9 Feeding Biology
Advances from Field-Based Observations, Physiological Studies, and Molecular Techniques

T. Todd Jones and Jeffrey A. Seminoff

CONTENTS

9.1 Introduction 211
9.2 Diet Composition 213
9.2.1 Leatherback Turtle, D. coriacea 213
9.2.2 Green Turtle, C. mydas 213
9.2.3 Loggerhead Turtle, Caretta caretta 217
9.2.4 Hawksbill Turtle, E. imbricata 219
9.2.5 Olive Ridley Turtle, Lepidochelys olivacea 220
9.2.6 Kemp's Ridley Turtle, Lepidochelys kempii 221
9.2.7 Flatback Turtle, Natator depressus 221
9.3 Feeding Physiology 221
9.3.1 Intake Rate 222
9.3.2 Digestibility and Assimilation 223
9.3.3 Passage Rate 224
9.3.4 Specific Dynamic Action 225
9.4 Stable Isotope Analysis in Sea Turtles 226
9.4.1 Limitations of Stable Isotope Analysis 229
9.4.2 Isotopic Discrimination 232
9.4.3 Isotopic Residence Time 232
9.4.4 Diet and Trophic Status 233
9.4.5 Isoscapes and Foraging Movements 234
9.4.6 Compound-Specific Isotope Analysis of Amino Acids 234
9.5 Fatty Acid and Trace Element Analyses 235
9.5.1 Fatty Acid Analysis 235
9.5.2 Trace Element Analysis 236
9.6 Conclusions 236
Acknowledgments 237
References 237

9.1 INTRODUCTION

Since Archie Carr's seminal work in the 1960s and 1970s and efforts by Karen Bjorndal and others in the 1980s and 1990s, feeding biology has been a relatively well-studied facet of sea turtle biology. This is opportune for the science of sea turtles considering that nutrient acquisition

strategies are among the most important components of a sea turtle's life history, influencing key demographic parameters such as somatic growth, age-at-maturity, and timing of reproductive migrations. Over the past two decades, however, the advent of new research fields such as physiological monitoring, biologging, and stable isotope analysis (SIA) have helped strengthen this understanding even further. These tools have provided insights that have in some cases confirmed earlier wisdom about how a sea turtle makes a living, and in other cases have redefined long-standing biological paradigms.

Considering the new information that has come available, it is clear that the ecological strategies of some species are much more diverse than originally considered. For example, green turtles (*Chelonia mydas*), long-considered obligate neritic herbivores instead eat large amounts of animal matter in many places (e.g., Heithaus et al., 2002; Seminoff et al., 2002a,b; Cardona et al., 2009; Carrion-Cortez et al., 2010), and at least in the Pacific are commonly high-seas dwellers, even as adults (Hatase et al., 2006; Kelez, 2011; Parker et al., 2011). Hawksbill turtles (*Eretmochelys imbricata*), the "coral reef dwelling" turtle, are turning up in the strangest of places. In the eastern Pacific, for example, adult hawksbills inhabit mangrove estuaries during non-breeding periods, a huge departure from our belief that the species was tied to coral reefs (Gaos et al., 2012). In the Caribbean and Indian Ocean, hawksbills are now known to depend on seagrass pastures for foraging and residence (Bjorndal and Bolten, 2010; J. Mortimer, unpubl. data). Leatherbacks (*Dermochelys coriacea*), historically defined as "high-seas inhabitants," are now seen in coastal habitats more than ever before (James et al., 2006; Benson et al., 2011; Fossette et al., 2011). These and other novel revelations about feeding biology are at least partly due to the globalization of sea turtle research and an everexpanding toolbox at the disposal of field and laboratory scientists. Indeed, more research with both traditional and novel tools is conducted in more parts of the world than ever before, and we are now gaining an appreciation of just how complex and adaptive sea turtles can be.

Much new biological information has emerged in the published literature since *The Biology of the Sea Turtles* (Volume 1; Lutz and Musick, 1997) was first published and a thorough update is warranted, particularly for aspects relating to feeding biology. In this chapter we present new information for all seven sea turtle species, building on Karen Bjorndal's chapter on Feeding Biology in Volume 1 that summarized what was known at that time. In Section 9.2 we present the latest information about sea turtle diet and feeding biology. Here we describe new diet items and novel foraging tactics that are reshaping our perceptions about the types of prey consumed and methods by which sea turtles access food resources. In Section 9.3 we focus on the feeding physiology of sea turtles (e.g., specific dynamic action (SDA), digestive efficiency, and passage rates of digesta), a still-understudied area of sea turtle feeding biology, but one that is expanding thanks to additional field and lab-based scientific research. Understanding how sea turtle energy acquisition is constrained by physiological and environmental factors is important as these data factor into growth rates, residency times, population demographics, bioenergetics and energy budgets, and reproductive output. In Sections 9.4 (stable isotopes) and 9.5 (fatty acids and trace elements) we explore the "molecular-based" techniques that are showing great promise for establishing diet, trophic status, and foraging movements of sea turtles. Clearly, the advent of these approaches allows us to learn much about the types of foods consumed by turtles based on the analysis of their own body tissues.

As described earlier, the feeding biology of sea turtles is a broad topic with many nuisances. Together the established (e.g., stomach content analysis, esophageal lavage) and emerging (e.g., SIA, fatty acids) techniques give greater insight and understanding into the unique foraging strategies of sea turtles both intra- and interspecifically and through life-history stages. Studies of feeding physiology then begin to tie together what, when, and where sea turtles eat with why and how they eat to meet daily and yearly energy demands of maintenance, growth, and reproduction. In the end, our goal is to provide an update on the current knowledge of sea turtle feeding biology and share a perspective of how our understanding has evolved in the past decades.

9.2 DIET COMPOSITION

9.2.1 Leatherback Turtle, D. coriacea

Leatherback turtles feed primarily on gelatinous zooplankton from several days post-emergence (Salmon et al., 2004), through juvenile maturation (Iverson and Yoshida, 1956, authors personal observations), and adulthood (see Bjorndal, 1997). While observations of feeding during the pelagic juvenile years are rare, the authors had the opportunity to observe the stomach contents of several leatherback turtles (60–80 cm SCL) from fishery bycatch in the western Pacific Ocean, all of which contained remnants of gelatinous zooplankton. The majority of reports on leatherback diet come from direct observations of surface or water column feeding (Bacon, 1970; Duron, 1978; Eisenberg and Frazier, 1983; Grant and Ferrell, 1993; James and Herman, 2001; Salmon et al., 2004; Fossette et al., 2011; Heaslip et al., 2012), from alimentary tract contents from stranded or bycaught turtles (e.g., Bleakney, 1965; Brongersma, 1972; Den Hartog, 1980; Den Hartog and Van Nierop, 1984; Davenport and Balazs, 1991), and most recently from SIA (Dodge et al., 2011; Seminoff et al., 2012). The observed prey items consist mostly of the phylum Cnidaria, class Scyphozoa (i.e., true jellies) including *Aurelia* spp., *Catostylus* spp., *Chrysaora* spp., *Cyanea* spp., *Pelagia* spp., *Rhizostoma* spp., and *Stomolophus* spp. (Duguy, 1982; Den Hartog and Van Nierop, 1984; Duron-Dufrenne, 1987; Grant and Ferrel, 1993; Limpus and McLachlan, 1994; Davenport, 1998; James and Herman, 2001; Salmon et al., 2004). To date we only know of three reports indicating that leatherbacks forage on the class Hydrozoa, orders Leptomedusae (*Aequorea* spp.) and Siphonophorae (*Apolemia* spp., *Physalia* spp.) (Bacon, 1970; Den Hartog, 1980; Den Hartog and Van Nierop, 1984). Further it was suggested that the presence of the Leptomedusae (*Aequorea* spp.) in the leatherback alimentary tract may be a result of contamination, as Scyphomedusae (targeted leatherback prey) feed on *Aequorea* spp. (Den Hartog and Van Nierop, 1984). Leatherbacks have also been reported to feed on pyrosomes (Thaliacea) (Davenport and Balazs, 1991; pers. observ.) as well as ctenophores (Nuda) and gelatinous fish egg sacs (Actinopterygii eggs) (Salmon et al., 2004). Most recently, Dodge et al. (2011) have noted sea butterflies (Gastropoda) as a diet item of leatherbacks foraging in the eastern North Atlantic Ocean through SIA. This is the first documentation of a marine gastropod (family Cymbulioidea) in the leatherback diet. Squid, octopus, and fish have been noted in the alimentary tract of three leatherbacks caught in fishing gear (Brongersma, 1969, 1972; Limpus, 1984; Bello et al., 2011) as well as numerous crab species (e.g., *Libinia spinosa*) (Brongersma, 1969; Frazier et al., 1985). Frazier et al. (1985), however, clarified that the species of small crab and even the fish are probably jelly commensals and ingested incidentally.

Leatherbacks have long been thought to be oceanic-pelagic throughout their life-history (Bolten, 2003); however, recent evidence suggests that leatherback subadults and adults frequent coastal foraging areas (James et al., 2006; Benson et al., 2011) feeding on a vast array of dense gelatinous zooplankton. While these findings may be a departure from the strict oceanic paradigm what has not shifted is the epipelagic foraging strategy used by leatherbacks whether they are foraging in oceanic or neritic waters. The gelatinous diet of leatherbacks is varied across several phyla and classes (Table 9.1); however, the majority of data from feeding observations, gut content analysis, and use of SIA suggests that Scyphozoa (i.e., true jellies) remain the main diet component and that leatherbacks are obligate jelly (gelatinous zooplankton) consumers throughout their ontogeny.

9.2.2 Green Turtle, C. mydas

Green turtles occur in tropical and temperate waters worldwide and have been shown to consume a wide variety of seagrass, marine algae, and invertebrates (see Bjorndal, 1997). They have an oceanic–neritic developmental pattern (Bolten, 2003) that comes with a concomitant diet shift from omnivory to primarily herbivory (Table 9.1) at neritic recruitment (20–35 cm carapace length [CL] in the Atlantic [Bjorndal and Bolten, 1988]; 35+ cm CL in the Pacific [Seminoff et al., 2002a,b; Arthur et al., 2008]). However, central North Pacific green turtles have recently been

TABLE 9.1
Diet and Foraging Habitat of Sea Turtles throughout Development

Developmental Stage/Habitat	Leatherback	Green	Loggerhead	Hawksbill	Olive Ridley	Kemp's Ridley	Flatback
Post-hatchling diet	Scyphozoa, Nuda, Actinopterygii eggs	Seagrass, algae, Thaliacea, Actinopterygii eggs	Hydrozoa, Scyphozoa, Bryozoa, Gastropoda, Polychaeta, Maxillpoda, Malacostraca, Insecta, Actinopterygii, algae	Not observed	Not observed	Gastropoda, Malacostraca, algae	Not observed
Oceanic diet (juvenile)	Thaliacea (pyrosomes)	Gastropoda, Scyphozoa, Thaliacea, Malacostraca, Maxillopoda, algae, Insecta	Hydrozoa, Scyphozoa, Thaliacea, Actinopterygii eggs, Cephalopoda, Gastropoda, Malacostraca, Maxillopoda, Insecta, Polychaeta, algae	Algae, Maxillopoda, Malacostraca, Thaliacea, Actinopterygii eggs	Thaliacea, Gastropoda, Actinopterygii	Not observed	N/A
Neritic diet (juvenile)	N/A	N/A	N/A	N/A	N/A	N/A	Gastropoda, Hydrozoa, Scyphozoa, Anthozoa, Bryozoa
Neritic diet (post-recruitment)	N/A	Seagrass, algae, mangrove fruit/ leaves, Gastropoda, Thaliacea, Porifera, Polychaeta, Anthozoa, Malacostraca, Cyanophyceae	Malacostraca, Merostomata, Actinopterygii (fisheries), Maxillopoda, Gastropoda, Bivalvia, Echinoidea, Anthozoa, Holothuroidea, Chondrichthyes, Scyphozoa, Cephalopoda, Bryozoa, Polychaeta, Porifera, Foraminifera, Porifera, Ophiuroidea, Brachiopoda, Demospongiae, Turbellaria, Sipunculida, Ascidiacea, seagrass, algae	Porifera, Anthozoa, Gastropoda, Polychaeta, Hydrozoa, Bryozoa, Scyphozoa, Malacostraca, Echinoidea, Actinopterygii, algae, seagrass	Gastropoda, Malacostraca	Malacostraca, Bivalvia, Gastropoda, Ascidiacea, seagrass, algae, Merostomata, Ctenophora, Actinopterygii	N/A

Oceanic diet (adult)	Scyphozoa, Hydrozoa, Thaliacea, Gastropoda	N/A	N/A	N/A	Thaliacea, Gastropoda, Actinopterygii	N/A	N/A
Neritic diet (adult)	See Oceanic diet (adult)[b]	See Neritic diet (post-recruitment)	See Neritic diet (post-recruitment)	See Neritic diet (post-recruitment)	Gastropoda, Malacostraca, Bryozoa, Sipunculidea, Ascidiacea, Actinopterygii, algae	Malacostraca, see Neritic diet (post-recruitment)	Gastropoda, Hydrozoa, Scyphozoa, Anthozoa, Bryozoa

[a] See Section 9.2 for complete details and cited references. Diet items listed in order of importance, abundance, or frequency when possible.
[b] Recent observations suggest that adult leatherbacks feed in epipelagic–neritic waters (Benson et al., 2011; Fossette et al., 2011; James et al., 2012).

found to forage in oceanic waters up to 70 cm CL (Parker et al., 2011) suggesting alternate life-history patterns. Little is known of the green turtle diet during oceanic development with only a few observations of surface or shallow depth foraging (Frick, 1976; Salmon et al., 2004), gut content analysis (Hughes, 1974; Boyle and Limpus, 2008), and more recently SIA (Reich et al., 2007; Arthur et al., 2008). Salmon et al. (2004) observed post-hatchling green turtles (<10 weeks of age) in the Gulf Stream (off the coast of eastern Florida, United States) feeding at the surface on floating bits of seagrass and algae (*Thalassia* sp. and *Sargassum* sp.) and at shallow depths on ctenophores (Nuda) and gelatinous egg sacs (unknown species) but they avoided larger Scyphozoa such as *Aurelia* sp. This corroborates a sighting of a green turtle hatchling eating a ctenophore 1 m below the surface off the shore of Bermuda (Frick, 1976). Gut content analysis revealed marine gastropod mollusks (Gastropoda) in green turtles off South Africa and eastern Australia (Hughes, 1974; Boyle and Limpus, 2008), as well as Scyphozoa, crustaceans (Malacostraca), plant material, and terrestrial insects (Insecta) (eastern Australia, Boyle and Limpus, 2008). North Atlantic green turtles have stable isotope signatures consistent with carnivory for their first 3–5 years of life while occupying the oceanic zone (Reich et al., 2007). Similar signatures were found for green turtles <44 cm CL of the southwestern Pacific (Arthur et al., 2008). Parker et al. (2011) described the gut contents of 10 oceanic green turtles (30–70 cm CL) from the central North Pacific (commercial fishery bycatch). The diet items included pyrosomes (Thaliacea), goose barnacles (Maxillopoda), amphipods (Malacostraca), sea snails and butterflies (Gastropoda), Ctenophora (Nuda), and jellyfish (Scyphozoa) (Parker et al., 2011); however, the carapace lengths are indicative of turtles recruiting to neritic zones (Bjorndal, 1997; Bolten, 2003). Therefore, plasticity may exist in recruitment length or turtles may shuttle between neritic and oceanic habitats.

Once green turtles recruit to neritic waters they primarily forage on benthic organisms (see Table 9.1). As reviewed by Bjorndal (1997), the diet mostly consists of seagrass and algae. Lopez-Mendilaharsu et al. (2005) recorded (through esophageal lavage) that eastern Pacific green turtles on the Pacific Coast of the Baja peninsula fed primarily on red algae in the inner bays but that larger turtles fed on seagrass along the outer coastline. On the other side of the Baja California Peninsula (Gulf of California), also using esophageal lavage, Seminoff et al. (2002a,b) documented that neritic green turtles fed primarily on the red algae *Gracilariopsis lemaneiformis*; however, they also noted high animal matter consumption, including sponges (Porifera), tube worms (Polychaeta), sea pens (Anthozoa), and sea hares (Gastropoda). This was later corroborated by Crittercam analysis (Seminoff et al., 2006a,b) observing the consumption of algae as well as previously undocumented species of Cnidaria (yellow-polyp black coral, *Antipathes galapagensis*) and Annelida (fanworm, *Bispiria* sp.). Further south, off of the South American coast, Carrion-Cortez et al. (2010) recorded mostly algae species and red mangrove in esophageal lavage samples of eastern Pacific green turtles of the Galapagos Islands, whereas Amorocho and Reina (2007) found (in order of abundance) tunicates (Thaliacea), red mangrove fruits, algae (Rhodophyta, Chlorophyta, Cyanophyta), small crustaceans (Malacostraca), and plant leaves as well as coral/shell fragments in esophageal contents of juveniles and adults (average 58 cm CL) in Gorgona National Park, Colombia. The gut content analysis of green turtles from the Sultanate of Oman also revealed a high rate of animal matter consumption (Ferreira et al., 2006), with algae and animal matter constituting 49% and 26% of the gut contents dry weight, respectively.

In southeast Queensland, Australia, the dominant diet item of green turtles is seagrass with algae a close second (Brand-Gardner et al., 1999; Limpus et al., 2005). Limpus et al. (2005) reported that 96.6% of lavage samples of green turtles from Shoalwater Bay had seagrass present (*Halodule* sp., *Zostera* sp., and *Halophila* sp.) and when present it constituted 50% or more of the sample. Mangrove leaves, fruits, and seedlings have also been reported in the diet of Australian green turtles (Pendoley and Fitzpatrick, 1999; Limpus and Limpus, 2000; Limpus et al., 2005) to the extent that Limpus (1998) described the herbivorous diet of green turtles in Australia as "seagrasses, algae, and mangroves." Three studies employing the use of animal-borne video cameras have documented the previously unreported consumption of gelatinous zooplankton by green turtles off Western

Australia (Heithaus et al., 2002) and eastern Australia (Arthur et al., 2007), and in the Gulf of California, Mexico (Seminoff et al., 2006a,b). Arthur et al. (2006) documented the consumption of the toxic filamentous cyanobacterium *Lyngbya majuscula* in the gut contents of green turtles in Shoalwater Bay, Queensland, Australia. Fifty-one percent of green turtles sampled had the cyanobacteria present (during a 2002 bloom), however, it only constituted 2% of stomach contents (Arthur et al., 2006) and did not relate to lessened body condition.

Non-native (alien) algae have been observed in green turtle diets in Hawaii, such as *Acanthophora spicifera* and *Hypnea musciformis* (Russell and Balazs, 1994), and with increasing abundance are becoming the dominate diet item (Russell and Balazs, 1994; Arthur and Balazs 2008). Green turtles in Australia were found to selectively consume algae that were low in fiber and high in nitrogen (Brand-Gardner et al., 1999) typical of invasive species. This preference for high nitrogen-invasive species may be of consequence for green turtle populations as Van Houtan et al. (2010) recently linked the consumption of invasive algae (high in nitrogen and arginine) to fibropapilloma tumors.

9.2.3 Loggerhead Turtle, Caretta caretta

Loggerhead turtles follow an oceanic–neritic developmental pattern (Bolten, 2003) departing nesting beaches and entraining in prevailing oceanic currents as float-and-wait foragers (Witherington, 2002) until recruiting to neritic foraging grounds at >25 cm CL (Bjorndal et al., 2000; Gardner and Nichols, 2001; Lazar et al., 2008). Although recent evidence suggests a prolonged oceanic stage or perhaps a plasticity in shuttling between habitats (Parker et al., 2005) persisting even through the commencement of breeding (Hatase et al., 2002, 2006, 2010). During the oceanic stage (generally lasting 7–10 years; Bjorndal et al., 2000) loggerhead post-hatchlings and juveniles are primarily carnivorous (Bjorndal, 1997). Post-hatchlings (4–8 cm CL) leaving the beaches of southeast Florida swim offshore to the Gulf Stream where they feed on a diet of Hydrozoa, Scyphozoa (jellyfish), Bryozoa, Gastropoda, Polychaeta, Maxillopoda (copepods), Malacostraca (crabs, shrimp), Insecta, Actinopterygii (fish), as well as feeding on bits of floating seagrasses, algae, and filamentous cyanobacteria (Witherington, 2002). Loggerhead post-hatchlings (5–11 cm CL) of the southwest Pacific feed on similar items (unidentified Cnidaria, Gastropoda, Malacostraca, and seagrasses; Boyle and Limpus, 2008). Frick et al. (2009) examined the gut content of larger oceanic loggerheads (9–56 cm CL) near the Azores; the turtles had remnants of Hydrozoa, Scyphozoa, Thaliacea, Actinopterygii eggs, Cephalopoda, Gastropoda, Malacostraca, Maxillopoda, and Insecta. Oceanic loggerheads (14–74 cm CL) of the central North Pacific feed solely on epipelagic items largely including Gastropoda (sea snails), Hydrozoa, Maxillopoda (goose barnacles), Malacostraca (hitchhiker crab, *Planes* spp.), and Thaliacea (tunicates) as well as bits of Cephalopoda, Actinopterygii, Actinopterygii eggs, Polychaeta, and algae (Parker et al., 2005). The diet of oceanic stage loggerheads is purely pelagic/epipelagic unlike the mixed diet of neritic stage loggerheads (Bolten, 2003). Recruitment to the neritic, however, may not come with a concomitant change in diet. There is a transitional stage where new recruits continue to feed on epipelagic organisms while gradually including benthic organisms in their diet (Bolten, 2003; Casale et al., 2008). The length that loggerheads recruit to neritic areas also varies geographically 25 to >60 cm CL (Bjorndal et al., 2000; Seminoff et al., 2004; Boyle and Limpus, 2008; Casale et al., 2008; Wallace et al., 2009).

Peckham et al. (2011) studied the movements, habitat selection, and diet of neritic loggerheads (Baja California Peninsula) of the same length (50–90 cm CL) as oceanic loggerheads of the central North Pacific (Parker et al., 2005). The diets differed considerably between the study groups with neritic loggerheads feeding mostly on fish (Actinopterygii) and crabs (Malacostraca), mostly the pelagic red crab (*Pleuroncodes planipes*). The average energy density of diet items was 60% greater (on dry mass basis) for the neritic loggerheads (Peckham et al., 2011) than for the diet of oceanic loggerheads (Parker et al., 2005). Peckham et al. (2011) suggested that loggerheads that recruit to neritic waters benefit from greater productivity and energy-dense diet items; however, neritic

foraging comes with a cost of greater mortality rates. The energy densities were compared on a dry mass basis, however, and this may underestimate the handling and volume of food needed to meet energy demands. Wet mass energy densities and handling costs associated with capture and/or dealing with exoskeletons may offset lessening the energy density disparity found between the habitats or increase them. The increased fish in the diet was surmised to be from fishery discard of the local gillnet fishery (Peckham et al., 2011). The consumption of fish from commercial fisheries discard and gear is perhaps a regionally learned response observed in Baja California (Peckham et al., 2011), the Mediterranean (Tomas et al., 2001), and in the western North Atlantic (Seney and Musick, 2007). Across the Pacific to the nesting beaches and associated foraging grounds off Japan, Hatase et al. (2002) observed a relationship between adult body length and diet (through SIA of deposited eggs). Larger loggerheads were associated with a neritic-benthic diet from the East China Sea whereas smaller loggerheads had diet signatures associated with oceanic-pelagic organisms of the Kuroshio Current; the researchers suggested the relationship reflects recruitment of immature loggerheads where early recruitment to neritic environments is rewarded by faster growth rates due to nutrient-rich prey vs. the loggerheads that remain in the oceanic habitats (Hatase et al., 2002). This study corroborates the observations of Peckham et al. (2011) that neritic recruitment exposes the loggerheads to a greater abundance of energy-dense food.

The diet records of immature and adult loggerheads of eastern and western Australia include over 100 taxa, but the principle diet consists of Gastropoda, Bivalvia, and Malacostraca (portunid and hermit crabs). Of lesser abundance are Scyphozoa, Echinoidea (sea urchins), Anthozoa (anemones), Holothuroidea (sea cucumbers), and Actinopterygii (Limpus, 2008a,b).

In the western North Atlantic along the U.S. east coast loggerhead diet is dominated by crabs (Malacostraca). Seney and Musick (2007) analyzed the gut contents of 297 loggerheads (33–99 cm CL) from 1983 to 2002, with the gut contents consisting of Merostomata (horseshoe crabs), Malacostraca (e.g., blue crab, rock crab, spider crab), Maxillopoda (e.g., Acorn barnacle, crab barnacle), Gastropoda (e.g., whelks, mud snail), Bivalvia (e.g., razor clam, blue mussel), Actinopterygii, Chondrichthyes (e.g., clearnose skate, Atlantic sharpnose shark) as well as seagrass, algae, Cephalopoda, Bryozoa, Polychaeta, Porifera (sponges), and other unidentified gelatinous organisms. Diets were dominated by horseshoe crab and blue crabs in the 1980s and early1990s, but after 1993 diets were dominated by fish species, a trend perhaps the result of declining crab populations causing loggerheads to forage in nets or on discarded fishery bycatch (Seney and Musick, 2007). Further south (North Carolina coast) SIA of 42–102 cm CL neritic loggerheads suggested a preference for Malacostraca (blue crabs), Gastropoda (whelks), and Scyphozoa (cannonball jellyfish) and that the loggerheads rarely supplemented their diet with fish discards or fish caught in gear of commercial fisheries. McClellan et al. (2010) revealed through SIA that loggerheads (53–82 cm CL) shuttle between foraging habitats; loggerheads that had recruited to neritic environments maintained oceanic diet signatures during overwintering periods and juvenile loggerheads first recruiting to neritic habitats continued to feed on oceanic-pelagic organisms.

Interestingly, in the western South Atlantic Carranza et al. (2011) reported the diet of neritic loggerheads (51–112 cm CL) in the Rio de la Plata Estuary (Uruguay) to consist solely of the invasive whelk (*Rapana venosa*, Gastropoda). The five loggerheads examined had on average 136 opercula in their stomach.

In the past decade studies have revealed a range of strategies for loggerheads that settle in the Mediterranean, including strict oceanic vs. neritic strategies as well as shuttling between strategies. Lazar et al. (2008) examined the gut contents of early recruitment loggerheads (25–39 cm CL) of the Adriatic Sea and found that the diet was composed of benthic and epipelagic organisms. The benthic organisms consisted of Foraminifera, Porifera, Echinoidea, Ophiuroidea, Malacostraca, Brachiopoda, Anthozoa, Bryozoa, Gastropoda, Polychaeta, seagrasses, and algae while the epipelagic organisms consisted of Cephalopoda, Actinopterygii, and Insecta (Lazar et al., 2008). The most abundant diet items by rank were Anthozoa (anemones), Malacostraca, and Gastropoda (Lazar et al., 2008). Analysis of the gut content and feces of larger neritic loggerheads (25–80 cm CL)

in the central Mediterranean Sea indicate an abundance of benthic organisms (Demospongiae, Turbellaria, Sipunculida, Bivalvia, Gastropoda, Cephalopoda, Polychaeta, Malacostraca, Bryozoa, Echinoidea, Holothuroidea, Ophiuroidea, Ascidiacea, Chondrichthyes, Osteichthyes, seagrasses, and algae) with the most abundant organisms encompassing Malacostraca, Gastropoda, and Echinoidea (Casale et al., 2008). Neritic loggerheads (34–69 cm CL) in the western Mediterranean feed on Actinopterygii, Ascidiacea, Thaliacea, Malacostraca, Polychaeta, Echinoidea, Ophiuroidea, Anthozoa, Porifera, Cephalopoda, Gastropoda, Insecta, seagrasses, and algae (Tomas et al., 2001). The prevalence of Actinopterygii (fish) in the gut contents of the western Mediterranean study, however, is probably due to consumption while captured or to bycatch waste from the fisheries (Tomas et al., 2001). In a study of similar length loggerheads of the Balearic Archipelago (Revelles et al., 2007a,b) SIA suggested the diet composition was primarily epipelagic organisms (Cephalopoda [squid] and Scyphozoa [Jellyfish]); furthermore, the stable isotope values did not differ from shelf and pelagic (assumed oceanic) loggerheads. Gut content analysis revealed the loggerheads also fed on Thaliacea, Malacostraca, Maxillopoda, and Actinopterygii—all of which were epipelagic. Revelles et al. (2007a,b) suggested that longline bait was a likely source of some of the prey species. In contrast, loggerheads of northwestern Mediterranean (off mainland Spain) had distinct isotopic values that differentiated between oceanic and neritic cohorts (CL data not provided), suggesting that gelatinous zooplankton is a primary diet item for oceanic loggerheads but not neritic turtles (Cardona et al. 2012).

Studies on the diet of immature and adult loggerheads have broadened the classic oceanic–neritic developmental pattern, expressing more plasticity in the use of habitats (Hatase et al., 2002; Revelles et al., 2007a,b; McClellan et al., 2010) and the ability to adapt to changing prey landscapes (Seney and Musick, 2007), which at times includes invasive species (Carranza et al., 2011). However, in all studies loggerheads were carnivorous from post-hatchling through adulthood with the main differences between populations coming from the proportion of benthic or pelagic fauna in the diet (see Table 9.1).

9.2.4 Hawksbill Turtle, E. imbricata

Hawksbill turtles are thought to follow the oceanic–neritic developmental pattern as observed in loggerheads and green turtles, although the evidence is not as strong (Bolten, 2003). Early reports of post-hatchling hawksbills suggest they associate with sargassum rafts in oceanic habitats (Carr 1987). Bjorndal (1997) summarized the gray literature noting that gut contents from stranded juvenile hawksbills (14–21 cm CL) in Florida (United States) had species of algae, Maxillopoda, Malacostraca, Thaliacea, and Actinopterygii eggs. This finding is similar to what Salmon et al. (2004) observed in post-hatchling green turtles feeding on in the Gulf Stream off the Florida coast. Limpus (2009) reports that the oceanic stage lasts for nearly 5 years for Australian hawksbills and that the post-hatchlings/juveniles feed on macroplankton.

Hawksbills recruit to neritic habitats at >20 cm CL in the Atlantic (Meylan, 1988) and at >30 cm CL in the Pacific (Limpus, 1992, 2009). Once recruiting to neritic habitats hawksbills have been observed foraging over coral reefs and rocky substrate, seagrass pastures, and in mangrove-fringed bays (Bjorndal and Bolten, 1988; Bjorndal, 1997). The main diet of Caribbean hawksbills after recruitment to neritic habitats is sponges (Porifera) with *Chondrilla nucula* the most abundant (Meylan, 1988). The diet of the hawksbill in the Caribbean and wider Atlantic region has been thoroughly reviewed (Meylan, 1988; Bjorndal, 1997), and Bjorndal (2003) further provides a case study on the impact of hawksbill spongivory in the Caribbean. Few accounts of the hawksbill diet have been given since. Other noted diet items (Table 9.1) include Actinopterygii, Gastropoda, Polychaeta, Hydrozoa, Bryozoa, Anthozoa, Malacostraca, Echinoidea (Carr and Stancyk, 1975; Den Hartog, 1980; Bjorndal, 1997). Blumenthal et al. (2009) observed recruitment to neritic habitats of the Cayman Islands at greater than 20 cm CL with diet components comprising benthic sponges (Porifera) and epipelagic jellyfish (Scyphozoa). A study of neritic hawksbills (19–50 cm CL) of

the Dominican Republic revealed that Cnidarian corals (Corallimorpharian) dominate the diet of hawksbills in certain habitats (81% of diet volume) while in other habitats the sponges were still the mainstay (59% by volume) and, to a much lesser extent, these hawksbills fed on algae (Leon and Bjorndal, 2002). The preference or selectivity for Corallimorpharian (*Ricordea florida*) was also noted by Rincon-Diaz et al. (2011) where hawksbills of Puerto Rico selected *R. florida* when it was of low abundance in the environment. Hawksbill turtles (20–50 cm CL) in the Caribbean waters off the coast of Honduras fed primarily on sponges (e.g., *Melophlus ruber*) comprising 59% of ingesta, smaller hawksbills, however, consumed mostly algae and this was suggested to reflect new recruits that were feeding mostly in the epipelagic waters (Berube et al., in press). Bjorndal and Bolten (2010) postulate that seagrass pastures may become important habitat for hawksbills as coral reef ecosystem health declines. A 30-year study of green and hawksbill turtles suggests that seagrass pastures can support healthy productive populations of hawksbills and that a sixfold increase in green turtle abundance did not affect the health or productivity of the associated hawksbills (Bjorndal and Bolten, 2010).

Neritic hawksbills (26–83 cm CL) of northern and western Australia (as well as in the Indian Ocean, Cocos Islands) feed in tidal and subtidal coral and rocky reef habitats (Limpus, 1992, 2009). The diet of Australian neritic hawksbills consists of algae, seagrass, and sponges (Porifera). Western Australian hawksbills rely less on spongivory than their Caribbean counterparts. Their diet is primarily algae (76%) with only 20% sponge consumption by volume (Limpus, 2009). Parker et al. (2009) reported the diet of Hawaiian hawksbills to consist of Porifera (sponge) and algae. In the eastern Pacific, hawksbills have also been reported to consume sponges (*Haliclona* sp.; Seminoff et al., 2003). A recent study by Gaos et al. (2011), although not reporting diet per se, indicated that hawksbills forage in mangrove estuaries, where sponges are presumably less frequent than in coral reef ecosystems.

Obura et al. (2010) observed that adult neritic hawksbills of the Aldabra Atoll feed on hard corals (Anthozoa) such as the bubble coral (*Physogyra lichtensteinii*). Reports of the same phenomena came from the Seychelles, Thailand, Madagascar, and the Red Sea. Obura et al. (2010) suggested that consumption of hard corals is widespread throughout the Indian Ocean and takes place in the Caribbean and Pacific but to a much lesser extent. Sponge health and abundance are closely related to reef health, and as coral bleaching and coral health continues to decline we may see a paradigm shift from hawksbills having a diet of sponge and corals (Leon and Bjorndal, 2002; Obura et al., 2010; Rincon-Diaz et al., 2011), to one including alternatives such as algae (Limpus, 2009), and reliance on seagrass pastures (Bjorndal and Bolten, 2010; J. Mortimer, unpublished data).

AQ3

9.2.5 Olive Ridley Turtle, Lepidochelys olivacea

Olive ridley turtles develop in oceanic waters and recruitment to neritic waters as juveniles/adults may be regional, with at least some individuals maintaining an oceanic existence (Bolten, 2003). Australian and western Atlantic populations have been widely reported to recruit to neritic habitats (Pritchard, 1976; Limpus, 2008a,b) whereas the eastern Pacific olive ridley may maintain an oceanic life-history pattern.

To our knowledge, there are no data on post-hatchling diet of olive ridley turtles. Oceanic olive ridleys in the central North Pacific prefer warmer water (23–28 C SST) and spend 40% of their time diving below 40 m (Polovina et al., 2004). Gut content analysis from olive ridleys of the central North Pacific suggests they feed on Thaliacea (pyrosomes and salps), Gastropoda (sea snails), and Actinopterygii (e.g., cowfish) (unpublished data, Pacific Islands Fisheries Science Center, NMFS).

In Australia immature and adult olive ridleys recruit to shallow benthic–neritic habitats, feeding mainly on Gastropoda and Malacostraca (Conway, 1994; Limpus, 2008a,b). Reports of stomach contents (Thaliacea, Gastropoda, Malacostraca, Bryozoa, Sipunculidea, Ascidiacea [sea squirts], Actinopterygii, and algae) of adult olive ridleys along the Mexican coast are of females near nesting beaches and not reflective of strict neritic foraging habitat (see Bjorndal, 1997, for review).

There remains a paucity of data on olive ridley life-history patterns, foraging habitat, and diet; however, all reports so far suggest an omnivorous diet (Table 9.1) throughout ontogeny and plasticity in use of oceanic and neritic habitats.

9.2.6 Kemp's Ridley Turtle, Lepidochelys kempii

Kemp's ridley turtles have an oceanic–neritic developmental pattern (Collard and Ogren, 1991; Bolten, 2003) recruiting to benthic–neritic habitats at 20+ cm CL (Snover et al., 2007; Seney and Landry, 2011). Post-hatchling Kemp's ridleys (~10 cm CL) that stranded in the Gulf of Mexico had Gastropoda (sea snails), Malacostraca (crabs), and algae (e.g., *Sargassum* sp.) in their gut (Shaver, 1991). No other reports of oceanic post-hatchlings/juveniles are available. Immature Kemp's ridleys recruiting to benthic habitats can be found from the western North Atlantic (e.g., New York state waters) to the Gulf of Mexico (Shaver, 1991; Burke et al., 1994). Benthic–neritic Kemp's ridleys (23–69 cm CL) of the western Atlantic and Gulf of Mexico continental shelf feed primarily on Malacostraca (e.g., blue crabs), Bivalvia (e.g., blue mussels), Gastropoda (e.g., mud snails, whelks), seagrass, and algae, and to a lesser extent Merostomata (i.e., horseshoe crab), Ctenophora (Nuda), and Actinopterygii (Shaver, 1991; Burke et al., 1993, 1994; Creech and Allman, 1998; Seney and Musick, 2005; Witzell and Schmid, 2005). Witzell and Schmid (2005) observed that immature Kemp's ridleys that recruited to benthic–neritic waters of southwestern Florida fed primarily on Ascidiacea (e.g., tunicates, *Molgula occidentalis*). Adult Kemp's ridleys are found primarily in continental shelf waters of the Gulf of Mexico and feed on Malacostraca (i.e., crabs) (Frick and Mason, 1998; Morreale et al., 2007). The aforementioned diet analyses and movement data suggest that Kemp's ridleys feed on epipelagic organisms during their oceanic period and once recruiting to benthic–neritic habitats, as juveniles, their diet is dominated by bottom-dwelling fauna throughout maturation and adulthood (see Table 9.1).

9.2.7 Flatback Turtle, Natator depressus

The flatback turtle is believed to have a completely neritic life history (Walker and Parmenter, 1990; Walker, 1991; Bolten, 2003), feeding within the waters of the Australian continental shelf (Limpus, 2007). Bolten (2003) suggested that juvenile sea turtles with a neritic developmental pattern probably feed at the surface and within the upper water column until buoyancy control is developed and dive depth-duration increased. The stomach content of juvenile and adult flatbacks had remnants of soft-bodied invertebrates (e.g., Gastropoda [sea snails], Hydrozoa [siphonophore], Scyphozoa [jellyfish], Bryozoa, Anthozoa [sea pens and soft corals]) (Walker and Parmenter, 1990; Walker, 1991). The foraging ecology of flatbacks remains poorly studied (Table 9.1), a biological review by Limpus (2007) summarized that post-hatchling flatbacks feed on macrozooplankton and that immature and adult flatbacks are carnivorous feeding primarily on soft-bodied invertebrates, adding holothurians (e.g., sea cucumbers) to the list of flatback diet items.

9.3 FEEDING PHYSIOLOGY

Paramount to sustaining life is the attainment, storage, and use of energy. Sea turtles obtain chemical energy through ingesting prey, that is, eating gelatinous zooplankton, crabs, mollusks, algae, plants, etc. (see Section 9.2). Once consumed, chemical energy is either used by the animal to fuel production and respiration or lost as heat and metabolic waste (Speakman, 1997). The terms used to describe this process (e.g., digestion, absorption, and assimilation) are often used broadly or incorrectly. For purposes of this chapter we define their use. In multicellular organisms with well-developed digestive tracts (e.g., the canal from mouth to cloaca opening of sea turtles), extracellular digestion takes place. Digestion is the process of breaking down large complex molecules with the aid of digestive enzymes secreted into the gut (Schimdt-Knielsen, 1997), making the chemical energy available to the animal. The energy is then absorbed through the digestive

tract lining (absorption). The non-absorbed energy travels through the digestive tract and is lost as feces or gas production (e.g., methane). Of the energy absorbed into the body, some will be lost through excretion as urine (e.g., urea, uric acid, and ammonia—nitrogenous wastes), the absorbed energy minus excretion is the assimilated energy. Assimilated energy is stored by the animal (e.g., glycogen and lipid stores), used for production (e.g., growth and biosynthesis), used to perform work external to the animal (e.g., locomotion), or lost to the environment as heat. How well the animal performs each of these processes (i.e., digestion, absorption, and assimilation) is termed efficiency and defined as the amount of ingested chemical energy actually made available to the organism. All of these processes combined lead to an increase in postprandial metabolic rate (MR), also known as SDA. While there have been many field based studies of the diet (see Section 9.2) of sea turtles, few studies have been undertaken to understand energy acquisition, and the costs associated with freeing chemical energy from diet items for use in energy consuming activities (e.g., maintenance, growth, locomotion, homeostasis, and reproduction). Nevertheless, knowledge about how physiological and environmental factors influence energy acquisition is critical, as these are among the most fundamental aspects of sea turtle ecology.

When describing the concepts for each section below, we also provide examples of the seminal studies that have paved the way for our understanding of sea turtle feeding physiology. We start with describing the current knowledge on intake rate as handling and consumption are the initial steps in the attainment of chemical energy. We then discuss the digestion and assimilation of food energy and the trade-offs between intake, passage rate, and efficiency. We finally discuss the big picture of the metabolic costs associated with the processes of feeding physiology (i.e., SDA).

9.3.1 Intake Rate

Of all the aspects of feeding physiology the study of food consumption rates (i.e., intake rates) have expanded the most in the past decade. Since the landmark studies of daily intake rates of 0.24%–0.33% of body mass for green turtles grazing on seagrass (Bjorndal, 1980), observation of a leatherback feeding in the North Atlantic Ocean consuming an estimated 200 kg day^{-1} (Duron, 1978), and post-hatchling leatherbacks needing to consume 100% of body mass per day of jellyfish to meet energy demands (Lutcavage and Lutz, 1986), new tools, and analyses have expanded our understanding. Several researchers have used energy budgets to estimate daily consumption rates, for instance, Jones et al. (2004) used a 36/64 resting vs. active diel activity model with measurements of oxygen consumption at rest and while active to estimate intake rates of 3.3% of body mass daily for eastern Pacific green turtles. Wallace et al. (2006a,b) estimated reproductive energy budgets for nesting female leatherbacks, suggesting that eastern Pacific and North Atlantic leatherbacks require 70–90 kg of jellyfish per day and up to 87–113 kg depending on nesting remigration intervals. Jones et al. (in press) measured gross food conversion of juvenile leatherbacks and estimated that adults need to consume prey quantities equivalent to 20%–30% of their body mass (60–108 kg of jellyfish) to meet daily energy requirements.

Biologging devices have allowed indirect and direct measurements of feeding bouts. Southwood et al. (2005) and Casey et al. (2010) measured possible feeding through stomach temperature pills that signal intake of cold prey or water. Casey et al. (2010) recorded limited daytime foraging events for internesting leatherbacks off St. Croix suggesting leatherbacks fed opportunistically, thus energy reserves required prior to nesting migrations are critical for success. Hochscheid et al. (2005) used Hall effect transducers and magnets attached to the beaks of loggerheads (intermandibular angle sensor [IMASEN]) to record mouth openings and general buccal movements. Validation of the sensor with video of foraging allowed for differentiation of consumption of hard or soft prey and moving and sessile prey (Hochscheid et al., 2005). Fossette et al. (2008) used IMASENs on gravid female leatherbacks nesting on French Guiana, the leatherbacks expressed various mouth-opening patterns for different dive patterns, and the authors interpreted that the turtles forage opportunistically on occasional prey, with possibly 17% of the dives hosting successful foraging bouts.

The use of turtle-borne video cameras in recent years has allowed direct observation of sea turtles foraging, many times negating previous assumptions of diet and foraging selectivity (Heithaus et al., 2002; Seminoff et al., 2006a,b; Arthur et al., 2007; see Section 9.2). Heaslip et al. (2012) used turtle-borne cameras on adult leatherbacks of the temperate North Atlantic recording ingestion rates of 330–840 kg day^{-1} of large Lion's mane jellyfish (*Cyanea* sp.) and moon jellies (*Aurelia aurita*) extrapolated from video clips of approximately 3.6 h or less. Fossette et al. (2011) used a hand-held submersible camera while diving to collect footage of leatherbacks feeding, analysis of the 39 s clip suggested that leatherbacks could consume up to 150 kg day^{-1} of small *Linuche unguiculata* jellyfish provided they ate continuously at the recorded rate of one jelly every 2.3 s. Even with the expansion in new technologies there still remains a fundamental lack of information on consumption rates across the turtle species. The handling and consumption of food items is the first and crucial step in the daily acquisition of energy requirements.

9.3.2 Digestibility and Assimilation

Bjorndal (1997) thoroughly reviewed the studies of digestibility and assimilation efficiency of green turtles feeding on natural diets of seagrasses and sponges (in the wild), and artificial diets of trout chow high in protein (in captivity). Many authors use assimilation efficiency and digestibility interchangeably, however, as urine is generally not accounted for in the studies then digestibility (the proportion of a feed or diet which can be digested by the normal animal of the subject species) or digestive efficiency is more appropriate (and what we will use here). The energy lost as nitrogenous wastes (urine) from a meal may be as high as that lost in feces (Merker and Nagy, 1984); therefore, the energy available to the turtles may be considerably less than reported in digestibility studies. For instance, Merker and Nagy (1984) found striped plateau lizards (*Sceloporus virgatus*) fed crickets and mealworms have digestive efficiencies of 0.82 ± 0.01 and assimilation efficiencies of 0.63 ± 0.01, thus only 63% of the energy in the meal was available to the lizards for respiration and production. Wild green turtles (8–66 kg) were found to have energy digestibilities of 22%–71% and protein digestibilities of 14%–57% for a diet of seagrass (Bjorndal, 1980). For green turtles (7–68 kg) feeding on the sponge *C. nucula* energy and protein digestibility ranged from $40\% \pm 15\%$ to $43\% \pm 9\%$ and $52\% \pm 11\%$ to $55\% \pm 7\%$, respectively (Bjorndal, 1990). These studies on wild turtles feeding on natural diets are in stark contrast with captive turtles fed pelleted (trout chow) diets. In a study of captive green turtles (4–22 kg) fed a pelleted diet to satiation (1.2% of body mass), Wood and Wood (1981) recorded protein digestive efficiencies of 82%–90% at 30°C. For juvenile green turtles (<0.9 kg) fed a high protein (40%–50%) diet of trout chow, at 25°C, the digestive efficiencies were $76\% \pm 6\%$ for energy and $86\% \pm 6\%$ for protein (Hadjichristophorou and Grove, 1983). These data corroborate with Davenport and Scott (1993) who recorded digestive efficiencies of juvenile green turtles (<0.8 kg), fed a similar diet of trout chow at 25°C, of $68.0\% \pm 5.9\%$, $89.3\% \pm 1.9\%$, and $60.9\% \pm 7.6\%$ for energy, protein, and lipids, respectively. Furthermore, Davenport and Scott (1993) observed a positive correlation between digestive efficiency and growth rate but not with MR, suggesting that the efficiency of physiological processes of digestion, absorption, and assimilation plays a greater role in growth rate, development, and stage-specific residency times than do consumption rate and MR. Turtles with low digestive efficiencies were associated with increased consumption rates (Davenport and Scott, 1993), presumably to offset poor digestion/assimilation to meet daily energy requirements.

In the only study since Bjorndal's (1997) review, Amorocho and Reina (2008) measured digestibilities of eastern Pacific green turtles (32.3 ± 6.7 kg) fed protein (fish), plant (mixed leaves), and mixed diets at 28°C in an in-water enclosure. The digestibilities for the protein, plant, and mixed diets were 85%–91%, 67%, and 77%, respectively (Amorocho and Reina, 2008). While the plant digestibility was similar to that found by Bjorndal (1980), the protein digestibility corroborated that of captive turtles fed trout chow. The lack of digestion and assimilation studies of the other six species of carnivorous sea turtle is troubling. Data on digestive and assimilation efficiency are

important for studies of physiological ecology and energetic budgeting that seek to understand energy acquisition and subsequent investment in various life-history demands (e.g., reproduction, growth, physiological regulation, etc.) (Wallace and Jones, 2008). Several authors have assumed assimilation efficiencies of 80% for studies of reproductive budgets and individual and population-level consumption rates of leatherbacks (Wallace et al., 2005; Jones et al., in press), and remigration intervals of loggerheads based on energy budgets (Hatase and Tsukomoto, 2008). The assumption of 80% assimilation efficiency was based on measurements of freshwater turtles (*Trachemys scripta*) fed a diet of similar protein content to that of jellyfish and the rapid rate of digestion of gelatinous organisms by fishes (Avery et al., 1993; Malej et al., 1993; Arai et al., 2003).

9.3.3 Passage Rate

The passage rate of food along the digestive tract and digestive efficiency are competing interests for the assimilation of energy. Animals need to move food along the digestive tract to make room for continued consumption, although the efficiency of digestive and absorptive processes is reduced at rapid passage rates (Karasov and Levy, 1990). Therefore, we might assume passage rates may vary significantly among sea turtle species that specialize in carnivorous (high digestive efficiency) and herbivorous (low digestive efficiency) diets. However, like the other processes of feeding physiology, these processes are poorly studied in sea turtles. The time a given meal spends in the alimentary canal of an animal has been called by many names, e.g., total gut clearance time, gastric emptying time (Hadjichristophorou and Grove, 1983; Davenport and Oxford, 1984), passage rate of digesta (Bjorndal, 1997), digesta retention time (Brand et al., 1999), total digestive transit time (Di Bello et al., 2006), ingesta passage time (Valente et al., 2008), and intake passage time (Amorocho and Reina, 2008). Furthermore, the names have slightly different meanings, for example, gastric emptying time is simply clearance of the stomach, whereas total digestive transit time is clearance of the entire digestive tract. The passage of food along the gut in 500–900 g green turtles, fed a satiation diet (2.5% of body mass) of trout chow, took 4.6 ± 0.5 days (gastric emptying) and 7.3 ± 0.7 days (total gut clearance) at 25°C (Hadjichristophorou and Grove, 1983) whereas 60 g post-hatchling green turtles fed a similar diet at 25°C had passage rates of 16 days for turtles continuously fed a daily satiation meal (2.6% of body mass) and 23 days for turtles that were fasted after feeding (Davenport and Oxford, 1984). Davenport and Oxford (1984) reported that feces production was halted after 16 days of starvation; however, in larger 22 kg green turtles feces production continued through 25 days of fasting in 24°C water temperature (T.T. Jones, personal observation; study Jones et al., 2009). Brand et al. (1999) observed that plastic markers were still in the gut of juvenile green turtles (50–55 cm CCL) 5–9 days after release into the wild; based on the passage of markers within the gut at time of recapture they estimated that the passage rate was 6.5–13.5 days (for 50% of markers to pass; water temperatures upward of 28°C). Using biodegradable colored ribbon, McDermott et al. (2006) measured mean initial passage time of 15 ± 1 day (range 5 to >35 days) for 42 ± 12 kg eastern Pacific green turtles, the turtles were allowed to feed ad libitum consuming 0.7%–1.75% of their body mass of red algae (*G. lemaneiformis*) daily (water temperature 27°C ± 2°C). In an experiment using an in-water enclosure to keep green turtles near shore, Amorocho and Reina (2008) observed passage rates of 23.3 ± 6.6 days (73% of markers had passed) for 32.3 ± 6.7 kg juveniles fed plastic markers along with various diets (water temperature 28°C). Birse and Davenport (1987) measured passage rates of 4–18 days for juvenile loggerheads (1–2 kg) fed a daily satiation ration of 3.7% of body mass of trout chow. Valente et al. (2008) observed the passage of markers in loggerheads (4–22 kg) fed a daily fish ration of 1.5%–2.5% of body mass. The time to first elimination was 9 ± 3 days and the time until 50% and 85% of the markers had passed was 12 ± 5 days and 13 ± 5 days, respectively. The Valente et al. (2008) study took place in water temperature ranging from 16°C to 24°C; however, there was no significant difference in passage rates with temperature whereas Birse and Davenport (1987) observed a 60% increase in passage rate from 20°C to 30°C. Di Bello et al. (2006) measured gastric emptying times of 1.4–11.0 days and total clearance times of 8–40 days;

however, the study was of post-surgery loggerheads. The data on intake passage rates are limited and the myriad experimental designs do not allow for clear determinations of diet types, species, and temperature effects on passage rate through the gut. As with all aspects of feeding physiology, there remain large gaps in our understanding of interspecific differences, the role of diet habituation, seasonal temperature fluctuations, and body mass or age on passage rate of food items along the gut or how this affects the fitness of the turtles.

9.3.4 Specific Dynamic Action

When animals consume food there is an accompanying increase in their MR. The postprandial increase in MR has been referred to as SDA and more recently as heat increment of feeding (HIF). Regardless of the name, the process refers to the increase in MR associated with consumption, digestion, absorption, and assimilation of food items (Secor, 2009). Only one study (Davenport et al., 1982) has directly measured SDA in sea turtles (i.e., the accumulated energy expended above standard metabolic rate [SMR]). Davenport et al. (1982) report SDA of 75–153 kJ for juvenile green turtles (0.8–2.2 kg) fed satiation meals (1.8%–2.0% of body mass) of trout chow (43.6% protein and 4.5% fiber). The SDA coefficient (SDA divided by the energy in the meal) ranged from 15% to 25% (Davenport et al., 1982). The SDA coefficient for juvenile green turtles is similar to that of freshwater turtles and tortoises (17.9% ± 1.3%) fed mealworms, kale, and beef (see Secor, 2009, for review). Several studies report the factorial scope of SDA (i.e., the peak postprandial MR divided by the SMR of the turtle); these data can also be gleaned from studies of MR of fasted and fed turtles. Davenport et al. (1982) reported a doubling of MR (factorial scope of 2) for post-absorptive (fasted) turtles fed a satiation meal; the peak in postprandial MR was 2 h post-consumption and the heightened MR lasted for 5 days. Kowalski (2006) measured a postprandial scope of 1.6–1.8 for green and loggerhead post-hatchlings. Jones et al. (2009) measured a scope of 2.1 for juvenile green turtles (22.4 ± 3.1 kg) fed a diet (trout chow, gelatin, vitamins [41% protein, 4% fiber]) 1%–2% of their body mass after 25 days of fasting. Postprandial MR scope for freshwater turtles and tortoises averages 1.9 ± 0.1 and the increased MR typically lasts for 3 days (Secor, 2009). While a doubling of MR is considerable, *Boa constrictors* have postprandial scopes up to 19 times SMR (Secor and Diamond, 2000) and 100% of their scope of activity. The scope of activity for sea turtles is up to four times SMR (Wallace and Jones, 2008), therefore SDA can cause increases in MR of 50% of the turtles maximum MR. SDA accounts for all the energetic costs associated with consumption to assimilation including numerous pre-absorptive, absorptive, and post-absorptive physiological processes (McCue, 2006). If the post-absorptive processes associated with SDA do not include biosynthesis (somatic growth), then the higher the SDA the less energy available to the organism for growth and reproduction (Secor, 2009). Therefore, the more efficient turtles are at consumption, digestion, absorption, and assimilation the lower the cost of SDA and the greater amount of energy available to the turtle for production (e.g., growth, biosynthesis), storage (e.g., fat), and work (e.g., locomotion, migration).

As with other emerging areas of scientific inquiry, our knowledge about these and other aspects of feeding physiology in sea turtles will benefit from continued research. So far, however, the majority of studies have focused on green turtles and we know very little about the feeding physiology of carnivorous sea turtles. We encourage both field studies and controlled laboratory experiments on all species, particularly species other than green turtles. These multiple lines of inquiry will hopefully shed light on the biological and ecological drivers that result in the varying behaviors and physiologies of each species. Basic research on intake rates, energy assimilation, and associated costs elucidate how sea turtles meet the energy demands of their various developmental patterns and ever changing environments. These data also allow inferences on distribution and demographic patterns of sea turtles based on current and future resource availability. Research on diet components and acquisition and use of chemical energy can be greatly expanded upon by the use of emerging technologies such as stable isotope, fatty acid, and trace element analysis.

These technologies may reveal differential use of stored energy in diet items (e.g., fat, proteins), as well as the spatial and temporal timing of feeding events and diet composition. Thus by melding feeding physiology with emerging technologies, we can better understand the dynamic and often complex nature of the foraging ecology of sea turtles.

9.4 STABLE ISOTOPE ANALYSIS IN SEA TURTLES

Among the various new tools that are available to sea turtle researchers, perhaps no application has blossomed more than SIA (Table 9.2). Stable isotopes are various forms of the same element (e.g., carbon, nitrogen, oxygen, sulfur) that differ in the numbers of neutrons in their atomic nucleus and therefore have minute differences in atomic mass (recall that the mass of an atom is constituted by total mass of protons, neutrons, and electrons in a single atom). The slight differences in atomic mass ultimately translate into variability in the way isotope ratios change in the environment, body tissues, and metabolic pathways (e.g., digestion, excretion) of animals (Miniwaga and Wada, 1984; Peterson and Fry, 1987) or in nutrient flow within ecosystems (Hobson and Rubenstein, 2004; Table 9.2). The predictable ways that isotope ratios change in body tissues as a result of these processes allow researchers to gain insights about a variety of biological aspects such as feeding biology, ontogeny, and habitat use (Miniwaga and Wada, 1984; Peterson and Fry, 1987). Because digestion and excretion processes are major influences on stable isotope ratios—especially of stable nitrogen and carbon—insights gained from SIA are often associated with consumer trophic status and diet. Indeed, SIA for sea turtle research has focused almost exclusively on stable carbon ($^{13}C/^{12}C = \delta^{13}C$) and stable nitrogen ($^{15}N/^{14}N = \delta^{15}N$), which are the most instructive elements for feeding studies, and are our primary focus in this chapter. It should be noted, however, that stable sulfur ($^{34}S/^{32}S = \delta^{34}S$) and stable oxygen ($^{18}O{:}^{16}O = \delta^{18}O$) analyses are becoming more widespread, and where appropriate we describe these studies later.

Stable isotope analysis in the context of animal ecology—including sea turtles—is based on the tenet that "you are what you eat." That is, dietary inferences based on stable isotopic profiles in animal tissues are possible because the isotope compositions of a consumer's body tissues are ultimately derived from those in its diet. However, rather than reflecting the exact stable isotope values of the foods they eat, predators such as sea turtles exhibit predictable differences (i.e., discriminate) from their prey. Because $\delta^{13}C$ signatures undergo only slight trophic enrichment, they are not necessarily good indicators of trophic levels, but more effectively describe different carbon sources and flow pathways (DeNiro and Epstein, 1978; Peterson and Fry, 1987; Table 9.2, Figure 9.1). On the other hand, due to their large enrichment factor, $\delta^{15}N$ signatures are useful for the identification of trophic level of the organism or trophic structure of the system of interest (DeNiro and Epstein, 1981; Miniwaga and Wada, 1984; Table 9.2). Stable sulfur and oxygen are also of value for studying wildlife, although in these cases there are spatial gradients in isotope concentrations, which make their study more appropriate for elucidating animal movements and habitat use rather than trophic status. For example, whereas $\delta^{34}S$ can discern the relative importance of estuarine vs. marine habitats and/or benthic vs. pelagic habitats for sea turtles (Thode, 1991), $\delta^{18}O$ elucidates latitudinal movements due to decreasing $\delta^{18}O$ in surface waters of higher latitudes (Lajtha and Marshall, 1994; Table 9.2)

Assuming discrimination values are known, the stable isotope technique is particularly useful when an organism's diet is difficult to establish with conventional approaches such as esophageal lavage (i.e., stomach flushing) and fecal analysis. Because isotope analysis provides information on nutrients assimilated over extended periods, the approach is much less affected by short-term temporal change in diet than other methods, which only provide dietary "snapshots" of recently consumed food items (Peterson and Fry, 1987; Hobson et al., 1996). When examined for multiple individuals within a population, or multiple organisms within an ecosystem, stable isotope analyses provide unique insights to trophic variability and niche width, or specificity with which an individual or population forages (Gu et al., 1997; Bearhop et al., 2004; Araújo et al., 2007), and nutrient transport within an ecosystem (e.g., Vander Zanden et al., 2012).

TABLE 9.2
Summary of Stable Isotopes Used in Sea Turtle Research

Stable Isotope Notation of Isotope Ratios	Natural Processes that Influence Isotope Abundance	Natural Environmental Patterns (i.e., without Human Influence)			
	Biological and/or Biochemical	Terrestrial	Marine	Terrestrial vs. Marine	Reference(s)
Carbon ^{13}C:^{12}C $\delta^{13}C$	Vary in plant tissue with Isotopic fractionation during photosynthesis[a] Ambient conditions that limit enzymatic reactions during photosynthesis or alter stomatal opening	Decrease with increasing latitude[b,c] Increase with increasing altitude[b] Mesic (i.e., dry) habitats more enriched compared to xeric (i.e., wet) habitats[d]	Decrease with increasing latitude[e] Northern oceans more enriched compared to southern oceans[e] Benthic more enriched compared to pelagic[e]	Marine more enriched compared to terrestrial[f]	Kelly (2000) Lajta and Marshall (1994) Hobson (1999)
Oxygen ^{18}O:^{16}O $\delta^{18}O$	Vary in meteoric waters with Precipitation patterns Temperature Elevation Relative humidity	Decrease with increasing latitude[g] Decrease with increasing altitude[g] Highest in summer and lowest in winter above 30° latitude[g] Decrease moving inland[g]	No patterns	Marine more enriched compared to terrestrial[h]	Lajta and Marshall (1994) Poage and Chamberlain (2001)

(*continued*)

TABLE 9.2 (continued)
Summary of Stable Isotopes Used in Sea Turtle Research

Stable Isotope Notation of Isotope Ratios	Natural Processes that Influence Isotope Abundance	Natural Environmental Patterns (i.e., without Human Influence)			
	Biological and/or Biochemical	Terrestrial	Marine	Terrestrial vs. Marine	Reference(s)
Nitrogen $^{15}N:^{14}N$ $\delta^{15}N$	Vary in plant tissue according to how plants fix N Symbiotic fixation Direct conversion of atmospheric N Increase with trophic level[i]	Xeric (i.e., wet) habitats more enriched compared to mesic (i.e., dry) habitats[j]	Northern oceans more enriched compared to southern oceans[k]	Marine more enriched compared to terrestrial[l]	Kelly (2000) Hobson (1999) Hobson (2003)
Sulfur $^{34}S:^{32}S$ $\delta^{34}S$	Vary in nature with Distribution of light and heavy sulfides in bedrock Quality of plant growing conditions (i.e., aerobic vs. anaerobic) Atmospheric deposition from natural sources	No patterns	Estuarine and marsh more enriched compared to marine[m] Benthic (i.e., inshore) more enriched compared to pelagic (i.e., offshore)[m]	Marine more enriched compared to terrestrial[n]	Thode (1991) Hobson (2003)

Source: Modified from Rubenstein, D.R. and Hobson, K.A., *Trends Ecol. Evol.*, 19, 256, 2004.

[a] Plants use one of three different types of photosynthetic pathway (C3, C4 or crassulacean acid metabolism [CAM]) that utilize different CO_2-fixing enzymes and result in varying ranges of d13C values (Latja and Marshall, 1994; Kelly, 2000).

[b] Due to temperature differences (Latja and Marshall, 1994; Kelly, 2000).

[c] Due to differences in abundance of C4 plants (Kelly, 2000).

[d] In C3-based systems 0 wing to difference in water use efficiency (Latja and Marshall, 1994).

[e] Due to temperature differences, surface-water CO_2 concentrations and differences in plankton biosynthesis or metabolism (Kelly, 2000).

[f] Due to bicarbonate as a carbon source and slower diffusion of CO_2 in marine environment (Kelly, 2000).

[g] Due to rainfall patterns and temperature differences (Latja and Marshall, 1994; Poage and Chamberlain, 2001).

[h] Due to evaporation of seawater and subsequent condensation of cloud moisture over land (Latja and Marshall, 1994).

[i] Due to discrimination and fractionation during prey nutrient assimilation by predators (DeNiro and Epstein, 1981).

[j] Reasons are unclear (Kelly, 2000).

[k] Due to inorganic nitrogen being an important contributing factor in marine environment (Hobson, 2003).

[l] Due to anoxic conditions (Thode, 1991).

[m] Due to bacterial sulfate reduction in marine environment (Thode, 1991).

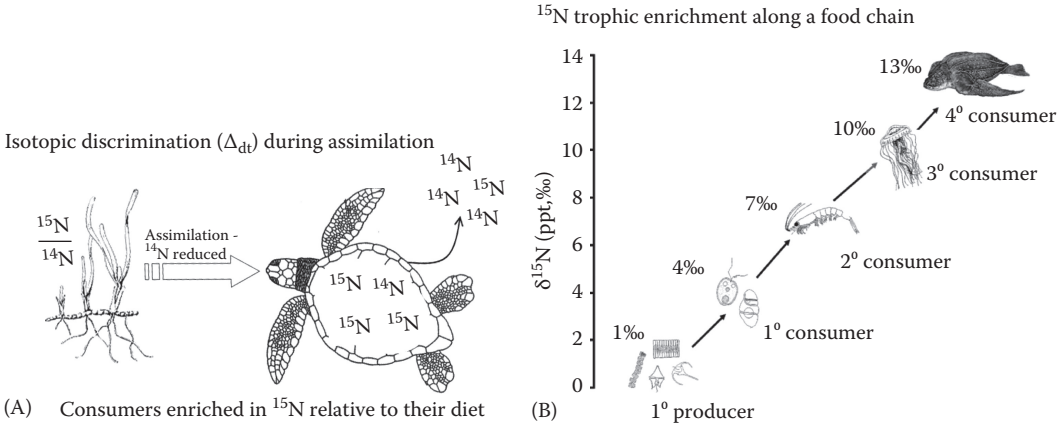

FIGURE 9.1 Schematic of ^{15}N trophic enrichment in sea turtles. (A) Conceptual presentation of retention of heavier ^{15}N isotopes and higher rate of purging of lighter ^{14}N isotopes. (B) Rendition of stepwise enrichment in ^{15}N at 3 ppt per trophic chain. AQ5

The initial sea turtle stable isotope study was conducted by Killingley and Lutcavage (1983) who measured stable oxygen profiles in commensal barnacle shells to reconstruct loggerhead movements, but it was not until Godley et al.'s (1998) efforts that isotopic measurements focused on sea turtle body tissues—in their case to explore trophic status of sea turtles in the Mediterranean. Since then, the application of this technique has rapidly expanded, and has resulted in deeper insights about sea turtle diet and trophic status, habitat use, movements, and demography (see later).

9.4.1 Limitations of Stable Isotope Analysis

The recent and rapid expansion of stable isotope applications to address questions about wildlife ecology has garnered panacea status for SIA. However, there are several limitations that must be considered prior to applying this research technique. Chief among these are for dietary investigations, the power of stable isotopes to determine the trophic level and/or specific prey of a consumer requires that isotopic discrimination and residence time be well understood. Yet for sea turtles these key aspects have not been determined for most species, diets, and life stages (see Table 9.3). A second challenge is that the ability of stable isotope analyses to decipher dietary complexity in a predator is only possible if the putative diet items differ appreciably in their isotope values (Boecklen et al., 2011). In other words, if all the potential foods in a foraging habitat have the same or similar stable isotope values, it is difficult to distinguish diet signals of each food type. Low isotopic diversity among species within a foraging habitat can thus limit the predictive power of stable isotope mixing models, and often requires that isotopically similar species are lumped into prey groups (Phillips and Gregg, 2003; Phillips et al., 2005), which thereby undermines the primary reason why mixing models are used. This problem can be ameliorated through incorporating elemental concentration dependency into modeling efforts (Phillips and Koch, 2002) and using a greater number of isotopes in such models (e.g., adding $\delta^{34}S$ to ongoing $\delta^{13}C$ and $\delta^{15}N$ analyses). However, expanding the palette of isotopes in a study is costly and may be prohibitive of maximizing sample sizes.

An additional challenge to the broad application of stable isotope analysis, particularly as it relates to studies of habitat use and animal movements, is that patterns of isotopic abundances (i.e., isoscapes) are poorly resolved for most ocean regions. While spatial gradients in stable isotope values at the base of food webs have been described on very large scales (Somes et al., 2010; Deutsch et al., 2011), few regional maps are available and little is known about temporal shifts in isotope abundances in natural systems (Faure, 1986; Boecklen et al., 2011). For high-order consumers, the

TABLE 9.3
Summary of Stable Isotope Discrimination and Isotope Retention Time in Turtles

Species	Lifestage	Size (SCL) cm	Diet Type	Tissue Type	Δdt Carbon	Δdt Nitrogen	C Turnover (d)	N Turnover (d)	References
Caretta caretta	Hatchling	4.3–4.9	Soy protein pellet	Skin	2.62 ± 0.34	1.65 ± 0.12	83.0 ± 7.02	66.7 ± 7.36	Reich et al. (2008)
				Scute	–0.86 ± 0.57	0.61 ± 0.16	62.5 ± 7.31	45.5 ± 5.48	
				RBC	–0.64 ± 0.73	–0.25 ± 0.30	76.9 ± 11.34	71.4 ± 10.66	
				Plasma	0.29 ± 0.20	0.32 ± 0.09	20.0 ± 6.34	18.5 ± 4.25	
				Whole blood	0.19 ± 0.08	0.92 ± 0.34	43.5 ± 2.34	35.7 ± 2.73	
Caretta caretta	Juvenile	9.0–13.1	Animal protein pellet	Skin	1.11 ± 0.17	1.60 ± 0.07	46.1 ± 7.02	44.9 ± 3.1	Reich et al. (2008)
				Scute	1.77 ± 0.58	–0.64 ± 0.09	50.9 ± 13.14	16.2 ± 2.3	
				RBC	1.53 ± 0.17	0.16 ± 0.08	40.1 ± 3.4	36.3 ± 3.4	
				Plasma	–0.38 ± 0.21	1.50 ± 0.17	39.6 ± 9.1	22.5 ± 5.1	
				Whole blood	1.11 ± 0.18	0.14 ± 0.06	46.1 ± 8.9	27.7 ± 3.5	
Chelonia mydas	Juvenile	43.0–47.5	Soy and fish-meal protein pellet	Skin	0.17 ± 0.03	2.80 ± 0.11			Seminoff et al. (2006a,b)
				RBC	–1.11 ± 0.05	0.22 ± 0.03			
				Plasma	–0.12 ± 0.03	2.92 ± 0.03			
				Whole blood	–0.92 ± 0.06	0.57 ± 0.09			
C. mydas	Juvenile	28.5–35.8	Soy protein pellet	Plasma	2.62 ± 0.66	3.18 ± 0.66			Seminoff et al., in review
Dermochelys coriacea	Juvenile	25.8 ± 1.0a	Fortified squid gelatin	Skin	2.26 ± 0.61a	1.85 ± 0.50a			Seminoff et al. (2009)
				RBC	0.46 ± 0.35a	1.49 ± 0.76a			
				Plasma	–0.58 ± 0.53a	2.86 ± 0.82a			
				Whole blood	0.35 ± 0.33a	1.98 ± 1.14a			

Trachemys scripta	Adult male	15.5–24.0	Soy pellet	RBC		1.9±0.2b			Seminoff et al. (2007)
				Plasma		3.8±0.1b			
				Whole blood		2.2±0.2b			
				Liver		3.0±0.3b			
				Brain		2.9±0.3b			
				PM muscle		2.7±0.3b			
				PI muscle		3.4±0.4b			
Trachemys scripta	Adult male	15.5–24.0	Fish-meal pellet	Plasma		–0.8±0.8b		38.7c	Seminoff et al. (2007)
				Whole blood		2.5±0.8b		35.6c	
				Liver		0.4±0.5b		52.5c	
Gopherus agassizii	Adults		Soy-plant based	Red Blood	0.2±0.3		126.7±40.3		Murray and Wolf (2012)
				Cells	1.0±0.2		32.9±14.5		
				Plasma	0.8±0.1				
				Scute					

a=SD, b=SE, c=halflife.

elaboration of foraging habitats is further obscured by the substantial difference in stable isotope values between their tissues and those of basal producers (Post, 2002; Phillips et al., 2009; Boecklen et al., 2011). These differences are due to stepwise isotope enrichment occurring at each trophic level (DeNiro and Epstein, 1981) along with poorly understood extrinsic and intrinsic factors affecting isotope enrichment along the food chain (Post, 2002; Phillips et al., 2009; Boecklen et al., 2011).

9.4.2 Isotopic Discrimination

Fundamental to the interpretation of stable isotope data is the need to understand the patterns by which diet isotopic values are reflected in consumer tissues (i.e., isotope discrimination, or Δ_{di}; Cerling and Harris, 1999). For example, $\delta^{13}C$ and $\delta^{15}N$ of consumer and prey tissues are usually not identical, and instead exhibit predictable differences due to selectivity for lighter isotopes during a consumer's metabolic processes (DeNiro and Epstein, 1978, 1981). Although there is variation among species, most endothermic species show an isotopic increase of 0‰–1‰ for $\delta^{13}C$ and 3‰–5‰ for $\delta^{15}N$ per trophic level (DeNiro and Epstein, 1978, 1981; Miniwaga and Wada, 1984; Post, 2002; Figure 9.1). However, stable isotopic discrimination may vary widely, with some species ^{13}C-depleted by ~1‰ and ^{13}C-enriched by ~3‰ relative to their prey, and ^{15}N-enriched by less than 3 ‰ (Hesslein et al., 1993; Pinnegar and Polunin, 1999; McCutchan et al., 2003; Reich et al., 2008).

The mechanisms for this enrichment are not thoroughly understood, but may result from a variety of biochemical pathways. For example, there is relatively greater differential excretion of ^{14}N in urine; resulting in a net gain of ^{15}N in consumer tissues (Miniwaga and Wada, 1984; Peterson and Fry, 1987) (Figure 9.1). Fractionation during amino acid (AA) amination and transamination further contributes to isotopic enrichment (Abelson and Hoering, 1961; Macko et al., 1986; Tieszen and Boutton, 1989; Hobson and Clark, 1992; Tieszen and Fagre, 1993). Variations in stable isotope ratios between consumer tissues and mean diet may also be influenced by consumer age (Roth and Hobson, 2000), nutrition status (Sealy et al., 1987; Hobson and Clark, 1992; McCue and Pollock, 2008), diet (Caut et al., 2009), trophic level (Tieszen et al., 1983; Hobson and Clark, 1992; Pearson et al., 2003), body temperature (Pinnegar and Polunin, 1999), digestive strategy (Macrae and Reeds, 1980), and (or) environmental conditions (Michener and Lajtha, 2007).

Within a given organism, stable isotope ratios may differ substantially among different tissue types. Such differences have been attributed to variations in the protein and AA compositions of different tissues because these components can differ in their nitrogen isotope content (Peterson and Fry, 1987). Selective routing of exogenous nutrients during tissue maintenance and construction, and differential mobilization of endogenous resources into tissues or tissue components, may also contribute to these tissue-level differences (Macrae and Reeds, 1980; Peterson and Fry, 1987; Gannes et al., 1997).

To date, discrimination in sea turtles has been established only for post-hatchling and small juvenile loggerheads (Reich et al., 2008), juvenile and adult green turtles (Seminoff et al., 2006a,b; Vander Zanden et al., 2012), and juvenile leatherbacks (Seminoff et al., 2009) (Table 9.3). As found in other taxa, there is evidence that discrimination varies with size class, somatic growth rates, and diet (Seminoff et al., 2006a,b; Reich et al., 2008; Vander Zanden et al., in press). Clearly there are numerous influences on predator–prey isotope discrimination, many of which remain poorly understood. Additional controlled sea turtle studies that focus on novel taxa, different life stages, and varied diets will be vital for providing discrimination values that will enable effective and accurate determinations of prey isotope values based on sea turtle bulk tissue data.

9.4.3 Isotopic Residence Time

Another key aspect is the determination of the isotopic residence time (i.e., turnover rate) in turtle body tissues. That is, when a turtle adopts a new diet, how long does it take for the old dietary signal to be completely turned over to the new diet signal. Incorporation of diet-derived stable isotopic

signatures into consumer body tissues occurs at varying rates based primarily on tissue-specific metabolism (Gannes et al., 1997). As a result, different tissues may provide dietary information that is integrated over different time scales. Tissues with higher metabolic activity (liver, whole blood) will reflect more recent diet history, and those with lower metabolism (integument, bone) will represent an integration of diet over a substantially longer period, perhaps approaching the full life of the consumer (Tieszen et al., 1983; Hobson and Clark, 1992).

Isotopic residence times have so far been established for relatively few sea turtle species and life stages (Table 9.3). Within sea turtles, isotopic residence times have only been established for juvenile loggerhead turtles (Reich et al., 2008) and green turtles (Vander Zanden et al., 2012), although there have also been studies of freshwater turtles (Seminoff et al., 2007) and tortoises (Murray and Wolf, 2012) that are instructive. In all cases it is evident that the turnover rates in turtles are much slower than for mammals and birds (Hobson and Clark, 1992; B. Wolf unpubl. data). There is also a general trend within the reptilia that stable carbon turnover rates are much slower than those for stable nitrogen (Seminoff et al., 2007; Reich et al., 2008; Murray and Wolf, 2012).

9.4.4 Diet and Trophic Status

Applications of stable isotope analytical techniques have provided many new insights about the ecology of sea turtles and other marine consumers. Among the most fundamental questions that can be addressed are those relating to trophic status and/or diet of a species. That is, what is the trophic level of a turtle or general population, and what are the specific prey species or prey groups consumed. This assumes knowledge is available regarding the turtle life stage and diet-specific isotope discrimination as well as the stable isotope baseline for primary producers within the marine system in which study animals forage. If information is available on the stable isotope values of individual putative prey species, stable isotope mixing models can be used to determine the relative contribution of various potential prey species to the overall diet composition of a consumer (Phillips, 2001; Semmens and Moore, 2008; Inger et al., 2010).

Stable isotope analyses have complemented conventional diet techniques to decipher dietary contributions for sea turtles in many localities worldwide. Stable carbon and nitrogen have been used to study the diet of loggerheads in the western North Atlantic (Wallace et al., 2009) and Mediterranean (Revelles et al., 2007a,b); green turtles in the eastern Pacific (Lemons et al., 2011), Australia (Arthur et al., 2009), and Japan (Hatase, 2006), hawksbills in Hawaii (Graham, 2009) and the Bahamas (Bjorndal and Bolten, 2010); and leatherbacks in the western North Atlantic (Dodge et al., 2011). In several cases, isotopic inquiry has also revealed novel insights otherwise unknown via conventional techniques. For example, green turtles are not obligate neritic herbivores throughout their range as once thought (Hatase et al., 2006; Arthur et al., 2009; Kelez, 2011), whereas hawksbill turtles appear to have a greater dependency on seagrass habitats than previously believed (Bjorndal and Bolten, 2010).

Stable isotopes have also been used to illustrate ontogenic shifts in diet and habitat use, as well as differences in foraging behavior of individuals within a population. For instance, stable isotope analysis revealed polymodal foraging in adult female loggerheads in Florida (Reich et al., 2009) and individual dietary specialization in loggerheads from the same region (Vander Zanden et al., 2010). A study by Reich et al. (2007) was the first to confirm the oceanic foraging by "lost year" turtles based on isotope analysis of sequential scute layers. Likewise, Arthur et al. (2008) used $\delta^{13}C$ and $\delta^{15}N$ to reveal ontogenic changes in foraging behavior in Australian green turtles, and Cardona et al. (2009, 2010) used $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ to reveal ontogenic diet shifts in green turtles from West Africa and the Mediterranean. Size-related differences in feeding habitat use and foraging dichotomies in adult loggerhead turtles around Japan have also been revealed via SIA (Hatase et al., 2002, 2010). In one of the first isotope studies to shed light on reproductive output parameters, Caut et al. (2006) used $\delta^{13}C$ and $\delta^{15}N$ to show that French Guianan nesting groups with differing remigration intervals had significantly different $\delta^{13}C$ and $\delta^{15}N$ values, likely owing to isoscape differences between each groups' unique foraging areas.

9.4.5 Isoscapes and Foraging Movements

In addition to the value of isotopes for determining the trophic status and diet of sea turtles, SIA can decipher the key foraging habitats used by sea turtles. While not as precise as satellite telemetry, SIA is much lower in cost, and a viable tool for tracking animal movements because the isotopic compositions of consumer tissues integrate isoscape information from foraging environments (DeNiro and Epstein, 1981). Thus, when a sea turtle moves among spatially discrete food webs that are isotopically distinct (i.e., isoscapes), stable isotope values of its tissues can provide unambiguous information about its previous location (Hobson, 1999; Rubenstein and Hobson, 2004; Hobson and Wassenaar, 2008; Newsome et al., 2010).

There have been several studies that have shed light on marine isoscapes, and this is an area of rapid advancement. The first such example was a study of leatherback turtles by Wallace et al. (2006a,b) that revealed significantly higher $\delta^{15}N$ in body tissues of leatherbacks nesting in the eastern Pacific (Playa Grande, Costa Rica) compared to those nesting in the western North Atlantic (St. Croix, USVI). The $\delta^{15}N$ disparity was likely due to differences in the prevailing nitrogen cycling regimes between the two ocean regions, with high levels of denitrification driving down $\delta^{15}N$ values in the eastern Pacific and greater N_2 fixation reducing the $\delta^{15}N$ values in the Atlantic (Montoya, 2007). Pajuelo et al. (2010) later found the same pattern in loggerhead turtles from Peru vs. those found near the Azores Islands, and also attributed this dichotomy to effects from baseline differences in nitrogen cycling between the two regions. However, while these two studies were paramount in showing that the influence of baseline stable isotope signatures is conserved up the food chain within a particular region, they lacked the ability to unequivocally determine the specific whereabouts of turtles when they incorporated observed stable isotope values.

Elucidating the whereabouts of a turtle during the assimilation of specific isotope signatures would appear to be a key need in isotopic research. An ideal, if not costly tool, to provide this spatial information is satellite telemetry, and studies blending isotope and satellite tracking are increasing, the result of which is a firmer understanding of marine isoscape patterns (Hobson and Wassenaar, 2008). A study by McClellan et al. (2010) of loggerhead turtles in the eastern United States was the first to our knowledge that used satellite telemetry to establish the spatial patterns of marine isoscapes; in their case, showing an isotopic dichotomy between juvenile loggerhead sea turtles that foraged coastally vs. those that foraged in offshore waters. Zbinden et al. (2011) similarly showed a migratory dichotomy and associated phenotypic variation in Mediterranean loggerhead turtles, and Pajuelo et al. (in review) found that variation in $\delta^{13}C$ and $\delta^{15}N$ in post-nesting Florida loggerheads can be explained by differences in food-web baseline isotopic signatures rather than differences in loggerhead trophic levels. Seminoff et al. (2012) provided similar insights for Indonesian leatherbacks that used eastern and western Pacific foraging areas.

9.4.6 Compound-Specific Isotope Analysis of Amino Acids

As a complimentary tool to bulk tissue stable isotope analysis, compound-specific isotope analysis of individual AAs (CSIA) can provide additional information that can separate source and metabolic changes in the bulk isotopic signature. The CSIA technique has been utilized in the fields of geology and paleoecology for over four decades (Evershed et al., 2007), but only recently has it been applied to studies of marine vertebrates and turtles specifically. CSIA is the measurement of the isotopic composition of specific AAs in body tissues and it can substantially enhance the value of bulk tissue stable isotope measurements for understanding the trophic status of marine species. This is possible because some AAs, such as phenylalanine, retain the isotopic composition of source nitrogen at the base of the food web (i.e., "source" AAs), whereas other AAs such as glutamic acid are significantly enriched in ^{15}N as they move through the food web (i.e., "trophic" AAs; McClelland and Montoya, 2002). Baseline and trophic information can thus be obtained from a consumer's tissue without

need for analyses of prey items or of basal food web samples (McClelland and Montoya, 2002; Popp et al., 2007). It is believed that these "trophic" AAs are either synthesized by the consumer or undergo significant transamination and deamination reactions that preferentially favor the retention of the heavier isotope (McClelland and Montoya, 2002), and it is assumed that this is also the mechanism underlying ^{15}N enrichment observations in bulk tissues (Figure 9.1).

Compound-specific isotope analysis of AAs has been conducted in a small number of ecological studies, being applied to differentiate metabolic and trophic-level relationships in a food web from changes in isotopic composition at the base of the food web (Uhle et al., 1997; Fantle et al., 1999; McClelland and Montoya, 2002; Popp et al., 2007). To our knowledge there have only been two studies that have applied CSIA technique to sea turtles. Vander Zanden et al. (in review) investigated the $\delta^{15}N$ of AAs and bulk tissues in green turtles nesting at Tortuguero, Costa Rica, in an effort to discern the foraging destinations of individual nesters. Similarly, Seminoff et al. (2012) used CSIA coupled with satellite telemetry and bulk tissue SIA to track the foraging migrations of leatherback turtles nesting at Jamursba Medi, Indonesia. Both studies show great promise for the CSIA technique, and it is clear that this approach is a powerful complement to bulk tissue SIA.

9.5 FATTY ACID AND TRACE ELEMENT ANALYSES

9.5.1 Fatty Acid Analysis

Traditional methods for determining diet have relied on visually identifying the contents of the gastro-intestinal (GI) tract and the degree to which the components in the diet have been digested often complicate this assessment. Establishing dietary composition by monitoring fatty acid profiles for organisms has become increasingly common as a means for overcoming these difficulties and determining the relative importance of a dietary constituent for wildlife species (Iverson et al., 1997).

Fatty acids (FAs), the primary components of most lipids, are composed of a hydrocarbon chain with a methyl group (CH_3) at one end and a carboxyl group (COOH) at the other. Fatty acids with no double bonds are considered saturated because they contain the maximum number of hydrogen atoms. Those with one or more double bonds are referred to as monounsaturated or polyunsaturated, respectively, and the number and position of double bonds, as well as the length of the hydrocarbon chain, give a FA its particular biochemical properties. FAs are most commonly referred to by the following shorthand notation: A:Bn-C where A is the number of carbon atoms in the hydrocarbon chain, B is the number of double bonds, and C is the position of the first double bond relative to the methyl end (IUPAC-IUB Commission on Biochemical Nomenclature, 1967).

Unlike proteins and carbohydrates that are degraded during digestive processes, dietary FAs are often deposited in the fat stores of a consumer with little or no modification (Ackman, 1989). Thus, predators have biochemical limitations on the types of FA they can synthesize, and FAs longer than 14:0 are predictably incorporated into consumer tissue (Cook, 1985; Galli and Rise, 2006). As a result, the FA composition of the diet is thought to be reflected in the stored fat of consumers (Holland et al., 1990). The FA composition of a consumer can therefore provide insight into the types of foods that were previously consumed.

There have been relatively few studies on sea turtles that employ fatty acid analysis. The technique was first applied in a study of leatherback diet by Holland et al. (1990) that linked the FAs in sea jellies to those in the fat tissue of leatherback turtles. Guitart et al. (1999) studied loggerhead turtles to similarly determine their prior diet. Green turtles have been the sea turtle species for which FA analysis has been most common, with Ackman et al. (1992) exploring FAs in green turtles from the Hawaiian Islands and Johnston Atoll, Seaborn et al. (2005) measuring FAs in green turtles from Hawaii, and Craven et al. (2008) exploring FAs in the yolks of captive green turtles.

Despite some rapid advancement over the past decade, FA signature analysis is still in development. Many important physiological and statistical issues need to be resolved to maximize

its applicability to studies of sea turtle ecology. For example, much as with stable isotopes, if potential food sources all have very similar FA compositions, consumers will likely be relatively uniform in their FA signatures and the FA approach will have low power for discriminating diet source. Conversely, if a consumer group ingests a wide variety of different foods that each has highly variable FA compositions, predator signatures may be too variable to reflect meaningful ecological patterns. Another challenge to the FA approach is that the exact temporal scale of FA information is still unclear in most cases. Evidence from captive feeding studies indicates that the FA signatures of seals reflect diet composition integrated over weeks to months (Kirsch et al., 2000), but more information on the FA temporal window for other species is necessary. For sea turtles, calibration of this timing, as well as greater understanding about the effects of dietary FA variability on the power of FA analysis, could be determined via captive feeding studies.

9.5.2 Trace Element Analysis

The value of trace elemental analysis (TEA) is less resolved than for SIA and FA analysis. The theory behind the TEA is similar to that of stable isotopes and FA in that it is expected that prey species' and spatially explicit background chemical signatures in the water column and/or food source are incorporated into body tissues of consumers. For diet investigations, it is believed that the minute trace levels of a host of heavy metals and pollutants (including but not limited to arsenic, antimony, cadmium, cobalt, copper, lead, mercury, selenium, and zinc) in foods ingested by consumers will bioaccumulate in the consumer tissues. Thus, when both consumer tissues and prey are analyzed for trace element concentrations, the elemental "signatures" of these groups can be linked to determine which potential prey species were featured in the diet. Likewise, for studies of animal movements, trace element concentrations in consumer tissues are presumed to be an integration of trace elements present in foraging environments, and thus, when an animal moves among spatially discrete food webs that have different trace element occurrences, TEA can provide unambiguous information about an animal's previous location (Ramos et al., 2009).

Few TEA studies have been conducted on sea turtles to our knowledge, although there are many studies underway (e.g., Lopez Castro, unpubl. data). Bergeron et al. (2007) studied diet composition in four species of freshwater turtles using trace elements, Ikonomopoulou et al. (2011) studied trace element concentrations in nesting flatback turtles in Australia, and van de Merwe et al. (2010) studied long-distance migrations of green turtles from Southeast Asia. Although TEA is in its infancy, this approach shows promise as another tool to examine foraging ecology and animal movements across broad spatial scales.

9.6 CONCLUSIONS

Since publication of *The Biology of the Sea Turtles* (Volume 1; Lutz and Musick, 1997), there have been many advances in our understanding of sea turtle biology. These insights have been gained via continued application of many tried and true, and traditionally "low tech" research tools and benefited more recently from the development of new research fields such as biologging, fine-scale physiological measurements, stable isotope analysis, and fatty acid analysis. However, despite their value in sea turtle research, there are still improvements that can be achieved.

More than a decade ago in Volume 1, Karen Bjorndal (Chapter 7, Foraging ecology and nutrition of sea turtles) stressed the importance of studies on all aspects of feeding physiology and in quantifying nutritional requirements, since that time only a handful of studies have emerged (see Section 9.3). The reproductive success of turtles, and inevitably their rebound from past declines, requires the successful attainment of chemical energy and the conversion of that energy into useable components to fuel somatic and reproductive growth, trans-oceanic migrations, temperate water foraging, and all the physiological processes of life (i.e., homeostasis). With impending changes in climate and temperature, prey landscapes are changing (Mills, 2001); human perturbations such as

commercial fishing reduce target species (e.g., crabs) but offer free lunch in the form of fisheries discard (Seney and Musick, 2007). How well turtles adapt to these changes both behaviorally and physiologically and how they maintain energy intake and absorption despite ever changing conditions such as dietary dilution from plastic ingestion (McCauley and Bjorndal, 1999), is yet to be determined. Therefore, a decade and a half later, we end with a call for more studies into the diet selection and feeding physiology of sea turtles and an incorporation of emerging techniques and technologies to elucidate aspects of feeding biology.

In the realm of molecular analyses, we need greater emphasis on technical aspects such as tissue preservation for sea turtle stable isotope studies (e.g., Barrow et al., 2008; Lemons et al., 2012). Knowledge like this, coupled with efforts to standardize tissue collection and analytical protocols will benefit molecular approaches. For analysis of consumer and prey isotope values, the disparities in discrimination factors and isotope retention time found among taxa underscore the need for additional feeding trials under controlled conditions for the technique to be reliably used in unstudied groups. Likewise, we need a more solid understanding of the spatiotemporal isotopic patterns in marine fauna at basal and higher-order trophic levels. Clarification about the baseline influence on isotopic compositions of tissues of higher-order marine consumers is also required for maximizing the value of isotopic analyses (Graham et al., 2010). In the coming years we encourage studies to address these issues and believe that through greater emphasis on controlled experimental studies and additional data collected in situ, we will be able to maximize the value of SIA for addressing questions about sea turtle ecology (see Gannes et al., 1997; Newsome et al., 2007; Martínez del Rio et al., 2009). We also urge additional studies that combine techniques (e.g., biologging with SIA, SIA with FA analysis). Research efforts will yield their greatest insights when tools are used in combination. It is our hope that another 15 years will see the increase in numbers of sea turtles and that novel and traditional tools will result in even larger data streams, with a need to provide another update on the biology and ecology of feeding.

ACKNOWLEDGMENTS

We thank the editors of this book for inviting us to contribute this chapter. It is an honor to build off of the foundation created in Volume 1 by Karen Bjorndal. We gratefully acknowledge Garrett Lemons, Brad MacDonald, Elizabeth Whitman for assistance with the drafting of this chapter. An anonymous reviewer provided valuable comments that improved earlier versions of this chapter. JAS thanks Karen Bjorndal and Alan Bolten of the Archie Carr Center for Sea Turtle Research, where he initially got involved with stable isotope analysis. TTJ is indebted to Michael Salmon, Peter Lutz, and David Jones for nurturing his interest and giving him the tools to study "how" sea turtles fuel their behaviors.

REFERENCES

AQ6

Abelson, P. H. and T. C. Hoering. 1961. Carbon isotope fractionation in formation of amino acids by photosynthetic organisms. *Proc. Natl Acad. Sci. U.S.A*. 47:623–632.

Ackman, R. G. 1989. Fatty acids. In *Marine Biogenic Lipids, Fats, and Oils*, ed. R. G. Ackman, pp. 103–137. Boca Raton, FL: CRC Press.

Ackman, R. G., T. Takeuchi, and G. H. Balazs. 1992. Fatty-acids in depot fats of green turtles *Chelonia mydas* from the Hawaiian-islands and Johnston Atoll. *Comp. Biochem. Physiol. B* 102(4):813–819.

Amorocho, D. F. and R. D. Reina. 2007. Feeding ecology of the East Pacific green sea turtle *Chelonia mydas agassizii* at Gorgona National Park, Colombia. *Endanger. Species Res*. 3:43–51.

Amorocho, D. F. and R. D. Reina. 2008. Intake passage time, digesta composition and digestibility in East Pacific green turtles (*Chelonia mydas agassizii*) at Gorgona National Park, Colombian Pacific. *J. Exp. Mar. Biol. Ecol*. 360:117–124.

Arai, M. N., D. W. Welch, A. L. Dunsmuir, M. C. Jacobs, and A. R. Ladouceur. 2003. Digestion of pelagic Ctenophora and Cnidaria by fish. *Can. J. Fish. Aquat. Sci*. 60:825–829.

Araújo, M. S., D. I. Bolnick, G. Machado, A. A. Giaretta, and S. F. dos Reis. 2007. Using d^{13}C stable isotopes to quantify individual-level diet variation. *Oecologia* 152:643–654.

Arthur, K. E. and G. H. Balazs. 2008. A comparison of immature green turtle (*Chelonia mydas*) diets among seven sites in the main Hawaiian Islands. *Pac. Sci*. 62(2):205–217.

Arthur, K. E., M. C. Boyle, and C. J. Limpus. 2008. Ontogenetic changes in green sea turtle (*Chelonia mydas*) foraging behaviour as demonstrated by δ^{13}C and δ^{15}N stable isotope analysis. *Mar. Ecol. Prog. Ser*. 362:303–311.

Arthur, K. E., C. J. Limpus, C. M. Roelfsema, J. W. Udy, and G. R. Shaw. 2006. A bloom of *Lyngbya majuscula* in Shoalwater Bay, Queensland, Australia: An important feeding ground for the green turtle (*Chelonia mydas*). *Harmful Algae* 5(3):251–265.

Arthur, K. E., K. M. McMahon, C. J. Limpus, and W. C. Dennison. 2009. Feeding ecology of green turtles (*Chelonia mydas*) from Shoalwater Bay, Australia. *Mar. Turtle Newslett*. 123:6–11.

Arthur, K. E., J. M. O'Neil, and C. J. Limpus. 2007. Using animal-borne imaging to assess green turtle (*Chelonia mydas*) foraging ecology in Moreton Bay, Australia. *Mar. Technol. Soc. J*. 41(4):9–13.

Avery, H. W., J. R. Spotila, J. D. Congdon, R. U. Fischer Jr., E. A. Standora, and S. B. Avery. 1993. Roles of diet protein and temperature in the growth and nutritional energetics of juvenile slider turtles, *Trachemys scripta. Physiol. Zool*. 66:902–925.

Bacon, P. R. 1970. Studies on the leatherback turtle, *Dermochelys coriacea* (L.), in Trinidad, West Indies. *Biol. Conserv*. 2:213–217.

Barrow, L. M., K. A. Bjorndal, and K. Reich. 2008. Effects of preservation method on stable carbon and nitrogen isotope values. *Physiol. Biochem. Zool*. 81:688–693.

Bearhop, S., C. E. Adams, S. Waldron, R. A. Fuller, and H. Macleod. 2004. Determining trophic niche width: A novel approach using stable isotope analysis. *J. Anim. Ecol*. 73:1007–1012.

Bello, G., A. Travaglini, and F. Bentivegna. 2011. *Histioteuthis bonnellii* (Cephalopoda: Histioteuthidae): A new prey item of the leatherback turtle *Dermochelys coriacea* (Reptilia: Dermochelidae). *Mar. Biol. Res*. 7(3):314–316.

Benson, S. R., T. Eguchi, D. G. Foley et al. 2011. Large-scale movements and high-use areas of western Pacific leatherback turtles, *Dermochelys coriacea. Ecosphere* 2(7):art84.

Bergeron, C. M., J. F. Husak, J. M. Unrine, C. S. Romanek, and W. A. Hopkins. 2007. Influence of feeding ecology on blood mercury concentrations in four species of turtles. *Environ. Toxicol. Chem*. 26(8):1733–1741.

Berube, M. D., S. G. Dunbar, K. Rutzler, and W. K. Hayes. In press. Home range and foraging ecology of juvenile
AQ7 hawksbill sea turtles (*Eretmochelys imbricata*) on inshore reefs of Honduras. *Chelonian Conserv. Biol*.

Biasatti, D. M. 2004. Stable carbon isotopic profiles of sea turtle humeri: Implications for ecology and
AQ8 physiology. *Paleoggeogr. Paleoclimatol. Paleoecol*. 206:203–216.

Birse, R. F. and J. Davenport. 1987. A study of gut function in young Loggerhead sea turtles, *Caretta caretta* L. at various temperatures. *Herpetol. J*. 1:170–175.

Bjorndal, K. A. 1980. Nutrition and grazing behavior of the green turtle, *Chelonia mydas. Mar. Biol*. 56:147–154.

Bjorndal, K. A. 1990. Digestibility of the sponge *Chondrilla nucula* in the green turtle, *Chelonia mydas. Bull. Mar. Sci*. 47(2):567–570.

Bjorndal, K. A. 1997. Foraging ecology and nutrition of sea turtles. In *The Biology of Sea Turtles*, eds. P. Lutz and J. Musick, pp. 199–232. Boca Raton, FL: CRC Press.

Bjorndal, K. A. and A. B. Bolten. 1988. Growth rates of immature green turtles, *Chelonia mydas*, on feeding grounds in the southern Bahamas. *Copeia* 1988:555–564.

Bjorndal, K. A. and A. B. Bolten. 2010. Hawksbill sea turtles in seagrass pastures: Success in a peripheral habitat. *Mar. Biol*. 157:135–145.

Bjorndal, K. A., A. B. Bolten, and H. R. Matins. 2000. Somatic growth model of juvenile loggerhead sea turtles *Caretta caretta*: Duration of pelagic stage. *Mar. Ecol. Prog. Ser*. 202:265–272.

Bleakney, J. S. 1965. Reports of marine turtles from New England and Eastern Canada. *Can. Field Nat*. 79(2):120–128.

Blumenthal, J. M., T. J. Austin, C. D. L. Bell et al. 2009. Ecology of Hawksbill turtles, *Eretmochelys imbricata*, on a western Caribbean foraging ground. *Chelonian Conserv. Biol*. 8(1):1–10.

Boecklen, W. J., C. T. Yarnes, B. A. Cook, and A. C. James. 2011. On the use of stable isotopes in trophic ecology. *Annu. Rev. Ecol. Evol. Syst*. 42:411–440.

Bolten, A. B. 2003. Variation in sea turtle life history patterns: Neritic vs. oceanic developmental stages. In *The Biology of Sea Turtles*, eds. P. Lutz, J. Musick, and J. Wyneken, Vol. II, pp. 243–258. Boca Raton, FL: CRC Press.

Boyle, M. C. and C. J. Limpus. 2008. The stomach contents of post-hatchling green and loggerhead sea turtles in the southwest Pacific: An insight into habitat association. *Mar. Biol*. 155(2):233–241.

Brand, S. J., J. M. Lanyon, and C. J. Limpus. 1999. Digesta composition and retention times in wild immature green turtles, *Chelonia mydas*: A preliminary investigation. *Mar. Freshwater Res*. 50:145–147.

Brand-Gardner, S. J., J. M. Lanyon, and C. J. Limpus. 1999. Diet selection by immature green turtles, *Chelonia mydas*, in subtropical Moreton Bay, south-east Queensland. *Aust. J. Zool*. 47(2):181–191.

Brongersma, L. D. 1969. Miscellaneous notes on turtles. IIA, IIB. *Proc. K. Ned. Akad. Wet. C* 72:76–102.

Brongersma, L. D. 1972. European Atlantic turtles. *Leiden Zool. Verhandel*. 121:1–318.

Burke, V. J., S. J. Morreale, and E. A. Standora. 1994. Diet of the Kemp's ridley sea turtle, *Lepidochelys kempii*, in New York waters. *Fish. Bull*. 92:26–32.

Burke, V. J., E. A. Standora, and S. J. Morreale. 1993. Diet of juvenile Kemp's ridley and loggerhead sea turtles from Long Island, New York. *Copeia* 1993:1176–1180.

Cardona, L., I. Alvarez de Quevedo, A. Borrell, and A. Aguilar. 2012. Massive consumption of gelatinous zooplankton by Mediterranean apex predators. *PLoS One* 7(3):e31329.

Cardona, L., P. Campos, Y. Levy, A. Demetropoulos, and D. Margaritoulis. 2010. Asynchrony between dietary and nutritional shifts during the ontogeny of green turtles (*Chelonia mydas*) in the Mediterranean. *J. Exp. Mar. Bio. Ecol*. 393(1–2):83–89.

Cardona, L., L. Pazos, and L. Aguilar. 2009. Delayed ontogenic dietary shift and high levels of omnivory in green turtles (*Chelonia mydas*) from the NW coast of Africa. *Mar. Biol*. 156:1487–1495.

Carr, A. 1987. New perspectives on the pelagic stage of sea turtle development. *Conserv. Biol*. 1:103–121.

Carr, A. and S. Stancyk. 1975. Observations on the ecology and survival outlook of the hawksbill turtle. *Biol. Conserv*. 8:161–172.

Carranza, A., A. Estrades, F. Scarabino, and A. Segura. 2011. Loggerhead turtles *Caretta caretta* (Linnaeus) preying on the invading gastropod *Rapana venosa* (Valenciennes) in the Rio de la plata estuary. *Mar. Ecol*. 32(2):142–147.

Carrion-Cortez, J. A., P. Zarate, and J. A. Seminoff. 2010. Feeding ecology of the green sea turtle (*Chelonia mydas*) in the Galapagos Islands. *J. Mar. Biol. Assoc. U.K*. 90(5):1005–1013.

Casale, P., G. Abbate, D. Freggi, N. Conte, M. Oliverio, and R. Arganto. 2008. Foraging ecology of loggerhead sea turtles: *Caretta caretta* in the central Mediterranean Sea: Evidence for a relaxed life history model. *Mar. Ecol. Prog. Ser*. 372:265–276.

Casey, J., J. Garner, S. Garner, and A. S. Williard. 2010. Diel foraging behavior of gravid leatherback sea turtles in deep waters of the Caribbean Sea. *J. Exp. Biol*. 213:3961–3971.

Caut, S., E. Angulo, and F. Courchamp. 2009. Variation in discrimination factors ($\delta^{15}N$ and $\delta^{13}C$): The effect of diet isotopic values and applications for diet reconstruction. *J. Appl. Ecol*. 46:443–453.

Caut, S., E. Guirlet, E. Angula, K. Das, and M. Girondot. 2008. Isotope analysis reveals foraging area dichotomy for Atlantic leatherback turtles. *PLoS One* 3:1845–1853.

Cerling, T. E. and J. M. Harris. 1999. Carbon isotope fractionation between diet and bioapatite in ungulate mammals and implications for ecological and paleontological studies. *Oecologia* 120:347–363.

Collard, S. B. and L. H. Ogren. 1990. Dispersal scenarios for pelagic post-hatchling sea turtles. *Bull. Mar. Sci*. 47:233–243.

Conway, S. P. 1994. Diets and feeding biology of adult olive ridley (*Lepidochelys olivacea*) and loggerhead (*Caretta caretta*) sea turtles in Fog Bay (Northern Territory). Unpublished Dip. Sci. Diss., Northern Territory University, Darwin, Australia.

Cook, H. W. 1985. Fatty acid desaturation and chain elongation in Eukaryotes. In *Biochemistry of Lipids and Membranes*, eds. D. E. Vance and J. E. Vance, pp. 181–212. Menlo Park, CA: Benjamin/Cummings.

Craven, K. S., J. Parsons, S. A. Taylor, C. N. Belcher, and D. W. Owens. 2008. The influence of diet on fatty acids in the egg yolk of green sea turtles, *Chelonia mydas. J. Comp. Physiol. B* 178(4):495–500.

Creech, L. and P. E. Allman. 1998. Stomach and gastrointestinal contents of stranded kemp's ridley (*Lepidochelys kempii*) sea turtles in Georgia. In *Proceedings of the Seventeenth Annual Sea Turtle Symposium*, Orlando, FL, compilers S. P. Epperly and J. Braun, NOAA Tech Memo NMFS-SEFSC-415, March 4–8, 1997, p. 167.

Davenport, J. 1998. Sustaining endothermy on a diet of cold jelly: Energetics of the leatherback turtle *Dermochelys coriacea. Br. Herpetol. Soc. Bull*. 62:4–8.

Davenport, J. and G. H. Balazs. 1991. "Fiery pyrosomas"—Are pyrosomas an important item in the diet of leatherback turtles? *Br. Herpetol. Soc. Bull*. 37:33–38.

Davenport, J., G. Inagle, and A. K. Hughes. 1982. Oxygen uptake and heart rate in young green turtles (*Chelonia mydas*). *J. Zool*. 198(3):399–412.

Davenport, J. and P. J. Oxford. 1984. Feeding, gut dynamics, digestion and oxygen consumption in hatchling green turtles (*Chelonia mydas*). *Br. J. Herpetol*. 6:351–358.

Davenport, J. and C. R. Scott. 1993. Individuality of growth, appetite, metabolic rate and assimilation of nutrients in young green turtles (*Chelonia mydas* L.). *Herpetol. J*. 3:26–31.

Den Hartog, J. C. 1980. Notes on the food of sea turtles: *Eretmochelys imbricata* (Linnaeus) and *Dermochelys coriacea* (Linnaeus). *Neth. J. Zool*. 30(4):595–610.

Den Hartog, J. C. and M. M. Van Nierop. 1984. A study on the gut contents of 6 leathery turtles *Dermochelys coriacea* (Linnaeus) (Reptilia: Testudines: Dermochelyidae) from British Waters and The Netherlands. *Zool. Verhandel*. 209:1–31.

DeNiro, M. J. and S. Epstein. 1978. Influence of diet on the distribution of carbon isotopes in animals. *Geochim. Cosmochim. Acta* 42:495–506.

DeNiro, M. J. and S. Epstein. 1981. Influence of diet on the distribution of nitrogen isotopes in animals. *Geochim. Cosmochim. Acta* 45:341–351.

Deutsch, C. A., N. P. Gruber, R. M. Key, J. L. Sarmiento, and A. Ganachaud. 2011. Denitrification and N_2 fixation in the Pacific Ocean. *Global Biogeochem. Cycles* 15:483–506.

Di Bello, A., C. Valastro, F. Staffieri, and A. Crovace. 2006. Contrast radiography of the gastrointestinal tract in sea turtles. *Vet. Radiol. Ultrasound* 47:351–354.

Dodge, K. L., J. M. Logan, and M. E. Lutcavage. 2011. Foraging ecology of leatherback sea turtles in the Western North Atlantic determined through multi-tissue stable isotope analyses. *Mar. Biol*. 158:2813–2824.

Duguy, R. 1982. Note sur les méduses des Pertuis Charentais. *Annales de la Sociéte des Sciences Naturelles de la Charente-Maritime* 6:1029–1034.

Duron, M. 1978. Contribution à l'étude de la biologie de *Dermochelys coriacea* (Linné) dans les Pertuis Charentais. Thèse Universite Bordeaux, France.

Duron-Dufrenne, M. 1987. Premier suivi par satellite en Atlantique d'une tortue luth *Dermochelys coriacea. Comptes Rendus de l'Academie des Sciences Paris* 304:339–402.

Eisenberg, J. F. and J. Frazier. 1983. A leatherback turtle (*Dermochelys coriacea*) feeding in the wild. *J. Herpetol*. 17(1):81–82.

Evershed, R. P., I. D. Bull, L. T. Corr et al. 2007. Compound-specific stable isotope analysis in ecology and paleoecology. In *Stable Isotopes in Ecology and Environmental Science*, eds. R. H. Michener and K. Lajtha, pp. 480–540. Malden, MA: Blackwell Publishing Ltd.

Fantle, M. S., A. I. Dittel, S. M. Schwalm, C. E. Epifanio, and M. L. Fogel. 1999. A food web analysis of the juvenile blue crab, *Callinectes sapidus*, using stable isotopes in whole animals and individual amino acids. *Oecologia* 120:416–426.

Faure, G. 1986. *Principles of Isotope Geology*, 2nd edn. New York: John Wiley & Sons Ltd.

Ferreira, B., M. Garcia, B. P. Jupp, and A. Al-Kiumi. 2006. Diet of the green turtle (*Chelonia mydas*) at Ra's Al Hadd, Sultanate of Oman. *Chelonian Conserv. Biol*. 5:141–146.

Fossette, S., P. Gaspar, Y. Handrich, Y. Le Maho, and J.-Y. Georges. 2008. Dive and beak movement patterns in leatherback turtles *Dermochelys coriacea* during internesting intervals in French Guiana. *J. Anim. Ecol*. 77(2):236–246.

Fossette, S., A. C. Gleiss, J. P. Casey, A. R. Lewis, and G. C. Hays. 2011. Does prey size matter? Novel observations of feeding in the leatherback turtles (*Dermochelys coriacea*) allow a test of predator-prey size relationships. *Biol. Lett*. 8(3):351–354.

Frazier, J., M. D. Meneghel, and F. A. Achaval. 1985. A clarification on the feeding habits of *Dermochelys coriacea. J. Herpetol*. 19(1):159–160.

Frick, J. 1976. Orientation and behavior of hatchling green turtles (*Chelonia mydas*) in the sea. *Anim. Behav*. 24:849–857.

Frick, M. G. and P. A. Mason. 1998. *Lepidochelys kempii* (Kemp's ridley sea turtle) diet. *Herpetol. Rev*. 29:166–168.

Frick, M. G., K. L. Williams, A. B. Bolten, K. A. Bjorndal, and H. R. Martins. 2009. Foraging ecology of oceanic-stage loggerhead turtles *Caretta caretta. Endanger. Species Res*. 9:91–97.

Galli, C. and P. Rise. 2006. Origin of fatty acids in the body: Endogenous synthesis versus dietary intakes. *Eur. J. Lipid Sci. Technol*. 108:521–525.

Gannes, L. Z., C. Martinez del Rio, and P. Koch. 1997. Stable isotopes in animal ecology: Assumptions, caveats, and a call for more laboratory experiments. *Ecology* 78:1271–1276.

Gaos, A. R., R. R. Lewison, I. L. Yañez et al. 2012. Shifting the life-history paradigm: Discovery of novel habitat use by hawksbill turtles. *Biol. Lett*. 8:54–56.

Gardner S. C. and W. J. Nichols. 2001. Assessment of sea turtle mortality rates in the Bahia Magdalena region, Baja California Sur, Mexico. *Chelonian Conserv. Biol*. 4:197–199.

Godley, B. J., D. R. Thompson, S. Waldron, and R. W. Furness. 1998. The trophic status of marine turtles as determined by stable isotope analysis. *Mar. Ecol. Prog. Ser*. 166:277–284.

Graham, S. C. 2009. Analysis of the foraging ecology of hawksbill turtles (*Eretmochelys imbricata*) on Hawaìi Island: An investigation utilizing satellite tracking and stable isotopes. MS thesis, University of Hawaìi at Hilo, Hawaìi.

Graham, B. S., P. L. Koch, S. D. Newsome, K. W. McMahon, and D. Aurioles. 2010. Using isoscapes to trace the movements and foraging behavior of top predators in oceanic ecosystems. In *Understanding Movement, Pattern, and Process on Earth through Isotope Mapping*, eds. J. B. West, G. J. Bowen, T. E. Dawson, and K. P. Tu, pp. 299–318. New York: Springer.

Grant, G. S. and D. Ferrell. 1993. Leatherback turtle, *Dermochelys coriacea* (Reptilia, Dermochelidae)—Notes on near-shore feeding behavior and association with Cobia. *Brimleyana* 19:77–81.

Gu, B., C. L. Schelske, and M. V. Hoyer. 1997. Intrapopulation feeding diversity in blue tilapia: Evidence from stable-isotope analysis. *Ecology* 78:2263–2266.

Guitart, R., A. M. Silvestre, X. Guerrero, and R. Mateo. 1999. Comparative study on the fatty acid composition of two marine vertebrates: Striped dolphins and loggerhead turtles. *Comp. Biochem. Physiol. B Biochem. Mol. Biol*. 124(4):439–443.

Hadjichristophorou, M. and D. J. Grove. 1983. A study of appetite, digestion and growth in juvenile green turtle (*Chelonia mydas L.*) fed on artificial diets. *Aquaculture* 30:191–201.

Hatase, H., K. Omuta, and K. Tsukamoto. 2010. Oceanic residents, neritic migrants: A possible mechanism underlying foraging dichotomy in adult female loggerhead turtles (*Caretta caretta*). *Mar. Biol*. 157(6):1337–1342.

Hatase, H., K. Sato, M. Yamaguchi, K. Takahashi, and K. Tsukamoto. 2006. Individual variation in feeding habitat use by adult female green sea turtles (*Chelonia mydas*): Are they obligately neritic herbivores? *Oecologia* 149:52–64.

Hatase, H., N. Takai, Y. Matsuzawa et al. 2002. Size-related differences in feeding habitat use of adult female loggerhead turtles *Caretta caretta* around Japan determined by stable isotope analyses and satellite telemetry. *Mar. Ecol. Prog. Ser*. 233:273–281.

Heaslip, S. G., S. J. Iverson, W. D. Bowen, and M. C. James. 2012. Jellyfish support high energy intake of leatherback sea turtles (*Dermochelys coriacea*): Video evidence from animal-borne cameras. *PLoS One* 7(3): e33259. doi:10.1371/journal.pone.0033259.

Heithaus, M. R., J. L. McLash, A. Frid, L. M. Dill, and G. J. Marshall. 2002. Novel insights into green sea turtle behavior using animal-borne video cameras. *J. Mar. Biol. Assoc. U.K*. 82(6):1049–1050.

Hesslein, R. H., K. A. Hallard, and P. Ramlal. 1993. Replacement of sulfur, carbon, and nitrogen in tissue of growing broad whitefish (*Coregonus nasus*) in response to a change in diet traced by d34S, d13C, and d15N. *Can. J. Fish. Aquat. Sci*. 50:2071–2076.

Hobson, K. A. 1999. Tracing origins and migration of wildlife using stable isotopes: A review. *Oecologia* 120:314–326.

Hobson, K. A. and R. G. Clark. 1992. Assessing avian diets using stable isotopes II: Factors influencing diet-tissue fractionation. *Condor* 94:189–197.

Hobson, K. A., D. M. Schell, D. Renoug, and E. Noseworthy. 1996. Stable carbon and nitrogen isotopic fractionation between diet and tissues of captive seals: Implications for dietary reconstructions involving marine mammals. *Can. J. Fish. Aquat. Sci*. 53:528–533.

Hobson, K. A. and L. I. Wassenaar. 2008. *Tracking Animal Migration with Stable Isotopes*. London, U.K.: Academic Press.

Hochscheid, S., F. Maffucci, F. Bentivegna, and R. P. Wilson. 2005. Gulps, wheezes, and sniffs: How measurement of beak movement in sea turtles can elucidate their behaviour and ecology. *J. Exp. Mar. Biol. Ecol*. 316:45–53.

Holland, D. L., J. Davenport, and J. East. 1990. The fatty acid composition of the leatherback turtle *Dermochelys coriacea* and its jellyfish prey. *J. Mar. Biol. Assoc. U.K*. 70:761–770.

Hughes, G. R. 1974. The sea turtles of south-east Africa II. The biology of the Tongaland loggerhead turtle *Caretta caretta* L. with comments on the leatherback turtle *Dermochelys coriacea* L. and the green turtle *Chelonia mydas* L. in the study region. Oceanography Research Institute, Durban, South Africa, Investigative Report No. 36, pp. 1–96.

Ikonomopoulou, M. P., H. Olszowy, C. Limpus, R. Francis, and J. Whittier. 2011. Trace element concentrations in nesting flatback turtles (*Natator depressus*) from Curtis Island, Queensland, Australia. *Mar. Environ. Res*. 71(1):10–16. AQ9

Inger, R., A. Jackson, A. Parnell, and S. Bearhop. 2010. SIAR V4: Stable isotope analysis in R. An ecologist's guide. AQ10

IUCN. 2011. The IUCN red list of threatened species. Version 2011.2. http://www.iucnredlist.org (accessed November 12, 2011).

Iverson, S. J., Frost, K. J., and Lowry, L. F. 1997. Fattyacid signatures reveal fine scale structure of foraging distribution of harbor seals and their prey in Prince William Sound, Alaska. *Mar. Ecol. Prog. Ser*. 151:255–271.

Iverson, E. S. and H. O. Yoshida. 1956. Longline fishing for tuna in the Central Equatorial Pacific, 1954. Washington, DC: USFWS, Special Scientific Report Fisheries No. 184.

James, M. C. and T. B. Herman. 2001. Feeding of *Dermochelys coriacea* on medusae in the Northwest Atlantic. *Chelonian Conserv. Biol*. 4:202–205.

James, M. C., S. A. Sherill-Mix, K. Martin, and R. A. Myers. 2006. Canadian waters provide critical foraging habitat for leatherback sea turtles. *Biol. Conserv*. 133:347–357.

Jones, T. T., B. Bostrom, M. Carey et al. 2011. Determining transmitter drag and best-practice attachment procedures for sea turtle biotelemetry studies. NOAA Technical Memorandum. NOAA-NMFS-SWFSC-480.

Jones, T. T., B. L. Bostrom, M. D. Hastings, K. S. Van Houtan, D. P. Pauly, and D. R. Jones. In press. Resource requirements of the Pacific leatherback turtle population. *PLoS One*.

Jones, T. T., M. D. Hastings, B. L. Bostrom, R. D. Andrews, and D. R. Jones. 2009. Validation of the use of doubly labeled water for estimating metabolic rate in the green turtle (*Chelonia mydas L.*): A word of caution. *J. Exp. Biol*. 212:2635–2644.

Karasov W. H. and D. J. Levey. 1990. Digestive system trade-offs and adaptations of frugivorous passerine birds. *Physiol. Zool*. 63(6):1248–1270.

Kelez, S. 2011. Bycatch and foraging ecology of sea turtles in the Eastern Pacific. PhD dissertation, Duke University, Durham, NC.

Kelly, J. F., V. Atudorei, Z. D. Sharp, and D. M. Finch. 2002. Insights into Wilson's Warbler migration from analyses of hydrogen stable-isotope ratios. *Oecologia* 130:216–221.

Killingley, J. S. and M. Lutcavage. 1983. Loggerhead turtle movements reconstructed from ^{18}O and ^{16}O profiles from commensal barnacle shells. *Estuar. Coast. Shelf Sci*. 16:345–349.

Kirsch, P. E., S. J. Iverson, and W. D. Bowen. 2000. Effect of a low-fat diet on body composition and blubber fatty acids of captive juvenile harp seals (*Phoca groenlandica*). *Physiol. Biochem. Zool*. 73:45–59.

Kowalski, A. 2006. Specific dynamic action in hatchling and posthatchling green (*Chelonia mydas*) and loggerhead (*Caretta caretta*) sea turtles. MS thesis, Florida Atlantic University, Boca Raton, FL.

Lajtha, K. and J. D. Marshall. 1994. Sources of variation in the stable isotopic composition of plants. In *Stable Isotopes in Ecology and Environmental Science*, eds. K. Lajtha and R. H. Michener, pp. 1–21. Oxford, U.K.: Blackwell Scientific Publications.

Lazar, B., R. Gracan, D. Zavodnik, and N. Tvrtkovic. 2008. Feeding ecology of "pelagic" loggerhead turtles, *Caretta caretta*, in the northern Adriatic Sea: Proof of an early ontogenetic habitat shift. In *Proceedings of the Twenty-Fifth Annual Symposium on Sea Turtle Biology and Conservation*, compilers H. Kalb, A. S. Rohde, K. Gayheart, and K. Shanker. NOAA Technical Memorandum NMFS-SEFSC-582.

Lemons, G., T. Eguchi, B. D. Lyon, R. LeRoux, and J. A. Seminoff. 2012. Effects of blood preservatives on stable isotope values ($\delta^{13}C$ and $\delta^{15}N$) of sea turtle blood tissue: Implications for studies at remote field sites. *Aquat. Biol*. 14:201–206.

Lemons, G., R. Lewison, L. Komoroske et al. 2011. Trophic ecology of green sea turtles in a highly urbanized bay: Insights from stable isotopes and mixing models, *J. Exp. Mar. Biol. Ecol*. 405:25–32.

Leon, Y. M. and K. A. Bjorndal. 2002. Selective feeding in the hawksbill turtle, an important predator in coral reef ecosystems. *Mar. Ecol. Prog. Ser*. 245:249–258.

Limpus, C. J. 1984. A benthic feeding record from neritic waters for the leathery turtle (*Dermochelys coriacea*). *Copeia* 1984:522–523.

Limpus, C. J. 1992. The hawksbill turtle, *Eretmochelys imbricata*, in Queensland: Population structure within a southern Great Barrier Reef feeding ground. *Wildlife Res*. 19:489–505.

Limpus, C. J. 1998. Overview of marine turtle conservation and management in Australia. In *Marine Turtle Conservation and Management in Northern Australia*, eds. R. Kennett, A. Webb, G. Duff, M. Guinea, and G. Hill, pp. 1–8. Darwin, Australia: Northern Territory University.

Limpus, C. J. 2007. *A biological Review of Australian Marine Turtle Species. 5. Flatback Turtle*, Natator depressus Garman. Brisbane, Queensland, Australia: Queensland Environmental Protection Agency.

Limpus, C. J. 2008a. *A Biological Review of Australian Marine Turtle Species. 1. Loggerhead Turtle, Caretta caretta* Linnaeus. Brisbane, Queensland, Australia: Queensland Environmental Protection Agency.

Limpus, C. J. 2008b. *A Biological Review of Australian Marine Turtle Species. 4. Olive Ridley Turtle* Lepidochelys olivacea (Eschscholtz). Brisbane, Queensland, Australia: Queensland Environmental Protection Agency.

Limpus, C. J. 2009. *A Biological Review of Australian Marine Turtle Species. 3. Hawksbill Turtle,* Eretmochelys imbricata Linnaeus. Brisbane, Queensland, Australia: Queensland Environmental Protection Agency.

Limpus, C. J. and D. J. Limpus. 2000. Mangroves in the diet of *Chelonia mydas* in Queensland, Australia. *Mar. Turtle Newslett*. 89:13–15.

Limpus, C. J., D. J. Limpus, K. E. Arthur, and C. J. Parmenter. 2005. Monitoring green turtle population dynamics in Shoalwater Bay: 2000–2004. Australian Government, Great Barrier Reef Marine Park Authority, Research Publication No. 83.

Limpus, C. J. and McLachlan. 1994. The conservation status of the leatherback turtle, *Dermochelys coriacea*, in Australia. In *Proceedings of the Australian Marine Turtle Conservation Workshop*, Queensland, Australia, 1994, p. 68. AQ13

Lopez-Mendilaharsu, M., Gardner, S. C., Seminoff, J. A., and Riosmena-Rodriguez, R. 2005. Identifying critical foraging habitats of the green turtle (*Chelonia mydas*) along the Pacific coast of the Baja California peninsula, Mexico. *Aquat. Conserv*. 15(3):259–269.

Lutcavage, M. E. and P. L. Lutz. 1986. Metabolic rate and food energy requirements of the leatherback sea turtle *Dermochelys coriacea. Copeia* 1986:796–798.

Lutz, P. L. and J. Musick. 1997. *The Biology of the Sea Turtles*, Vol. 1. Boca Raton, FL: CRC Press.

Macko, S. A., M. L. Fogel-Estep, M. H. Engel, and P. E. Hare. 1986. Kinetic fractionation of nitrogen isotopes during amino acid transamination. *Geochim. Cosmochim. Acta* 50:2143–2146.

Macrae, J. C. and P. J. Reeds. 1980. Prediction of protein deposition in ruminants. In *Protein Deposition in Animals*, eds. P. J. Buttery and D. B. Lindsay, pp. 225–249. London, U.K.: Butterworths.

Malej, A., J. Faganeli, and J. Pezdič. 1993. Stable isotope and biochemical fractionation in the marine pelagic food chain: The jellyfish *Pelagia noctiluca* and net zooplankton. *Mar. Biol*. 116:565–570.

Marra, P. P., K. A. Hobson, and R. T. Holms. 1998. Linking winter and summer events in a migratory bird by using stable-carbon isotopes. *Science* 282:1884–1886.

Martínez del Rio, C. and B. Wolf. 2005. Mass balance models for animal isotopic ecology. In *Physiological and Ecological Adaptations to Feeding in Vertebrates*, eds. M. A. Starck and T. Wang, pp. 141–174. Enfield, U.K.: Science Publishers.

Martínez del Rio, C., N. Wolf, S. A. Carleton, and L. Z. Gannes. 2009. Isotopic ecology ten years after a call for more laboratory experiments. *Biol. Rev*. 84:91–111.

McCauley, S. J. and K. A. Bjorndal. 1999. Conservation implications of dietary dilution from debris ingestion: Sublethal effects in post-hatchling loggerhead sea turtles. *Conserv. Biol*. 13:925–929.

McClellan, C. M., J. Braun-McNeill, L. Avens, B. P. Wallace, and A. J. Read. 2010. Stable isotopes confirm a foraging dichotomy in juvenile loggerhead sea turtle. *J. Exp. Mar. Biol. Ecol*. 387:44–51.

McClelland, J. W. and J. P. Montoya. 2002. Trophic relationships and the nitrogen isotopic composition of amino acids in plankton. *Ecology* 83:2173–2180.

McCue, M. D. 2006. Specific dynamic action: A century of investigation. *Comp. Biochem. Physiol. A* 144:381–394.

McCue, M. D. and E. D. Pollock. 2008. Stable isotopes may provide evidence for starvation in reptiles. *Rapid Commun. Mass Spectrom*. 22:2307–2314.

McCutchan Jr., J. M., W. M. Lewis Jr., C. Kendall, and C. C. McGrath. 2003. Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. *Oikos* 102:378–390.

McDermott, A. J., J. A. Seminoff, T. T. Jones, and A. Resendiz. 2006. Food intake and retention time in green turtles (*Chelonia mydas*) from the Gulf of California: Preliminary development of a digestive model. In *Proceedings of the Twenty-Third Annual Symposium on Sea Turtle Biology and Conservation*, compilers N. J. Pilcher. Kuala Lumpur, Malaysia. NOAA Technical Memorandum NMFS-SEFSC-536, March 17–21, 2003.

Merker, G. P. and K. A. Nagy. 1984. Energy utilization by free-ranging *Sceloporus virgatus* lizards. *Ecology* 65(2):575–581.

van de Merwe, J. P., M. Hodge, J. M. Whittier, K. Ibrahim, and S. Y. Lee. 2010. Persistent organic pollutants in the green sea turtle *Chelonia mydas*: Nesting population variation, maternal transfer, and effects on development. *Mar. Ecol. Prog. Ser*. 403:269–278.

Meylan, A. 1988. Spongivory in hawksbill turtles: A diet of glass. *Science* 239:393–395.

Michener, R. and K. Lajtha. 2007. *Stable Isotopes in Ecology and Environmental Science*, 2nd edn. Malten, MA: Blackwell Publishing, 566 pp.

Miller, N. G., L. I. Wassenaar, K. A. Hobson, and D. R. Norris. 2011. Monarch butterflies cross the Appalachians from the west to recolonize the east coast of North America. *Biol. Lett*. 7:43–46.

Mills, C. E. 2001. Jellyfish blooms: Are populations increasing globally in response to changing ocean conditions? *Hydrobiologia* 451:55–68.

Miniwaga, M. and W. Wada. 1984. Stepwise enrichment of $d^{15}N$ along food chains: Further evidence of the relation between $d^{15}N$ and animal age. *Geochim. Cosmochim. Acta* 48:1135–1140.

Montoya, J. P. 2007. Natural abundance of ^{15}N in marine planktonic ecosystems. In *Stable Isotopes in Ecology and Environmental Science*, eds. R. Michener and K. Lajtha, pp. 176–201. Malden, MA: Blackwell Publishing Ltd.

Morreale, S. J., P. T. Plotkin, D. J. Shaver, and K. J. Kalb. 2007. Adult migration and habitat utilization: Ridley turtles in their element. In *Biology and Conservation of Ridley Sea Turtles*, ed. P. T. Plotjin, pp. 213–229. Baltimore, MD: John Hopkins University Press.

Murray, I. W. and B. O. Wolf. 2012. Tissue carbon incorporation rates and diet-to-tissue discrimination in ectotherms: Tortoises are really slow. *Physiol. Biochem. Zool*. 85:96–105.

Newsome, S. D., M. R. Clementz, and P. L. Koch. 2010. Using stable isotope biogeochemistry to study marine mammal ecology. *Mar. Mamm. Sci*. 26:509–572.

Newsome, S. D., C. M. del Rio, S. Bearhop, and D. L. Phillips. 2007. A niche for isotopic ecology. *Front. Ecol. Environ*. 5(8):429–436.

Obura, D. O., A. Harvey, T. Young, M. M. Eltayeb, and R. von Brandis. 2010. Hawksbill turtles as significant predators on hard coral. *Coral Reefs* 29:759.

Pajuelo, M., K. A. Bjorndal, J. Alfaro-Shigueto, J. A. Seminoff, J. Mangel, and A. B. Bolten. 2010. Stable isotope dichotomy in loggerhead turtles reveals Pacific-Atlantic oceanographic differences. *Mar. Ecol. Prog. Ser*. 417:277–285.

Pajuelo, M., K. A. Bjorndal, K. J. Reich, M. D. Arendt, and A. B. Bolten. In review. Foraging habitat use and movement patterns of male loggerhead turtles (*Caretta caretta*) as revealed by stable isotopes and satellite telemetry. *Mar. Biol*.

Parker, D. M., G. H. Balazs, C. S. King, L. Katahira, and W. Gilmartin. 2009. Short-range movements of hawksbill turtles (*Eretmochelys imbricata*) from nesting to foraging areas within the Hawaiian Islands. *Pac. Sci*. 63(3):371–382.

Parker, D. M., W. J. Cooke, and G. H. Balazs. 2005. Diet of oceanic loggerhead sea turtles (*Caretta caretta*) in the central North Pacific. *Fish. Bull*. 103:142–152.

Parker, D., P. H. Dutton, and G. H. Balazs. 2011. Oceanic diet and distribution of haplotypes for the green turtle, *Chelonia mydas*, in the central North Pacific. *Pac. Sci*. 65(4):419–431.

Peckham, S. H., D. Maldonado-Diaz, Y. Tremnlay et al. 2011. Demographic implications of alternative foraging strategies in juvenile loggerhead turtles *Caretta caretta* of the North Pacific Ocean. *Mar. Ecol. Prog. Ser*. 425:269–280.

Pendoley, K. and J. Fitzpatrick. 1999. Browsing on mangroves by green turtles in Western Australia. *Mar. Turtle Newslett*. 84:10.

Peterson, B. J. and B. Fry. 1987. Stable isotopes in ecosystem studies. *Annu. Rev. Ecol. Syst*. 18:293–320.

Phillips, D. L. 2001. Mixing models in analyses of diet using multiple stable isotopes: A critique. *Oecologia* 127:166–170.

Phillips, R. A., S. Bearhop, R. A. R. McGill, and D. A. Dawson. 2009. Stable isotopes reveal individual variation in migration strategies and habitat preferences in a suite of seabirds during the breeding period. *Oecologia* 160:795–806.

Phillips, D. L. and J. W. Gregg. 2003. Source partitioning using stable isotopes: Coping with too many sources. *Oecologia* 136:261–269.

Phillips, D. L. and P. L. Koch. 2002. Incorporating concentration dependence in stable isotope mixing models. *Oecologia* 130:114–125.

Phillips, D. L., S. D. Newsome, and J. W. Gregg. 2005. Combining sources in stable isotope mixing models: Alternative methods. *Oecologia* 144:520–524.

Pinnegar, J. K. and N. V. C. Polunin. 1999. Differential fractionation of $\delta^{13}C$ and $\delta^{15}N$ among fish tissues: Implications for the study of trophic interactions. *Funct. Ecol*. 13:225–231.

Poage, M. A. and C. P. Chamberlain. 2001. Empirical relationships between elevation and the stable isotope composition of precipitation and surface waters: Considerations for studies of paleoelevation change. *Am. J. Sci*. 301:1–15.

Polovina, J. J., G. H. Balazs, E. A. Howell, D. M. Parker, M. P. Seki, and P. H. Dutton. 2004. Forage and migration habitat of loggerhead (*Caretta caretta*) and olive ridley (*Lepidochelys olivacea*) sea turtles in the central North Pacific Ocean. *Fish. Oceanogr*. 13(1):1–16.

Popp, B. N., B. S. Graham, R. J. Olson et al. 2007. Insight into the trophic ecology of yellowfin tuna, *Thunnus albacares*, from compound-specific nitrogen isotope analysis of proteinaceous amino acids. In *Stable Isotopes as Indicators of Ecological Change*, eds. T. Dawson and R. Siegwolf, pp. 173–190. Amsterdam, the Netherlands: Elsevier Academic Press.

Post, D. M. 2002. Using stable isotopes to estimate trophic position: Models, methods, and assumptions. *Ecology* 83:703–718.
Pritchard, P. C. H. 1976. Post-nesting movements of marine turtles (Cheloniidae and Dermochelyidae) tagged in the Guianas. *Copeia* 1976:749–754.
Purcell, J. E. 2005. Climate effects on jellyfish and ctenophore blooms: A review. *J. Mar. Biol. Assoc. U.K.* 85:461–476.
Ramos, R., J. Gonzalez-Solis, J. P. Croxall, D. Oro, and X. Ruiz. 2009. Understanding oceanic migrations with intrinsic biogeochemical markers. *PLoS One* 4(7):e6236.
Reich, K. J., K. A. Bjorndal, and A. B. Bolten. 2007. The 'lost years' of green turtles: Using stable isotopes to study cryptic life stages. *Biol. Lett*. 3:712–714.
Reich, K. J., K. A. Bjorndal, M. G. Frick, B. E. Witherington, C. Johnson, and A. B. Bolten. 2009. Polymodal foraging in adult female loggerheads (*Caretta caretta*). *Mar. Biol*. 157:113–121.
Reich, K. J., K. A. Bjorndal, and C. Martínez del Rio. 2008. Effects of growth and tissue type on the kinetics of ^{13}C and ^{15}N incorporation in a rapidly growing ectotherm. *Oecologia* 155:651–663.
Revelles, M., L. Cardona, A. Aguilar, A. Borrell, G. Fernández, and M. San Félix. 2007a. Concentration of stable C and N isotopes in several tissues of the loggerhead sea turtle *Caretta caretta* from the western Mediterranean and dietary implications. *Sci. Mar*. 71:87–93.
Revelles, M., L. Cardona, A. Aguilar, and G. Fernández. 2007b. The diet of pelagic loggerhead sea turtles *Caretta caretta* off the Balearic archipelago (western Mediterranean): Relevance of long-line baits. *J. Mar. Biol. Assoc. U.K*. 87:805–813.
Rincon-Diaz, M. P., C. E. Diez, R. P. Van Dam, and A. M. Sabat. 2011. Foraging selectivity of the hawksbill sea turtle (*Eretmochelys imbricata*) in the Culebra Archipelago, Puerto Rico. *J. Herpetol*. 45(3):277–282.
Roth, J. D. and K. A. Hobson. 2000. Stable carbon and nitrogen isotopic fractionation between diet and tissue of captive red fox: Implications for dietary reconstruction. *Can. J. Zool*. 78:848–852.
Rubenstein, D. R. and K. A. Hobson. 2004. From birds to butterflies: Animal movement patterns and stable isotopes. *Trends Ecol. Evol*. 19:256–263.
Russell, D. J. and G. H. Balazs. 1994. Colonization by the alien marine alga *Hypnea musciformis* (Wulfen) J. Ag. (Rhodophyta: Gigartinales) in the Hawaiian Islands and its utilization by the green turtle, *Chelonia mydas* L. *Aquat. Bot*. 47:53–60.
Salmon, M., T. T. Jones, and K. Horch. 2004. Ontogeny of diving and feeding behavior in juvenile sea turtles: A comparison study of green turtles (*Chelonia mydas* L.) and leatherbacks (*Dermochelys coriacea* L.) in the Florida current. *J. Herpetol*. 38:36–43.
Seaborn, G. T., M. K. Moore, and G. H. Balazs. 2005. Depot fatty acid composition in immature green turtles (*Chelonia mydas*) residing at two near-shore foraging areas in the Hawaiian Islands. *Comp. Biochem. Physiol. B* 140(2):183–195.
Sealy, J. C., N. J. Van Der Merwe, J. A. L. Thorp, and J. A. Lanham. 1987. Nitrogen isotopic ecology in southern Africa: Implications for environmental and dietary tracing. *Geochim. Cosmochim. Acta* 51:2707–2717.
Secor, S. M. 2009. Specific dynamic action: A review of the postprandial metabolic response. *J. Comp. Physiol. B* 179:1–56.
Secor, S. M. and J. Diamond. 2000. Evolution of regulatory response to feeding in snakes. *Physiol. Biochem. Zool*. 73:123–141.
Seminoff, J. A., G. H. Balazs, T. Work, B. MacDonald, and S. Hargrove. In review. $\delta^{13}C$ and $\delta^{15}N$ in green sea turtle (*Chelonia mydas*) tissues and their diet: Impacts of growth rate on isotopic discrimination. *Pac. Sci*.
Seminoff, J. A., S. R. Benson, K. E. Arthur, P. H. Dutton, T. Eguchi, R. Tapilatu, and B. N. Popp. In press. Stable isotope tracking of endangered sea turtles: Validation with satellite telemetry and $\delta^{15}N$ analysis of amino acids. *PLoS One*.
Seminoff, J. A., K. A. Bjorndal, and A. B. Bolten. 2007. Stable carbon and nitrogen isotope discrimination and turnover in pondsliders *Trachemys scripta*: Insights for trophic study of freshwater turtles. *Copeia* 534–542. AQ14
Seminoff, J. A., T. T. Jones, T. Eguchi, D. R. Jones, and P. H. Dutton. 2006a. Stable isotope discrimination ($\delta^{13}C$ and $\delta^{15}N$) between soft tissues of the green sea turtle *Chelonia mydas* and its diet. *Mar. Ecol. Prog. Ser*. 308:271–278.
Seminoff, J. A., T. T. Jones, T. Eguchi, M. Hastings, and D. R. Jones. 2009. Stable carbon and nitrogen isotope discriminations in soft tissues of the leatherback turtle (*Dermochelys coriacea*): Insights for trophic studies of marine turtles. *J. Exp. Mar. Biol. Ecol*. 381(1):33–41.
Seminoff, J. A., T. T. Jones, and G. J. Marshall. 2006b. Underwater behavior of green turtles monitored with video-time-depth recorders: What's missing from dive profiles? *Mar. Ecol. Prog. Ser*. 322:269–280.

Seminoff, J. A., A. Resendiz, and W. J. Nichols. 2002a. Diet of east Pacific green turtles (*Chelonia mydas*) in the central Gulf of California, México. *J. Herpetol*. 36(3):447–453.

Seminoff, J. A., A. Resendiz, W. J. Nichols, and L. Brooks. 2003. Occurrence of hawksbill turtles, *Eremochelys imbricata*, near Baja California. *Pac. Sci*. 57:9–16.

Seminoff, J. A., A. Resendiz, W. J. Nichols, and T. T. Jones. 2002b. Growth rates of wild green turtles (*Chelonia mydas*) at a temperate foraging area in the Gulf of California, Mexico. *Copeia* 2002(3):610–617.

Seminoff, J. A., A. Resendiz, B. Resendiz, and W. J. Nichols. 2004. Occurrence of loggerhead sea turtles (*Caretta caretta*) in the Gulf of California, Mexico: Evidence of life-history variation in the Pacific Ocean. *Herpetol. Rev*. 35(1):24–27.

Semmens, B. X. and J. W. Moore. 2008. MixSIR: A bayesian stable isotope mixing model, Version 1.04. AQ15 http://www.ecologybox.org

Seney, E. E. and A. M. Landry Jr. 2011. Movement patterns of immature and adult female Kemp's ridley sea turtles in the northwestern Gulf of Mexico. *Mar. Ecol. Prog. Ser*. 440:241–254.

Seney, E. E. and J. A. Musick. 2005. Diet analysis of Kemp's ridley sea turtles (*Lepidochelys kempii*) in Virginia. *Chelonian Conserv. Biol*. 4:864–871.

Seney, E. E. and J. A. Musick. 2007. Historical diet analysis of loggerhead sea turtles (*Caretta Caretta*) in Virginia. *Copeia* 2007(2):478–489.

Shaver, D. J. 1991. Feeding ecology of wild and head-started Kemp's ridley sea turtles in South Texas waters. *J. Herpetol*. 25:327–334.

Snover, M. L., A. A. Hohn, L. B. Crowder, and S. S. Heppell. 2007. Age and growth in Kemp's ridley sea turtles: Evidence from mark-recapture skeletochronology. In *Biology and Conservation of Ridley Sea Turtles*, ed. P. T. Plotjin, pp. 89–105. Baltimore, MD: John Hopkins University Press.

Somes, C. J., A. Schmittner, E. D. Galbraith et al. 2010. Simulating the global distribution of nitrogen isotopes in the ocean. *Global Biogeochem. Cycles* 24:GB4019.

Southwood, A. L., R. D. Andrews, F. V. Paladino, and D. R. Jones. 2005. Effects of swimming and diving behavior on body temperatures of Pacific leatherbacks in tropical seas. *Physiol. Biochem. Zool*. 78:285–297.

Thode, H. G. 1991. Sulfur isotopes in nature and the environment: An overview. In *Stable Isotopes: Natural and Anthropogenic Sulfur in the Environment*, eds. H. R. Krouse and V. A. Grinenko, pp. 1–26. New York: John Wiley & Sons.

Tieszen, L. L. and T. W. Boutton. 1989. Stable carbon isotopes in terrestrial ecosystem research. In *Stable Isotopes in Ecological Research*, eds. P. W. Rundel, J. R. Ehleringer, and K. A. Nagy, pp. 167–195. New York: Springer-Verlag.

Tieszen, L. L., T. W. Boutton, K. G. Tesdahl, and N. A. Slade. 1983. Fractionation and turnover of stable carbon isotopes in animal tissues: Implications for $\delta^{13}C$ analysis of diet. *Oecologia* 57:32–37.

Tieszen, L. L. and T. Fagre. 1993. Effect of diet quality and composition on the isotopic composition of respiratory CO_2, bone collagen, bioapatite, and soft tissues. In *Molecular archeology of Prehistoric Human Bone*, eds. J. Lambert and G. Grupe, pp. 123–135. Berlin, Germany: Springer-Verlag.

Tomas, J., F. J. Aznar, and J. A. Raga. 2001. Feeding ecology of the loggerhead turtle *Caretta caretta* in the western Mediterranean. *J. Zool*. 255(4):525–532.

Uhle, M. E., S. A. Macko, H. J. Spero, M. H. Engel, and D. W. Lea. 1997. Sources of carbon and nitrogen in modern planktonic foraminifera: The role of algal symbionts as determined by bulk and compound specific stable isotopic analyses. *Org. Geochem*. 27:103–113.

Valente, A. L., I. Marco, M. L. Parga, S. Lavin, F. Alegre, and R. Cuenca. 2008. Ingesta passage and gastric emptying times in loggerhead sea turtles (*Caretta caretta*). *Res. Vet. Sci*. 84:132–139.

Van Houtan, K. S., S. K. Hargrove, and G. H. Balazs. 2010. Land use, macroalgae, and a tumor-forming disease in marine turtles. *PLoS One* 5(9):e12900.

Vander Zanden, H. B., K. E. Arthur, A. B. Bolten et al. In review. Interpreting the isotopic niche of a breeding AQ16 population to understand the trophic ecology of a highly migratory species. *Mar. Ecol. Prog. Ser*.

Vander Zanden, H. B., K. A. Bjorndal, P. W. Inglett, and A.B. Bolten. 2012. Marine derived nutrients from green turtle nests subsidize terrestrial beach ecosystems. *Biotropica* 44:294–301.

Vander Zanden, H. B., K. A. Bjorndal, W. Mustin, J. M. Ponciano, and A. B. Bolten. In press. Inherent variation in stable isotope values and discrimination factors in two age-classes of green turtles. *Physiol. Biochem. Zool*.

Vander Zanden, H. B., K. A. Bjorndal, K. J. Reich, and A. B. Bolten. 2010. Individual specialists in a generalist population: Results from a long-term stable isotope series. *Biol. Lett*. 6:711–714. doi:10.1098/rsbl.2010.0124.

Vander Zanden, M. J. and J. B. Rasmussen. 2001. Variation in $d^{15}N$ and $d^{13}C$ trophic fractionation: Implications for aquatic food web studies. *Limnol. Oceanogr*. 46:2061–2066.

Walker, T. A. 1991. Juvenile flatback turtles in proximity to coastal nesting islands in the Great Barrier Reef Province. *J. Herpetol*. 25:246–248.

Walker, T. A. and C. J. Parmenter. 1990. Absence of a pelagic phase in the life cycle of the flatback turtle, *Natator depressa* (Garman). *J. Biogeogr*. 17:275–278.

Wallace, B. P., L. Avens, J. Braun-McNeill, and C. M. McClellan. 2009. The diet composition of immature loggerheads: Insights on trophic niche, growth rates, and fisheries interactions. *J. Exp. Mar. Biol. Ecol*. 373:50–57.

Wallace, B. P. and T. T. Jones. 2008. What makes marine turtles go: A review of metabolic rates and their consequences. *J. Exp. Mar. Bio. Ecol*. 356:8–24.

Wallace, B. P., S. S. Kilham, F. V. Paladino, and J. R. Spotila. 2006a. Energy budget calculations indicate resource limitation in Eastern Pacific leatherback turtles. *Mar. Ecol. Prog. Ser*. 318:263–270.

Wallace, B. P., J. A. Seminoff, S. S. Kilham, J. R. Spotila, and P. H. Dutton. 2006b. Leatherback turtles as oceanographic indicators: Stable isotope analyses reveal a trophic dichotomy between ocean basins. *Mar. Biol*. 149:953–960.

Witherington, B. E. 2002. Ecology of neonate loggerhead turtles inhabiting lines of downwelling near a Gulf Stream front. *Mar. Biol*. 140:843–853.

Witt, M. J., A. C. Broderick, D. J. Johns et al. 2007. Prey landscapes help identify potential foraging habitats for leatherback turtles in the northeast Atlantic. *Mar. Ecol. Prog. Ser*. 337:231–244.

Witzell, W. N. and J. R. Schmid. 2005. Diet of immature Kemp's ridley turtles (*Lepidochelys kempii*) from Gullivan Bay, Ten Thousand Islands, southwest Florida. *Bull. Mar. Sci*. 77:191–199.

Zbinden, J. A., S. Bearhop, P. Bradshaw et al. 2011. Migratory dichotomy and associated phenotypic variation in marine turtles revealed by satellite tracking and stable isotope analysis. *Mar. Ecol. Prog. Ser*. 421:291–302.

AUTHOR QUERIES

[AQ1] Reference citations "Gaos et al., 2011; Ferriera et al., 2006; Carr, 1975; Collard and Ogren, 199l; Brandt et al., 1999; Secor, 2008; Minagawa and Wada, 1984; Cardona et al. 2011; Cook, 1991; Mills, 2011" have been changed to "Gaos et al., 2012; Ferreira et al., 2006; Carr and Stancyk, 1975; Collard and Ogren, 1990; Brand et al., 1999; Secor, 2009; Miniwaga and Wada, 1984; Cardona et al. 2010; Cook, 1985; Mills, 2001," respectively, to match the reference list. Please check.

[AQ2] Please provide citation for footnote "a" in Table 9.1.

[AQ3] Please check and suggest whether "*Physogyra lichtensteinii*" can be changed as "*Physogyra lichtensteini*."

[AQ4] Please provide footnote for "n" in Table 9.2.

[AQ5] The part label captions in the artwork of Figure 9.1 slightly differ from the ones in the caption. Please check and suggest whether the part label captions in the artwork can be deleted.

[AQ6] Please add the following references to the reference list: "Bjorndal 2003, Caut et al. 2006, Gaos et al. 2011, Hatase and Tsukomoto 2008, Hobson 2003, Hobson and Rubenstein 2004, IUPAC-IUB Commission on Biochemical Nomenclature, 1967, James et al. 2012, Jones et al. 2004, Kelly 2000, Pearson et al. 2003, Schimdt-Knielsen 1997, Seminoff et al. 2012, Speakman 1997, Wallace et al. 2005 and Wood and Wood 1981."

[AQ7] Please update "in press/in review" Refs. "Berube et al., Jones et al., Seminoff et al., Vander Zanden et al., Pajuelo et al., Pajuelo et al., Vander Zanden et al."

[AQ8] Please provide in text citation for the following Refs. "Biasatti 2004, Caut et al. 2008, IUCN 2011, Jones et al., 2011, Kelly, et al. 2002, Martínez del Rio and Wolf 2005, Marra, et al. 1998, Miller et al. 2011, Purcell 2005, Seminoff, et al. In Press, Vander Zanden and Rasmussen 2001, and Witt et al. 2007.

[AQ9] Please check the page range in reference Ikonomopoulou et al. (2011) for correctness.

[AQ10] Please provide further details if any for Ref. "Inger et al., 2010."

[AQ11] Please provide proceedings date and place of conference for Ref. "Lazar et al., 2008."

[AQ12] Please check the title identified in references Limpus (2007, 2008a, 2008b, 2009) for correctness.

[AQ13] Please provide initials for the author McLachlan in the reference Limpus and McLachlan (1994).

[AQ14] Please provide volume number, if any, for reference Seminoff et al. (2007).

[AQ15] Please provide accessed date for Ref. "Semmens and Moore 2008."

[AQ16] The text "*Vander Zanden et al., 2012 (line ~704)*" has been deleted from the Ref. "Vander Zanden et al. In review". Please check.