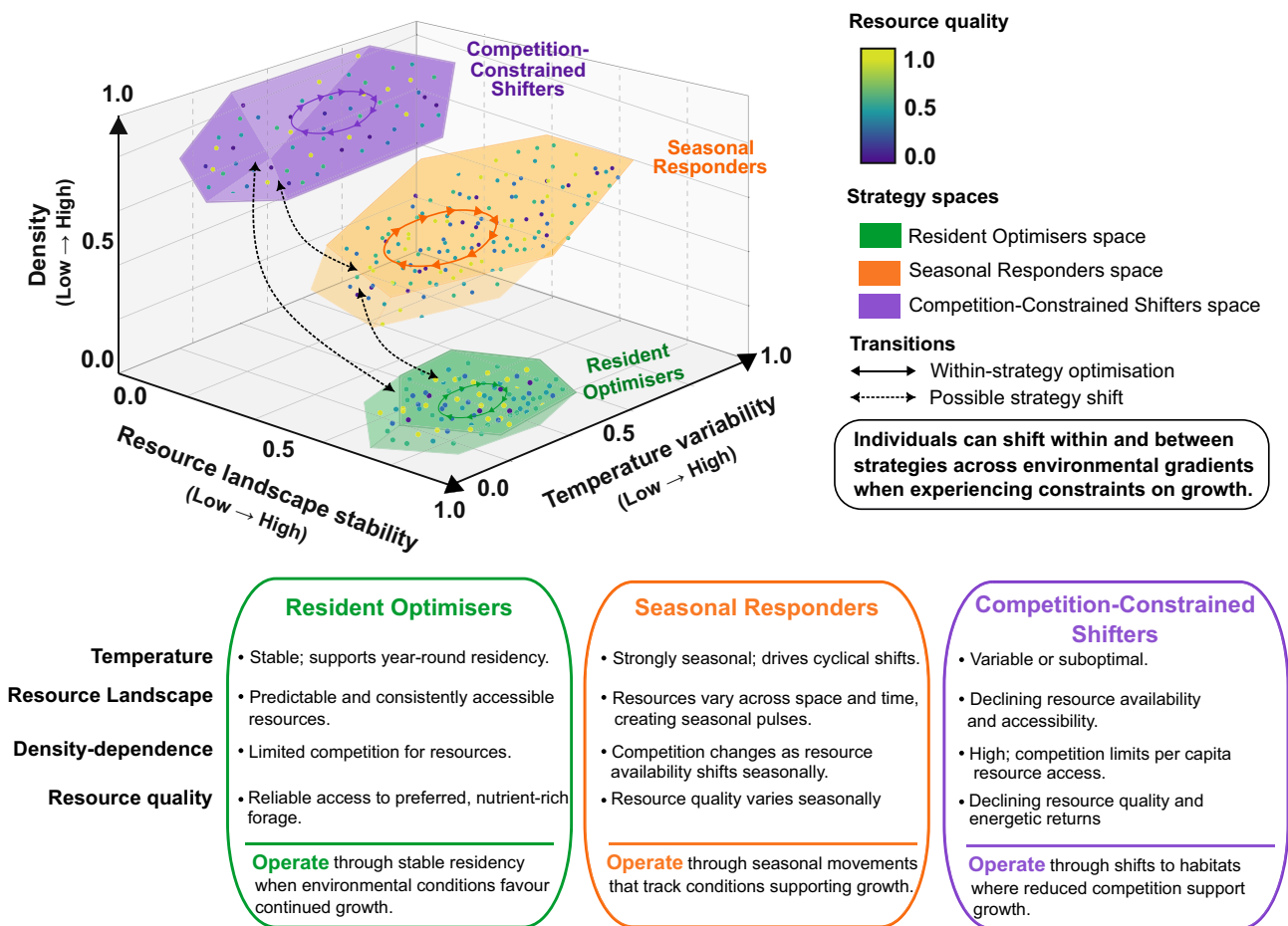


Figure 4 Conceptual representation of growth-response strategy space for juvenile green turtles (*Chelonia mydas*) within a three-dimensional environmental–demographic theoretical framework. Individuals are positioned according to **temperature variability** (x-axis; low to high), **resource landscape stability** (y-axis; low to high), and **density-dependence** (z-axis; low to high), while point colour indicates relative **resource quality**. Semi-transparent volumes represent the environmental space associated with each proposed strategy. **Resident Optimisers** occur where stable temperatures, predictable resources, limited competition, and high-quality forage support continued growth through stable residency. **Seasonal Responders** occur where seasonal variation in temperature and resource availability promotes cyclical movements that track conditions supporting growth. **Competition-Constrained Shifters** occur where high density, declining resource availability or quality, and reduced per-capita access to resources constrain growth, promoting shifts to habitats where reduced competition may better support growth. Solid lines indicate within-strategy optimization, whereas dashed arrows indicate potential shifts between strategies as environmental or demographic conditions change. The lower panels summarize the key temperature, resource landscape, density-dependent, and resource-quality conditions associated with each strategy, highlighting that these responses are dynamic and non-discrete.

Methodological considerations and future research priorities

Geographic and methodological biases continue to shape our understanding of juvenile green turtle ecology. Research remains concentrated in a few well-resourced regions, while large areas such as the Indian Ocean, eastern Atlantic, and several Pacific RMUs remain under-represented despite their conservation importance (Wildermann et al. 2018, Wallace et al. 2025). Restriction to English-language studies may have further introduced geographic and/or publication bias. Broader geographic coverage is therefore necessary to determine whether the patterns here extend across the species' range.

Methodological inconsistencies further limit cross-study comparisons. Gut content analysis provides short-term diet snapshots and underdetects soft-bodied prey such as jellyfish (González Car-

man et al. 2014), while stable isotope analysis offers longer-term insights but relies on regional baselines that are often lacking (Newsome et al. 2007, Vander Zanden et al. 2010, 2012). Satellite telemetry and capture-mark-recapture are constrained by tag loss, deployment duration, and cost (Wallace et al. 2011, Hussey et al. 2015, Hays and Hawkes 2018), and although acoustic telemetry offers fine-scale data, it is constrained by receiver coverage (Dwyer et al. 2015, Hardin and Fuentes 2021, Hardin et al. 2024). eDNA metabarcoding offers additional perspectives but remains limited by taxonomic resolution, DNA degradation, and difficulties in quantifying dietary contributions (Okuyama et al. 2013, Lamb et al. 2019, Kim et al. 2021, Díaz-Abad et al. 2022). Collectively, these limitations may bias observations towards nearshore residents and under-represent offshore use, habitat transitions, or long-distance shifts.

Evidence of morphotype-specific differences remains limited. Few studies have explicitly examined the ecology of the eastern Pacific ‘black’ morphotype, and proposed traits (e.g. prolonged offshore movements or more carnivorous diets) are not unique, having also been reported in other populations under similar environmental conditions (e.g. upwelling systems and prey pulses) (Parker et al. 2011). Given the limited samples and absence of standardized comparisons, morphotype-based analyses were excluded from this synthesis; currently environmental context appears to be a more reliable predictor of juvenile behaviour than morphotype.

Some recruited individuals likely spend more time in oceanic habitats than previously assumed (Turner Tomaszewicz et al. 2018), underscoring the importance of improving access to these stages. Collaborations with ocean-based industries—high-seas fisheries, offshore oil and gas platforms, and maritime NGOs—could provide cost-effective platforms for sampling and observation (Wildermann et al. 2018). Standardized monitoring records, including location, size class, biological samples and environmental context, would improve regional comparisons, accelerate understanding of juvenile habitat use, and reduce duplication effort (Fossette et al. 2014, Seminoff et al. 2021).

Few studies combine multiple approaches across contrasting environments, yet multi-method designs are essential to capture the full range of developmental strategies. Integrating telemetry with SIA using validated baselines, or dietary methods, animal-borne video, remote sensing, automated cameras, and machine learning would help better resolve habitat use and diet across scales (Fuentes et al. 2023). When combined with multi-year deployments, these approaches can also reveal ontogenetic flexibility and individual variability. Standardizing protocols for measuring diet, movement, growth, and habitat use would further improve cross-site comparability and enable large-scale syntheses.

Despite its central role in the proposed framework, growth remains under-reported: only 15 of the 172 studies measured individual growth rates, largely because of the difficulty recapturing in-water juveniles. This contrasts with broader marine turtle research, where growth data provide critical insights into life-stage transitions and population dynamics (Stubbs et al. 2022). Prioritizing growth metrics is critical, particularly when integrated with movement, diet, and SIA, and would strengthen links between behavioural strategies and developmental outcomes.

While some regions and questions may exceed the logistical scope of many field programmes, research capacity could be expanded through approaches that are feasible across a wider range of contexts. These include opportunistic sampling, long-term sentinel (i.e. index) foraging sites—analogous to the nesting beaches that underpin IUCN assessments—photo-identification and machine learning (Dujon and Schofield 2019), bycatch mapping (Cambie et al. 2013), and local ecological knowledge from fishers and coastal communities, which remains an invaluable, under-used resource for expanding spatial and seasonal data (Barrios-Garrido et al. 2017).

Together, these priorities would help move juvenile green turtle research beyond site-specific descriptions and towards a more integrated and globally comparable understanding of developmental flexibility. Linking movement, diet, growth, habitat use, and environmental context will be essential to test why strategies vary

among regions and how populations may respond to continued environmental change.

Conclusion

This review shows that juvenile green turtles do not follow a single, fixed developmental pathway. Instead, their movement, diet, and habitat use vary with local environmental conditions, resource availability, and the opportunities available for growth. Recognizing this flexibility is important for understanding how juveniles use foraging habitats, why developmental strategies differ among regions, and how populations may respond to future environmental change.

Author contributions

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Supplementary material

Supplementary data is available at *ICES Journal of Marine Science* online.

Conflicts of interest

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Data availability

All Supplementary material associated with this manuscript is available and has been provided through the journal.

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