ARIADNA ARNAU RODRÍGUEZ

ARE SEA TURTLES CAPITAL OR INCOME BREEDERS? A CASE STUDY AND A GLOBAL REVIEW

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UNIVERSIDADE DO ALGARVE

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Masters on Marine and Coastal Systems

Project done under the supervision of
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Declaration of authorship

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I declare I am the author of this thesis, that is original and unpublished. The authors and publications mentioned in this project are properly cited and are included in the reference list.

To Dr. Alan Bolten,
for all his contributions to the sea turtle world and ocean conservation

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Abstract

Understanding how organisms store energy is as important as the strategies developed for its acquisition. Some species store energy prior to starting their reproductive stage (*capital* breeders), while others use energy acquired during the reproductive period (*income* breeders). The idea that sea turtles are *capital* breeders has been accepted and repeated since the early literature. However, it seems reasonable to consider that inter and intraspecific differences may also dictate variations on their breeding strategies.

The aim of this study is to better understand the feeding strategies of sea turtles during inter-nesting intervals. That is, if nesting females forage between nesting events (*income* breeding strategy) or, conversely, they only rely on stored energy (*capital* breeding strategy). To evaluate the inter-nesting feeding strategy of loggerhead sea turtles (*Caretta caretta*) nesting on Wassaw Island, Georgia, USA, stable isotope values of carbon and nitrogen ($\delta^{13}C$ and $\delta^{15}N$, respectively) for blood and yolk samples were analyzed. Results obtained for blood showed that values of $\Delta^{13}C$ and $\Delta^{15}N$ (change in $\delta^{13}C$ and $\delta^{15}N$ values obtained from the last sample minus $\delta^{13}C$ and $\delta^{15}N$ values from the first sample, respectively) were positively correlated with time interval, indicating an increase in $\delta^{13}C$ and $\delta^{15}N$ values through the nesting season in most of the turtles. There was no relationship between $\Delta^{15}N$ values obtained from the yolk samples and time interval, maintaining stable values over time. For yolk ΔC_{LE} values (lipid-corrected yolk $\Delta^{13}C$), there was a significant negative correlation with time interval, indicating a progressive decrease in $\delta^{13}C$ values over the nesting season. Therefore, results obtained for loggerheads in this study support the *capital* breeding strategy.

An extensive literature review was also conducted to assemble all published evidence of the inter-nesting foraging behavior of sea turtles on a global scale. Summarized patterns of evidence suggest that there is not a simple *capital-income* breeding dichotomy for sea turtles but a complex *continuum*.

Keywords Sea turtle, *capital versus income* breeding, inter-nesting periods, stable isotopes, carbon, nitrogen.

Resumo Alargado

A necessidade energética e a disponibilidade de alimentos nem sempre são constantes no meio ambiente. A capacidade dos organismos de monitorar sua própria energia permite a priorização de diferentes opções comportamentais para refletir as flutuações na energia disponível. Entender como os organismos armazenam energia é tão importante como as estratégias desenvolvidas para a sua aquisição. Essas estratégias de armazenamento de energia têm consequências importantes para a sobrevivência dos indivíduos e, portanto, para as espécies. Esses mecanismos são hereditários, e é por isso que é difícil entender a fisiologia do balanço de energia sem entender a sua ligação com o sucesso reprodutivo. Algumas espécies armazenam energia antes de iniciar a sua etapa reprodutiva (*capital breeders*), e isso garante o sucesso reprodutivo independentemente da disponibilidade de alimento durante a estação de reprodução. Outras usam a energia adquirida durante o período reprodutivo ao invés da energia armazenada antes do período de reprodução e dependem inteiramente da ingestão simultânea de energia durante o período reprodutivo (*income breeders*).

Quando o alimento é abundante e as necessidades de energia são baixas, a energia está disponível para todos os processos necessários para a sobrevivência imediata (locomoção, ingestão, digestão e remoção de resíduos). No entanto, a imprevisibilidade energética pode ditar investimentos de longo prazo, como crescimento, função imunológica e reprodução. Quando a energia é um fator limitante, os mecanismos fisiológicos irão promover processos que garantam a continuidade do indivíduo sobre aqueles que facilitam o crescimento, longevidade e reprodução.

Em comparação com o que se sabe sobre as estratégias de *capital* e *income breeding* em animais endotérmicos, pouco se sabe sobre ectotérmicos. Além disso, as informações relacionadas com este último grupo são contraditórias e dispersas. Como os animais ectotérmicos têm taxas metabólicas mais baixas do que os endotérmicos, os primeiros podem sobreviver em períodos mais longos sem se alimentar, dadas as condições corporais e reservas de energia semelhantes. Além disso, já que a maioria dos ectotérmicos pode armazenar energia suficiente nos seus corpos para suportar sua produção reprodutiva, a sazonalidade térmica restringe a reprodução a um curto período do ano. Assim a estratégia de organismos *capital breeding* poderia, de facto, ser mais comum em organismos ectotérmicos.

As tartarugas marinhas são animais ectotérmicos de grande tamanho com baixas taxas metabólicas que migram centenas de quilómetros entre as áreas de alimentação e nidificação. Antes dessas migrações reprodutivas, as tartarugas marinhas passam longos períodos em áreas de alimentação. Lá, armazenam grande quantidade de energia que lhes permitirá cobrir a maior parte, senão todos, os custos energéticos associados à migração e reprodução.

A ideia de que as tartarugas marinhas usam a estratégia de *capital breeding* tem sido aceite e repetida na literatura, mas é inegável que cada uma das sete espécies de tartarugas marinhas que habitam nos oceanos apresenta diferenças morfológicas e comportamentais. Portanto, parece razoável considerar que tais diferenças também podem ditar variações nas suas estratégias de reprodução, mesmo dentro de populações da mesma espécie, porque estão sujeitas a uma diversidade considerável de fatores ambientais (por exemplo disponibilidade de alimentos ou distâncias migratórias).

O objetivo do presente estudo é melhorar a compreensão acerca das estratégias de alimentação das tartarugas marinhas durante os intervalos entre as posturas. Ou seja, se as fêmeas em nidificação se alimentam entre posturas (*income breeding strategy*) ou, inversamente, elas dependem apenas da energia armazenada, obtida antes de sua migração para as áreas de nidificação (*capital breeding strategy*). Usando a análise de isótopos estáveis (carbono e azoto) de amostras de sangue e gema de ovo obtidas de tartarugas marinhas cabeçudas (*Caretta caretta)* amostradas na Ilha de Wassaw, Geórgia, EUA, foi avaliada sua estratégia de alimentação. Os resultados obtidos para o sangue mostraram que os valores de $\Delta^{13}C$ e $\Delta^{15}N$ no plasma foram positivamente correlacionados com o intervalo de tempo, indicando um aumento nos valores de $\delta^{13}C$ e $\delta^{15}N$ ao longo da temporada de desova para a maioria das tartarugas. Não houve relação entre os valores de $\Delta^{15}N$ obtidos das amostras de gema dos ovos e o intervalo de tempo, mantendo os valores estáveis ao longo do tempo. Para os valores de $\Delta^{13}C_{LE}$ da gema dos ovos, houve uma correlação negativa significativa com o intervalo de tempo, indicando uma diminuição progressiva nos valores de $\delta^{13}C$ ao longo da estação de nidificação. Esses resultados estão de acordo com outros estudos, e parecem indicar que as tartarugas marinhas que nidificam na Ilha de Wassaw não estão a se alimentar durante os períodos entre posturas. Neste contexto, os resultados obtidos neste estudo para as tartarugas cabeçudas suportam a estratégia destes organismos como *capital breeding*.

Além disto, foi conduzida uma extensa revisão da literatura para reunir toda a informação publicada sobre o comportamento das tartarugas marinhas durante os períodos entre nidificações, para assim melhor compreender o seu comportamento e identificar tendências e/ou padrões. Os diferentes estudos foram classificados com base nas sete espécies de tartarugas marinhas (tartaruga de couro, tartaruga verde, tartaruga cabeçuda, tartaruga de pente, tartaruga de casco achatado, tartaruga oliva e tartaruga de kemp) e o tipo de evidência utilizada (morfológica, fisiológica, física, comportamental e visual).

Durante a época de reprodução, as tartarugas marinhas empregam muitas estratégias para minimizar o gasto de energia, por exemplo, enquanto mergulham, tendem a aumentar o tempo de descanso no fundo, a usar flutuabilidade neutra e até mesmo nadar no mesmo sentido das correntes. Portanto, permanece a questão porque é que as tartarugas não se alimentam quando há alimento disponível. Em conclusão, a revisão completa da literatura revelou que a questão das estratégias das espécies de tartarugas marinhas *capital breeders* versus *income breeders* não deve ser vista como uma simples dicotomia entre uma ou outra. Em vez disso, as tartarugas marinhas exibem uma gama de estratégias que se enquadram no *continuum* entre os dois extremos. Os benefícios energéticos e nutricionais da alimentação das tartarugas marinhas durante os períodos entre os ninhos ainda precisam de ser melhor quantificados. O conhecimento da extensão de tais benefícios guiará os esforços para proteger os habitats entre os ninhos e melhorar a compreensão dos ciclos reprodutivos das tartarugas marinhas.

Palavras-Chave: Tartaruga marinha, isótopos estáveis, azoto, carbono, período entre postas, *capital versus income breeding.*

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Objective and Scope of the Work

The aim of this master's thesis is to better understand the feeding strategies of sea turtles during inter-nesting intervals. That is, do nesting females forage between nesting events (*income* breeding strategy) or, conversely, do they only rely on stored energy obtained prior to their migration to the nesting sites (*capital* breeding strategy)? Moreover, this study aims to provide a global perspective on what is currently known on the subject within the scientific community in order to direct and improve future investigations.

The research goal has been to evaluate different sources of evidence to document the inter-nesting behavior of sea turtles through:

1. Stable isotope analysis of blood and yolk samples obtained from loggerhead sea turtles (*Caretta caretta*) nesting in Wassaw Island, Georgia, USA to evaluate their inter-nesting feeding strategy.

2. An extensive literature review to assemble all published accounts of sea turtle inter-nesting foraging behavior and summarize trends.

1. General Introduction

1.1. ENERGY AND REPRODUCTION

The key for survival relies on the acquisition, storage, and use of energy. Acquired energy is either used for production and maintenance or is lost as heat and metabolic waste (Speakman, 1997). The theory of evolution is the major foundation of biology that links energy balance and reproduction, both of which are controlled by physiological mechanisms suited to different metabolic requirements (Bronson, 2000; Schneider and Watts, 2002). Since those mechanisms are heritable, it is difficult to understand the physiology of energy balance without understanding its link to reproductive success (Schneider, 2004).

Energetic demands and food availability are not always constant in the environment. The ability of organisms to monitor their own energy permits the prioritization of differing behavioral options to reflect fluctuations in available energy. When food is abundant and energy requirements are low, energy is available for all the processes necessary for immediate survival (locomotion, foraging, ingestion, digestion, and waste removal). However, energetic unpredictability can dictate long-term investments, such as growth, immune function, and reproduction. When energy is a limiting factor, physiological mechanisms will promote processes that ensure the continuity of the individual over those that facilitate growth, longevity, and reproduction (Schneider, 2004).

Processes that support foraging and feeding behavior may have priority over breeding, especially in long-lived organisms. Mechanisms that increase feeding behavior often inhibit reproductive processes (Schneider, 2004). In many species, the same metabolic signals and chemical messengers that increase the motivation to engage in reproductive behaviors also attenuate the motivation to engage in foraging, hoarding, and eating (Wade and Schneider, 1996; Schneider and Watts, 2002). Some organisms even cease eating when they conduct breeding behaviors (Shine, 1988). In these cases, the body relies on energy reserves (Schneider, 2004). Because reproduction represents a great investment of energy, many species can delay reproduction until energy stores are sufficient to meet the demand without endangering the survival of the organism (Bronson, 2000).

All of these energetic fluctuations are monitored and controlled by metabolic sensory stimuli, hormones (e.g., insulin and leptin), and central feeding-stimulatory circuits that involve neuropeptides and proteins (Schneider, 2004). These mechanisms are fundamental for the survival of the organisms since they are responsible for determining the allocation to reproduction according to the availability of energy reserves. That is, such mechanisms are responsible for prioritizing particular behaviors and changing the motivation of individuals to engage in either reproductive or feeding behaviors, when available energy is plentiful or scarce, respectively. Some species increase energy intake during a period of intense parental care, whereas others increase both energy intake and storage in anticipation of the production of offspring (Schneider 2004).

1.2. CAPITAL *VS.* INCOME BREEDING

Understanding how organisms store energy is as important as the strategies developed for its acquisition. Energy storage strategies have important ramifications for the survival of individuals and therefore for the species. However, for many years, ecologists focused much more on evaluating energy allocation than on the acquisition itself, which is probably due to the strong influence of reproductive effort theory during the second half of the twentieth century (Jönsson, 1997). This theory, based on the consequences driven by the allocation of already acquired energy used for somatic and reproductive functions, did not consider the acquisition of the resources needed. This trend seems to have switched during the last two decades, and the topic of energy storage has generated considerable investigation into *capital* versus *income* breeding strategies (Jönsson, 1997; Bonnet et al.1998; Houston et al. 2007; Stephens et al., 2014).

The definition of *capital* and *income* breeding has since deviated from the original paper on energetics in breeding birds published by Drent and Daan (1980). Initially, the theory was interpreted as a set of rules regarding when breeding females would continue laying eggs or stop based on the available *capital*. The refined definition of a *capital* breeder that continues to be used is “an organism that uses stored energy for reproduction”. Conversely, an *income* breeder is described as “an organism that uses the energy acquired during the reproductive period rather than stored energy for reproduction” (Stearns, 1989, 1992).

For *capital* breeders, storing energy prior to breeding ensures reproductive success regardless of the availability of food during the breeding season. In contrast, *income* breeders rely entirely on the concurrent intake of energy during the reproductive period (Jönsson, 1997). Both intrinsic factors (related to physiology and morphology) and extrinsic factors (related to abundance and availability of food) seem to play important roles in which strategy is selected (Stephens et al., 2009). Behavioral trade-offs are also fundamental, allowing *capital* breeders to separate feeding and breeding in time and space, thereby, favoring the optimal conditions for each (Bonnet et al., 1998).

Compared to what is known about *capital* and *income* breeding strategies in endothermic animals (Bonnet, 1998; Kullberg et al., 2005; Meijer and Drent, 1999), little is known about ectotherms. Moreover, the information related to the latter is contradictory and scattered. Because ectotherms have lower metabolic rates than endotherms, the former can survive longer periods of food deprivation, given similar body conditions and energy stores (Pough, 1980; Hays et al., 2002a; Wang et al., 2006). Moreover, because most ectotherms can store enough energy within their bodies to support their reproductive output and thermal seasonality constrains reproduction to a short period of the year, *capital* breeding could in fact be a more common strategy in ectotherms (Bonnet et al., 1998).

Sea turtles are large ectotherms with low metabolic rates that migrate hundreds of kilometers between foraging and nesting areas (Limpus et al., 1992; Bolten et al., 1998; Hughes et al., 1998; Benson et al., 2007). The life history of these long-lived marine reptiles comprises a wide diversity of ecosystems and latitudes, ranging from open ocean (oceanic) and coastal waters (neritic) where migration, foraging, and mating take place to terrestrial habitats where reproductive females emerge to lay their eggs and hatchlings hatch a few weeks later, ready to start the cycle again (Bolten, 2003). Although many studies have addressed the diet of sea turtles, few have focused on energy acquisition and allocation (e.g., maintenance, growth, locomotion, homeostasis, and reproduction) (Lutz et al., 2002). Therefore, many uncertainties about their reproductive energetics remain.

Migration requires a high expenditure of energy; however, it is nearly an order of magnitude lower in ectotherms than endotherms of the same size and body temperature (Bennett and Ruben, 1979). In some sea turtles, migration can consume 80% of the resources allocated for reproduction (Wallace et al., 2006). Therefore, prior to making breeding migrations, sea turtles spend long periods of time in foraging areas. It is in those regions where sea turtles store large amount of energy that will allow them to cover most, if not all, of the energetic costs associated with migration and reproduction.

Whether a sea turtle will reproduce in a given year is influenced by conditions over the months or even years prior to migration (Limpus and Nichols, 1988; Bjorndal, 1995; Solow et al., 2002). Vitellogenesis, the process of yolk formation via nutrients deposited in the oocyte, begins up to one year prior to nesting (Congdon, 1989; Miller et al., 2003). During this period, sea turtles store energy to be used for both vitellogenesis and migration. Once the female is ready, she will travel to her nesting area, sometimes to the same beach where she hatched decades earlier, which can often be hundreds of kilometers away (Plotkin, 2003).

Following migration, adult sea turtles aggregate at mating sites near the nesting beach, where both sexes mate with one or more partners. With sperm stored along their oviducts, adult females commence nesting. During each nesting season, which in some nesting aggregations can last up to five months, adult females emerge from the ocean and crawl up the beach in search of nesting sites. Following oviposition, the female returns to the ocean where she remains until the next nesting event, usually for a period of 9 to 30 days (Hirth, 1980; Dodd, 1998; Van Buskirk and Crowder, 1994). These intervals are known as inter-nesting periods. All species of sea turtles lay multiple clutches during each nesting season, but their reproductive output differs depending on the species, age, and body condition (Hirth, 1980; Van Buskirk and Crowder, 1994). The energy that developing embryos and hatchlings require is now packaged within the egg (Bonnet et al., 1998; Congdon, 1989). Females then return to their foraging grounds to begin the cycle again. Sea turtles undertake multiple nesting seasons over their lifetime, often separated by 2 to 4 years in foraging areas.

Because sea turtles build energy stores prior to breeding and then migrate away from known foraging areas, many studies purport that sea turtles are *capital* breeders (i.e., females use only stored energy for reproduction). Furthermore, general acceptance of this hypothesis has led many to think that foraging during the nesting season either does not occur or, if it does, the energy acquired during foraging does not contribute to the current year's reproductive output (Bonnet et al., 1998). However, consistent evidence for this theory is still lacking.

There are seven species of sea turtles in the world: leatherback (*Dermochelys coriacea*), green turtle (*Chelonia mydas*), loggerhead (*Caretta caretta*), hawksbill (*Eretmochelys imbricata*), flatback (*Natator depressus*), olive ridley (*Lepidochelys olivacea*) and Kemp's ridley (*Lepidochelys kempii*). Six species are considered vulnerable or endangered by the International Union for the Conservation of Nature and Natural Resources (IUCN, 2020), and the seventh is considered data deficient (flatback). Despite sharing a common and complex life cycle, each species presents different morphological and ecological traits, as well as specific geographical ranges and behavior (Márquez, 1990; Musick and Limpus, 1997; Lutz et al., 2002). Research into the specific feeding habits of each species will contribute to our understanding of their ecological strategies. Such knowledge will then help to develop more effective conservation measures (i.e., define protected areas), as well as a better understanding of the ecological roles of sea turtles.

1.3. STABLE ISOTOPES ANALYSIS – CARBON AND NITROGEN

Stable isotope analysis (SIA) has been used for many years by physiologists and ecologists to investigate physiological, biochemical, and ecological processes. Carbon and nitrogen isotopes are fundamental to interpret ecological aspects such as diet, habitat use, and nutritional stress (DeNiro and Epstein, 1978, 1981; Hatch, 2012). For this reason, SIA has been used to study feeding ecology and migration in both marine and terrestrial organisms (Hobson and Welch, 1992; Hatase et al., 2002b; Post, 2002; Reich et al., 2008; Vander Zanden et al., 2013).

Within an individual, as well as between individuals of the same population, carbon and nitrogen stable isotopes ($\delta^{13}C$ and $\delta^{15}N$, respectively) vary among tissues (Vander Zanden et al., 2012). Factors such as body size, growth, protein turnover (rate at which proteins of a substance are replaced), and half-life (time required to replace half of the molecules) were suggested to influence the incorporation rates of stable isotopes (Martinez del Rio et al., 2009). Isotopic variation is influenced by what the individual consumes and where it consumed it (Newsome et al., 2007). The ratio of stable carbon isotopes (^{13}C:^{12}C) can often reveal information about the base of the food web, and in marine ecosystems, $\delta^{13}C$ values decrease from neritic to oceanic habitats (Rubenstein and Hobson, 2004). The ratio of stable nitrogen isotopes (^{15}N:^{14}N) identifies trophic levels; higher ratios indicate the organism ingests food at higher trophic levels (Post, 2002). However, many factors influence $\delta^{13}C$ and $\delta^{15}N$ values at the base of the food web, especially in marine ecosystems (Hannides et al., 2009; Graham et al., 2010; Pajuelo et al., 2010, 2012a) that can affect the interpretation of carbon and nitrogen ratios.

Some studies have also suggested that nitrogen isotope ratios are sensitive to nutritional stress (Martinez del Rio et al, 2009; Hatch, 2012). Nitrogen isotope ratios may increase with increased duration of starvation (i.e., the animal cannot consume sufficient food to maintain body condition and therefore enters a catabolic state) (McCue, 2010) or fasting (i.e., the animal has sufficient food available but chooses not to eat and also suffers catalysis) (Martínez del Rio and Wolf, 2005). This is explained by the fact that ^{14}N is excreted and ^{15}N is retained in the new proteins and amino acids synthesized (Steele and Daniel, 1978). Similar results have been shown for carbon stable isotopes because $\delta^{13}C$ values increase in an animal when fasting, due to the strong reliance on internal lipid reserves that are depleted in ^{13}C (Gaye-Siessegger et al., 2004).

SIA can be a powerful tool in studies of *capital* breeding, showing the route of the nutrients during periods of starvation or nutritional stress, either to tissue turnover, somatic tissue growth, or reproductive effort (Hatch, 2012). SIA has demonstrated that many endotherms once thought to be *capital* breeders actually use a mixed strategy, and SIA results have also revealed that ectotherms such as lizards and viviparous snakes employ a mixed strategy as well (Warner et al., 2008; Van Dyke and Beaupre, 2011). Thus, mixed energetic strategies during reproduction may be more common among ectotherms than initially thought (Warner et al., 2008; Van Dyke and Beaupre, 2011).

Sea turtles are highly migratory marine animals with complex life cycles. Hence, identifying their foraging areas and studying the strategies used is challenging. Together with studies based on satellite tracking and recapture of tagged animals, SIA has shown that individual sea turtles show high fidelity to different foraging grounds and breeding areas (Limpus et al., 1992; Broderick et al., 2007; Pajuelo et al., 2012b; Walcott et al., 2012, 2013; Vander Zanden et al., 2013). Thus, in a single nesting aggregation, a wide variety of foraging aggregations and diets are represented (Pajuelo et al., 2012b, Pfaller et al., 2020). Analysis based on $\delta^{13}C$ and $\delta^{15}N$ stable isotopes provide important information about the sites that sea turtles forage before their reproductive period (Zbinden et al., 2010; Pajuelo et al., 2012b). Moreover, few studies have also used SIA to address the breeding strategy, and however results are not conclusive, they seem to suggest that sea turtles are *capital* breeders (Barrow, 2006; Caut et al., 2008; Lonhton, 2014).

It could be assumed that if there are isotopic differences between individuals of the same nesting population, different breeding strategies may also be used according to their needs. This study first aims to use SIA to test whether there is evidence for *capital* or *income* breeding in loggerheads nesting in Georgia, USA. Second, this study summarizes all currently available published information related to the feeding strategies used by sea turtles during the breeding season. Based on these studies, does one common strategy exist among all sea turtles (*capital* or *income* breeding) or do sea turtles display a mixed or opportunistic strategy that varies to different degrees among different species and populations?

2. Materials and Methods

2.1 CASE STUDY: WASSAW ISLAND

2.1.1 ETHICS STATEMENT

The animal use protocol for this research was reviewed and approved by the University of Florida Institutional Animal Care and Use Committee and the Georgia Department of Natural Resources. Procedures were permitted by the individual state sea turtle management agencies under the authority of the United States Fish and Wildlife Service (North Carolina Wildlife Resources Commission, South Carolina Department of Natural Resources, and Georgia Department of Natural Resources).

2.1.2 STUDY SITE

With approximately 11 km of beach, Wassaw Island is located on the Atlantic Ocean, on the northern coast of Georgia, USA (31°52′59″N, 80°57′46″W) and, together with the adjacent salt marshes, is part of the Wassaw Island National Wildlife Refuge (Fig 2.1). Because of its limited access, the island has experienced minimal human impact.

The loggerhead sea turtle (*Caretta caretta*) is the most abundant of all marine turtles in U.S. waters. The Wassaw Island nesting population is part of the Northern Recovery Unit (NRU) (Shamblin et al., 2012, 2014), a distinct genetic stock of the Northwest Atlantic loggerhead Regional Management Unit. Loggerhead nesting activity has been monitored by Caretta Research Project (CRP) since 1973. Wassaw Island hosts 10% of Georgia's annual nests (Pfaller et al., 2013), and the nightly monitoring during the nesting season ensures that most of the nesting females are intercepted, tagged, and sampled during this period (from May to August).

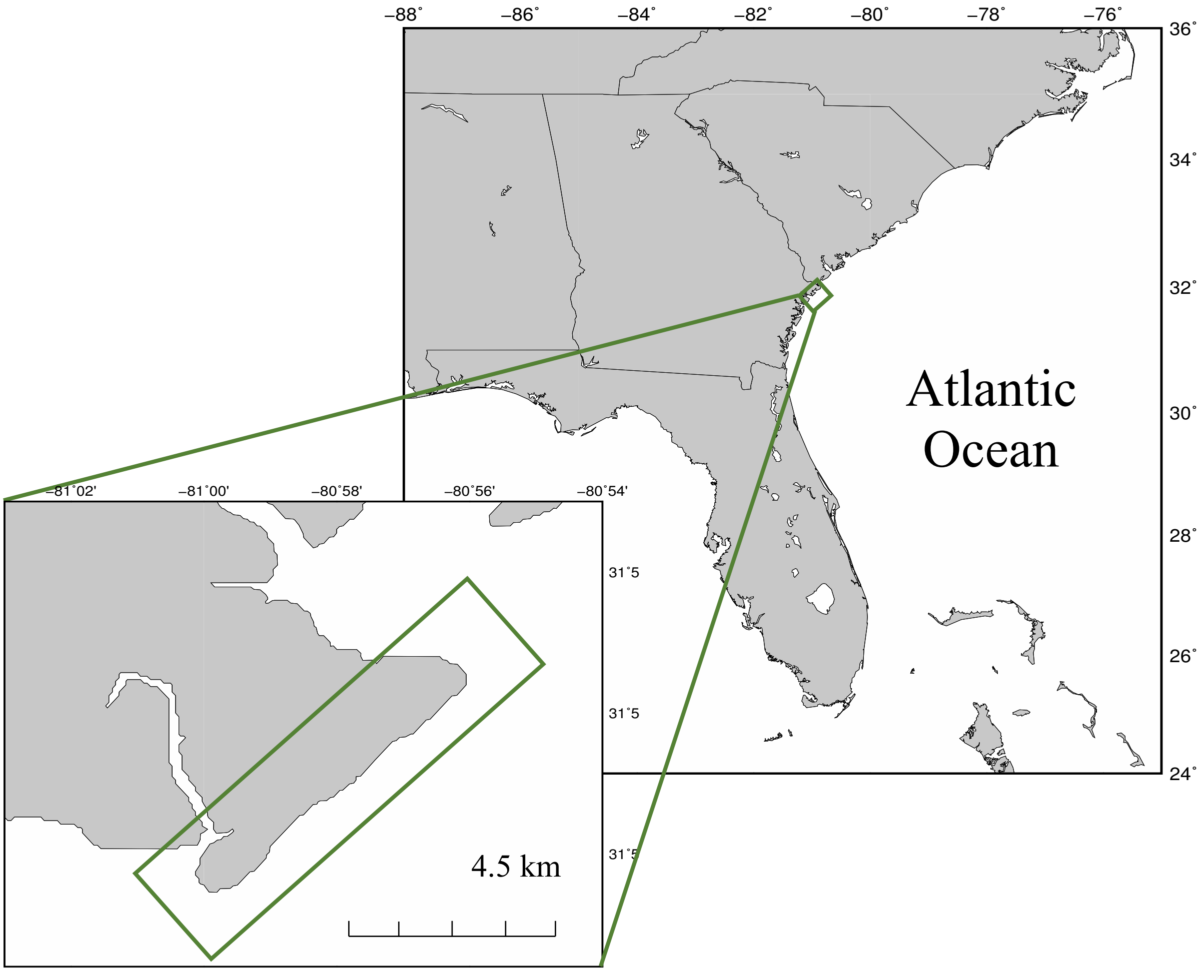

Figure 2.1. Map of Wassaw Island in Georgia, USA. The nesting area is highlighted in the green rectangle on the inset map.

2.1.3 SAMPLE COLLECTION AND PREPARATION

In 2004, CRP began collecting tissue samples from each individual sea turtle encountered on Wassaw for SIA. For the current study, blood and yolk samples were collected from females that were encountered repeatedly during the same nesting season. These two tissues were selected because they provide information that has been integrated over different time scales. Plasma samples provide information on more recent dietary changes of the nesting females, while yolk samples would likely reflect the energetic stores integrated over a longer period of time (Congdon, 1989; Miller et al., 2003)

i. Blood Samples

Two blood samples were collected from each individual. The first sample was collected at the beginning of the season, during the first observed nesting event. The second sample was collected at a subsequent nesting event, with a range of 11 to 47 days between samples. Blood was collected from the dorsal cervical sinus (Owens and Ruiz, 1980) from 25 nesting females during the 2005 and 2006 nesting seasons. A vacutainer tube with sodium heparin, fitted with a 21-gauge needle was used for the procedure, as sodium heparin does not affect isotopic values (Lemons et al., 2011). Blood was centrifuged for 5 min within 1 h of collection to isolate the plasma (PLA). Afterwards, PLA samples were stored in cryovials and frozen at -20ºC until preparation, at which point subsamples of plasma were dried 24 h at 60ºC. Lipid extraction was not performed on PLA, because the low concentrations of lipids in this tissue does not affect the final isotopic values. By using a mortar and pestle, dried PLA samples were ground to a fine powder, and approximately 500-600 μg was sealed in a 9 x 5mm tin capsule.

ii. Yolk Samples

During 2012 and 2013 nesting seasons, yolk samples from two different clutches of the same nesting female were collected for SIA (n=20). The first group of yolk samples were obtained from the earliest observed nesting events of the season. The second group of yolk samples were taken from another clutch of the same nesting female later in the season with a range of 39 to 70 days between samples. Yolks were obtained from eggs that were collected for genetic analysis of the shell and otherwise would have been discarded (Shamblin et al., 2017).

Yolks were preserved in 95% ethanol and mixed into a homogeneous solution in the field. Once in the lab, portions of the samples were pipetted into weigh boats and dried at 60ºC for 24-48h. Yolk samples were not lipid-extracted but were mathematically corrected (see below). To determine $\delta^{13}C$ and $\delta^{15}N$ composition, a subsample of 500-600 μg of each sample was sealed in a tin capsule before analysis.

2.1.4 ISOTOPIC ANALYSIS

Samples of PLA and yolk were analyzed for $\delta^{15}N$ and $\delta^{13}C$ in the Light Stable Isotope Mass Spec Lab in the Department of Geological Sciences at the University of Florida, Gainesville, USA. Samples were combusted in a COSTECH ECS 4010 elemental analyzer interfaced via a Finnigan-MAT ConFlow III device to a Finnigan-MAT DeltaPlus XL isotope ratio mass spectrometer.

Delta values (δ) are used to express the results of the stable isotopes calculated as $\delta X = [(R_{sample})/(R_{standard}) - 1]$ expressed as parts per thousand (‰). In the equation, X represents the heavy isotope (^{15}N or ^{13}C), R (R_{sample} and $R_{standard}$) is the ratio of the heavy isotope to light isotope ($^{15}N/^{14}N$ and $^{13}C/^{12}C$) for the sample and the standard, respectively. For ^{13}C the standard was Vienna Pee Dee Belemnite, and for ^{15}N the standard was atmospheric N_2.

Reference materials were used to normalize the results and assess precision. For blood samples from 2005, as well as all the yolk samples, the standards used were: L-glutamic acid USGS40 ($\delta^{13}C = -26.39$‰ and $\delta^{15}N = -4.52$‰). For blood samples from 2006, the standard used for ^{13}C was IAEA CH-6 sucrose ($\delta^{13}C = -10.4$ ‰) and for ^{15}N was IAEA N1 Ammonium Sulfate ($\delta^{15}N = 0.4$ ‰). Additionally, a laboratory reference material, homogenized loggerhead scute was used as a reference laboratory standard to measure precision in material similar to those used in the study.

The analytical precision of the measurements – calculated as the standard deviation of replicates of the reference materials – was 0.08‰ for $\delta^{13}C$ and 0.13‰ for $\delta^{15}N$ of USGS40 (N = 15), 0.12‰ for $\delta^{13}C$ IAEA CH-6 sucrose (n = 9), 0.12‰ for $\delta^{15}N$ for IAEA N1 Ammonium Sulfate (n = 9), 0.13‰ for $\delta^{13}C$ and 0.37‰ for $\delta^{15}N$ of loggerhead scute (n = 4).

2.1.5 STATISTICAL ANALYSIS

Samples with high lipid content such as egg yolks, are usually lipid extracted because lipids have lower $\delta^{13}C$ values than other components (i.e., proteins and carbohydrates) (DeNiro and Epstein, 1997) and as a result, tissues tend to present higher $\delta^{13}C$ values after lipid extraction. Without this procedure, the variation in isotopic values obtained as a result of differences in lipid content could be mistaken for differences in diet or location. In this case, δ^{13}C values were mathematically corrected for lipid content using the equation for loggerhead egg yolks preserved in 95% ethanol: $\delta^{13}C_{LE} = 0.62 * \delta^{13}C_W - 5.83$ where $\delta^{13}C_{LE}$ are lipid extracted δ^{13}C values and $\delta^{13}C_w$ are δ^{13}C values in whole yolk (Kaufman et al., 2014).

After calculating Δ^{15}N and Δ^{13}C (the change in δ^{15}N and δ^{13}C values obtained from the last sample minus δ^{15}N and δ^{13}C values from the first sample, respectively), for both blood and yolk, linear regression tests were used to examine the relationship between Δ^{15}N and Δ^{13}C and the time interval (number of days) between samples.

All analyses were conducted in R (R Core Team, 2020).

2.2 LITERATURE REVIEW

A literature review was conducted to compile the evidence supporting *capital versus income* breeding strategies during the inter-nesting period. For the review, searches on Web of Science and Google Scholar were carried out for the years 1900 through 2021 for the terms: *feeding ecology, feeding strategy, capital breeder, income breeder, diet, inter-nesting season, inter-nesting behavior, sea turtle,* and the genus and species names of the seven species of marine turtles. The literature cited sections of all of the publications were examined for additional pertinent references and these cited references were included in the review. The literature review includes published papers, as well as master's theses and PhD dissertations.

The resulting studies were classified by turtle species and geography (ocean basin and country). The type(s) of evidence used in each study were categorized as either morphological, physical, physiological, behavioral, or visual. Morphological evidence included studies describing body mass changes; physical evidence included gut content and gastrointestinal tract temperatures studies; physiological evidence included blood, hormones and stable isotopes; behavioral evidence included dive patterns, information obtained from time-depth recorders, satellite telemetry and mouth-opening patterns; and visual evidence included in-water observation and camera records. The number of samples was also extracted to provide context with regards to the strength of each study.

For each species by evidence type combination, the breeding strategy inferred by each study (*capital* or *income*) and the level of confidence (high or low) of that inference was determined. In cases where the author(s) provided robust results and/or specifically concluded that the results supported a certain breeding strategy, the inference was classified as having “high confidence”. Conversely, in cases where the results were not conclusive or the author(s) only suggested, directly or indirectly, a certain breeding strategy, the inference was classified as “low confidence”. Locations of the study sites by sea turtle species and by evidence provided were plotted on two maps to allow visual inspection of the distribution of studies and to identify poorly studied areas where additional studies would be useful.

3. Results

3.1 CASE STUDY: WASSAW ISLAND

3.1.1 BLOOD ANALYSIS

i. Carbon

The change in carbon isotope values ($\Delta^{13}C$) in successive PLA samples (n=25) increased with longer intervals between samples as expressed by a significant relationship between the two variables (Fig. 3.1., $R^2 = 0.1601$; $p = 0.018$). Values ranged from -0.38 to 1.17, where negative values represent a decrease of the $\delta^{13}C$ over time and, conversely, positive values represent an increase.

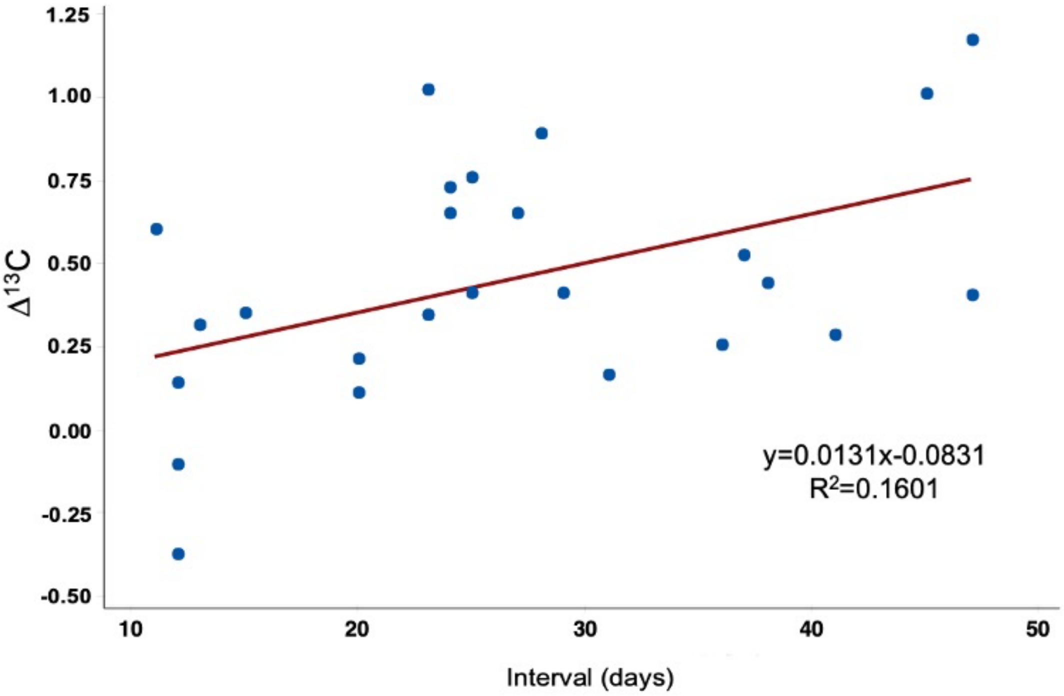

Figure 3.1. Scatter plot for $\Delta^{13}C$ (last $\delta^{13}C$ – first $\delta^{13}C$) values and time interval for plasma samples of nesting loggerhead sea turtles (N = 25). Longer intervals between plasma samples resulted in significantly larger $\Delta^{13}C$ values.

ii. Nitrogen

The change in nitrogen isotope values ($\Delta^{15}N$) in successive PLA samples also significantly increased with longer intervals between samples as depicted by the relationship between the two variables shown in Fig. 3.2 ($R^2 = 0.1774$; $p = 0.036$). The change in $\delta^{15}N$ values ranged from -0.83 to 0.94.

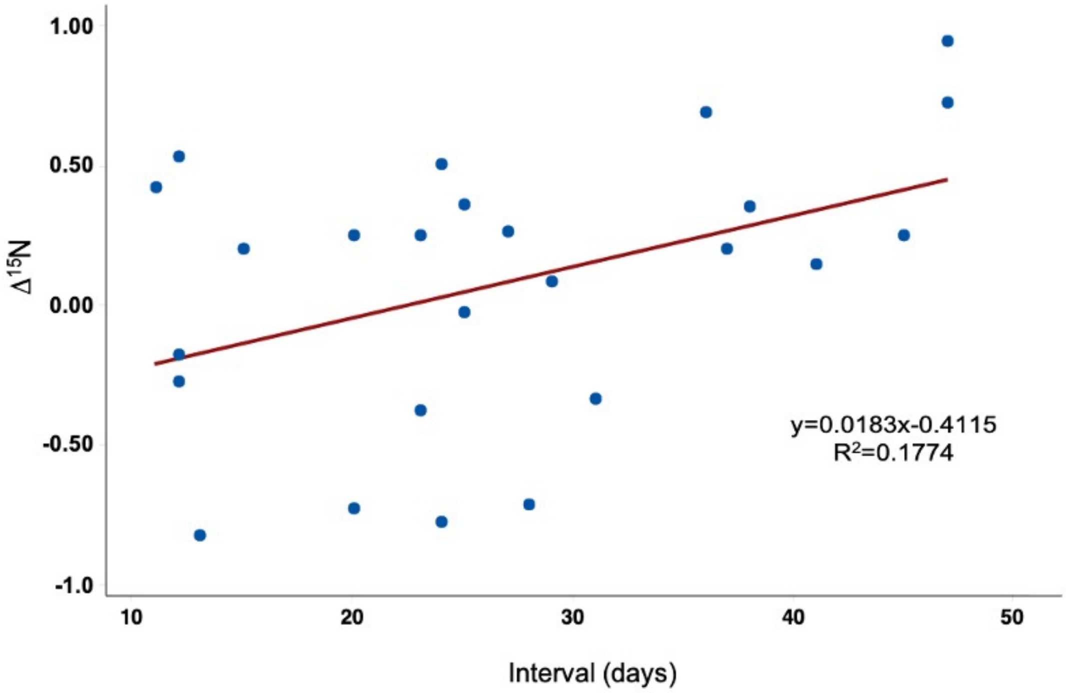

Figure 3.2. Scatter plot for $\Delta^{15}N$ (last $\delta^{15}N$ – first $\delta^{15}N$) values and time interval for plasma samples of nesting loggerhead sea turtles (n = 25). Longer intervals between plasma samples resulted in significantly larger $\Delta^{15}N$ values.

3.1.2 YOLK ANALYSIS

i. Carbon

Both lipid-corrected yolk $\Delta^{13}C_{LE}$ values and non-lipid-corrected yolk $\Delta^{13}C$ values were negatively and significatively related to the time interval between samples (n=20) (Fig. 3.3., $\Delta^{13}C_{LE}$ $R^2 = 0.4233$; $\Delta^{13}C$ $R^2 = 0.4224$; $p = 0.002$), which was opposite of the pattern observed in PLA. For non-lipid-corrected yolk $\Delta^{13}C$, values ranged from -1.58 to 0.06, while lipid-corrected yolk $\Delta^{13}C_{LE}$ values were, as expected, slightly lower ranging from -1.06 to 0.04.

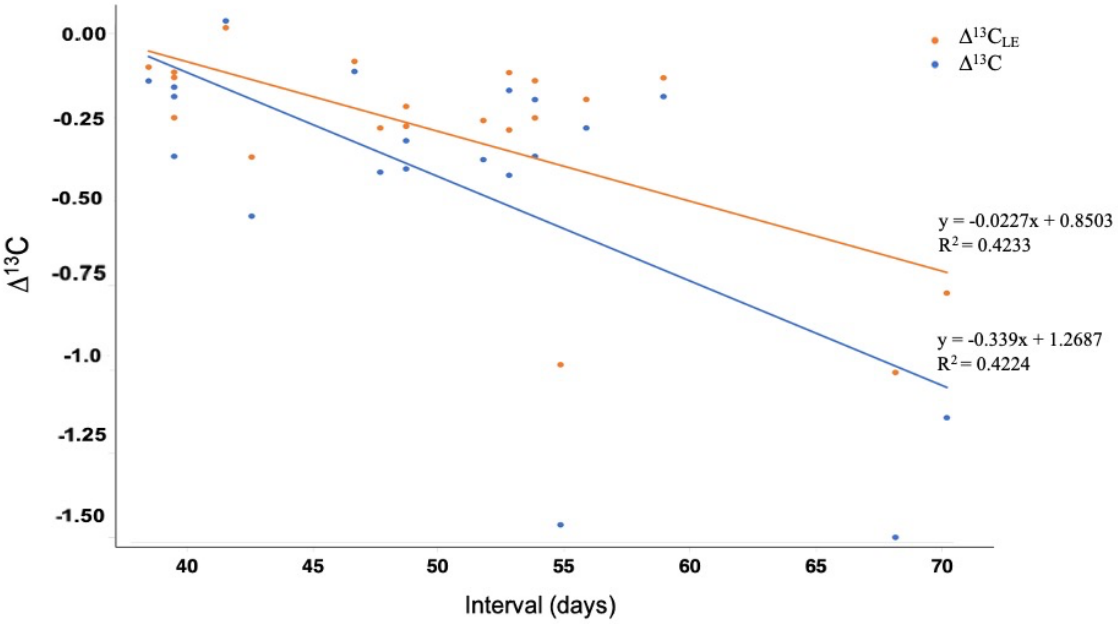

Figure 3.3. Lipid-corrected yolk $\Delta^{13}C_{LE}$ (last – first $\delta^{13}C$) and non-lipid-corrected yolk $\Delta^{13}C_{L}$ (last – first $\delta^{13}C$) values versus time interval in nesting loggerhead turtles (n = 20). Longer intervals between yolk samples resulted in larger decreases in $\delta^{13}C$ values.

ii. Nitrogen

No change was observed for nitrogen isotope values ($\Delta^{15}N$) in yolk samples over the time interval (Fig. 3.4., $R^2 = 0.0008$; $p = 0.907$). Values obtained from yolk samples for $\delta^{15}N$ ranged from -0.41 to 0.84.

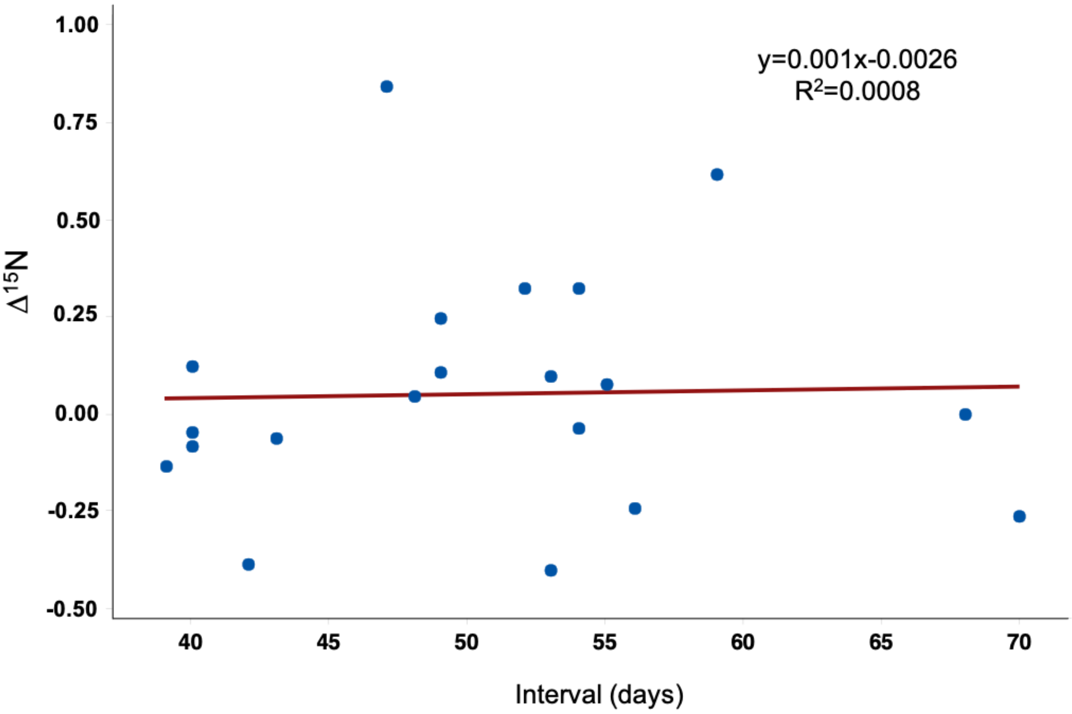

Figure 3.4. Yolk $\Delta^{15}N$ (last – first $\delta^{15}N$) values versus time interval in nesting loggerhead turtles (n = 20). There was no trend in yolk $\Delta^{15}N$ values with increasing time intervals.

3.2 LITERATURE REVIEW

Sixty-three publications were reviewed and classified by species, geographic region, and methods employed (Table 3.1). The most-studied sea turtle species are green turtles and leatherbacks with 21 studies each. For loggerheads, 12 publications were found on this topic, and only seven studies were conducted on hawksbills, and two on olive ridleys. No publications were found for flatbacks or Kemp’s ridleys.

Most of the research has been conducted in the Atlantic Ocean (n = 35), especially the Northwest region (n = 26) (Fig. 3.5). Leatherbacks are the most studied sea turtle in this area (n = 15), followed by loggerheads (n = 8) and green turtles (n = 5), and only one study was conducted on olive ridleys. In the Eastern region of the Mediterranean Sea (n = 7), most of the studies were performed in Cyprus (n = 5), but studies from Turkey (n = 1) and Greece (n = 1) were also included. The Mediterranean studies focused on green turtles (n = 4) and loggerheads (n =3). In the Pacific Ocean (n = 15), most of the studies conducted were on green turtles (n = 9) followed by leatherbacks (n = 5), and only one study was developed for olive ridleys. The Indian Ocean was the least explored (n = 4) with only two studies conducted on leatherbacks, one on green turtles, and one on hawksbills (Fig. 3.5).

There was a great variety in the type of evidence used to investigate inter-nesting feeding behaviors (Fig. 3.6), and in some cases more than one type of evidence or method was used in the same study (Table 3.1). However, behavioral (n = 27), physiological (n = 20), and physical (n = 13) evidence were the most common methods.

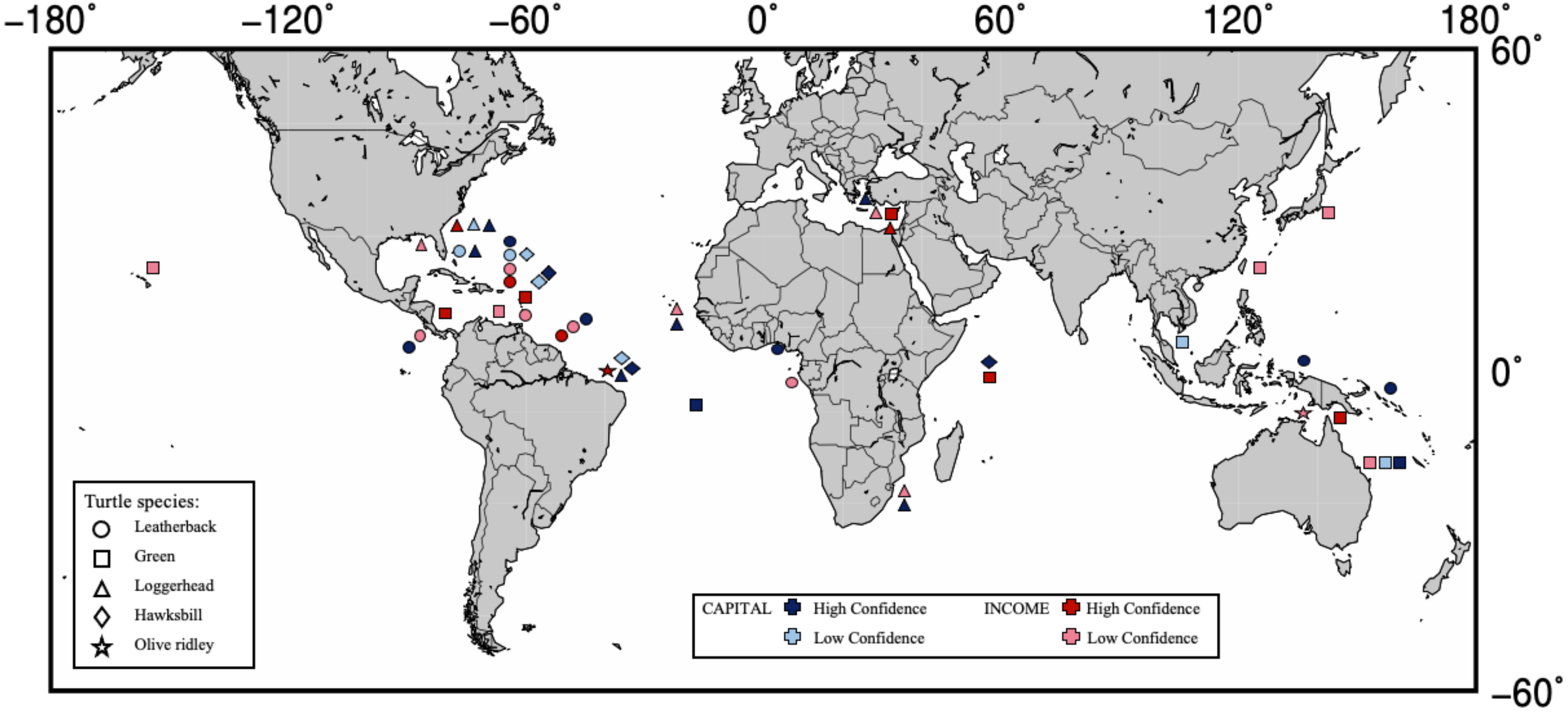

Figure 3.5. Locations of studies that investigated sea turtle breeding strategy. Symbols are colored by whether the evidence supported a *capital* or *income* breeding strategy with either high or low confidence. Studies investigated five of the seven sea turtle species worldwide.

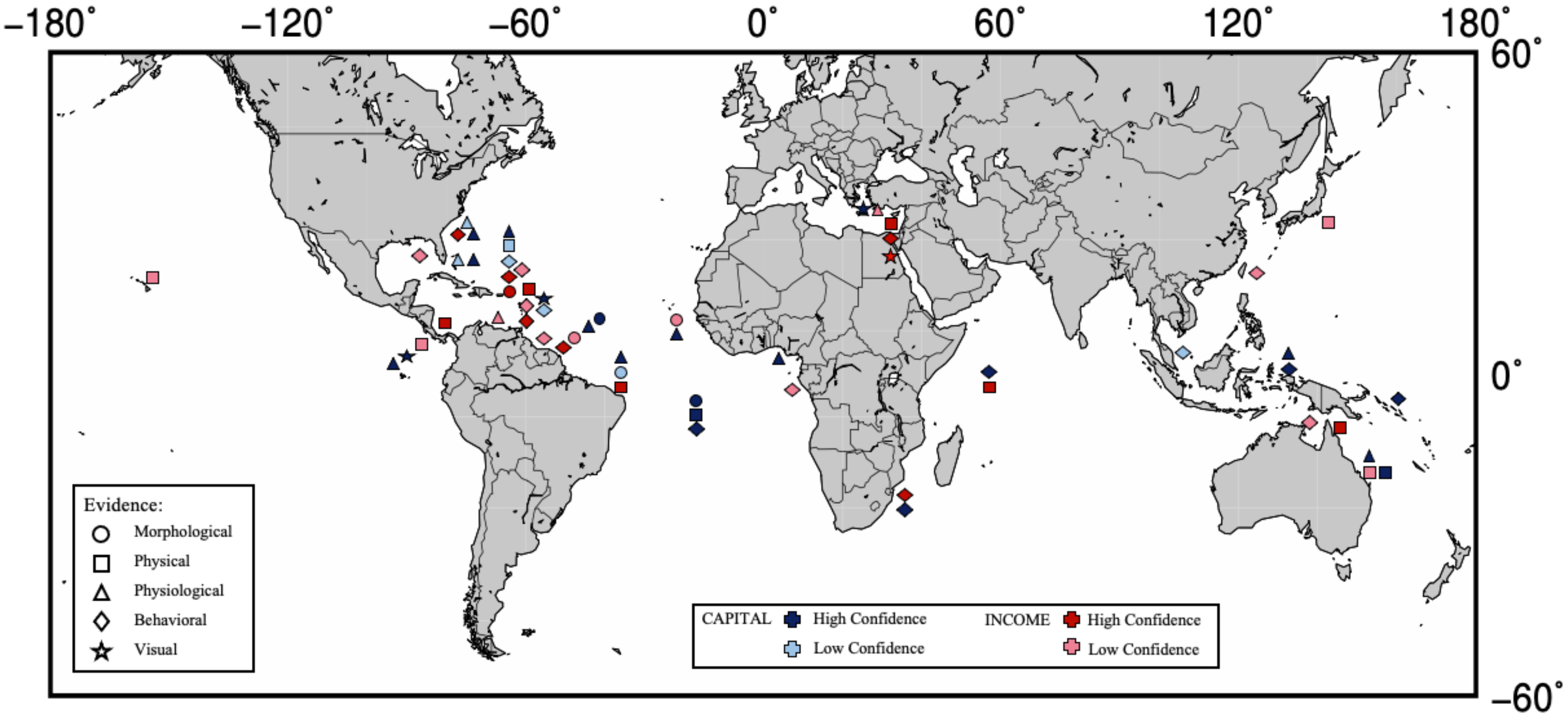

Figure 3.6. Locations of studies that investigated sea turtle breeding strategy by the type of evidence used. Symbols are colored by whether the evidence supported a *capital* or *income* breeding strategy with either high or low confidence.

Table 3.1. Summary of the 63 studies on sea turtles with evidence supporting either *capital* or *income* breeding strategies or both.

Species	Ocean	Site	Evidence	Method	Number of Individuals*	Breeding strategy	Level of confidence	Source
Leatherback	Atlantic	Florida, U.S.	Physiological	Stable isotopes	25	*Capital*	Low	Barrow, 2006
		Florida, U.S.	Physiological	Blood	60	*Capital*	Low	Perrault et al., 2012
		U.S. Virgin Islands	Morphological	Body mass	6	*Income*	High	Eckert et al., 1989
		U.S. Virgin Islands	Physical	T_{GT}	11	*Capital*	Low	Casey et al., 2010
		U.S. Virgin Islands	Physiological	Blood	76	*Capital*	High	Perrault et al., 2014
		U.S. Virgin Islands	Physiological	Blood	79	*Capital*	High	Perrault et al., 2016
		U.S. Virgin Islands	Physiological	Blood	12	*Capital*	High	Harris et al., 2011
		U.S. Virgin Islands	Behavioral	TDRs	2	*Income*	Low	Eckert et al., 1986
		U.S. Virgin Islands	Behavioral	TDRs	6	*Income*	High	Eckert et al., 1989
		U.S. Virgin Islands	Behavioral	Satellite telemetry	11	*Capital*	Low	Casey et al., 2010
		Grenada	Behavioral	Satellite telemetry	13	*Income*	Low	Georges et al., 2007
		Grenada	Behavioral	TDRs and IMASEN	11 TDR & 6 TDR+IMASEN	*Income*	Low	Myers and Hays, 2006
		French Guiana	Morphological	Body mass	49	*Income*	Low	Georges and Fossette, 2006

Species	Ocean	Site	Evidence	Method	Number of Individuals*	Breeding strategy	Level of confidence	Source
Leatherback	Atlantic	French Guiana	Morphological	Body mass	35	*Capital*	High	Plot et al., 2013
		French Guiana	Physiological	Blood	35	*Capital*	High	Plot et al., 2013
		French Guiana	Physiological	Stable isotopes	52	*Capital*	High	Caut et al., 2008
		French Guiana	Behavioral	TDRs Satellite telemetry	16 TDR + Satellite transmitters & 23 Satellite transmitters	*Income*	High	Fossette et al., 2007
		French Guiana	Behavioral	IMASEN	4	*Income*	High	Fossette et al., 2008
		French Guiana and Suriname	Behavioral	Satellite telemetry	5	*Income*	Low	Georges et al., 2007
		Equatorial Guinea	Physiological	Blood	23	*Capital*	High	Honarvar et al., 2011
		Gabon	Behavioral	Satellite telemetry	9	*Income*	Low	Georges et al., 2007
Leatherback	Indian	South Africa	Behavioral	Satellite telemetry	1	*Income*	High	Hughes et al., 1998
		South Africa	Behavioral	Satellite telemetry	10	*Capital*	High	Robinson et al., 2017
Leatherback	Pacific	Costa Rica (Pacific)	Physical	T_{GT} and TDRs	4 T_{GT} & 2 T_{GT} + TDRs	*Income*	Low	Southwood et al., 2005

Species	**Ocean**	**Site**	**Evidence**	**Method**	**Number of Individuals***	**Breeding strategy**	**Level of confidence**	**Source**
Leatherback	Pacific	Costa Rica (Pacific)	Physiological	Blood	8	*Capital*	High	Harris et al., 2011
		Costa Rica (Pacific)	Behavioral	TDRs Video images	11	*Capital*	High	Reina et al., 2005
		Papua Barat, Indonesia	Physiological	Stable isotopes	53	*Capital*	High	Lonhton, 2014
		Papua New Guinea	Physiological	Blood	11	*Capital*	High	Harris et al., 2011
		Papua Barat and Solomon Islands	Behavioral	Satellite telemetry Semi-archival tags	10	*Capital*	High	Okuyama et al., 2016
Green turtle	Atlantic	Guadeloupe, French West Indies	Physical	Gut contents	1	*Income*	High	Delcroix et al., 2009
		Venezuela	Physiological	Blood	48	*Income*	Low	Prieto-Torres et al., 2013
		Costa Rica (Caribbean)	Physical	Gut contents	11	*Income*	High	Meylan, 1978
		Ascension Island	Morphological	Body mass	14	*Capital*	High	Hays et al., 2002a
		Ascension Island	Physical	Gut contents	4	*Capital*	High	Hays et al., 2002a
		Ascension Island	Behavioral	TDRs	6	*Capital*	High	Hays et al., 2000
		Ascension Island	Behavioral	TDRs	6	*Capital*	High	Hays et al., 2002b

Species	**Ocean**	**Site**	**Evidence**	**Method**	**Number of Individuals***	**Breeding strategy**	**Level of confidence**	**Source**
Green turtle	Mediterranean	Captive	Physiological	Blood	5	*Income/Capital*	High	Price et al., 2013
		Cyprus	Physical	Gut contents	2	*Income*	High	Godley and Broderick, unpublished data
		Cyprus	Physical	Gut contents	2	*Income*	High	Hays et al., 2002b
		Cyprus	Behavioral	Data loggers	2	*Income*	High	Hochscheid et al., 1999
		Cyprus	Behavioral	TDRs	8	*Income*	High	Hays et al., 2002b
		Cyprus	Visual	Animal-borne cameras	2	*Income*	High	Fuller et al., 2009
Green turtle	Indian	Republic of Seychelles	Physical	Gut contents	17	*Income*	High	Stokes et al., 2019
Green turtle	Pacific	Hawaii, U.S.	Physical	Gut contents	3	*Income*	Low	Balazs, 1980
		Wan-an Island, Taiwan	Behavioral	TDRs	5	*Income*	Low	Cheng, 2009
		Taiwan	Behavioral	TDRs	10	*Income*	Low	Cheng et al., 2013
		Pulau Redang, Malaysia	Behavioral	Radio and ultrasonic telemetry	3	*Capital*	Low	Liew and Chan, 1992
		Raine Island, Australia	Physical	Gut contents	101	*Income*	High	Tucker and Read, 2001

Species	**Ocean**	**Site**	**Evidence**	**Method**	**Number of Individuals***	**Breeding strategy**	**Level of confidence**	**Source**
Green turtle	Pacific	Heron Island, Australia	Physical	Gut contents	-	*Income*	Low	Forbes, 1996
		Heron Island, Australia	Physical	Gut contents	20	*Capital*	High	Hamann et al., 2002
		Heron Island, Australia	Physiological	Blood	20	*Capital*	Low	Hamann et al., 2002
		Heron Island, Australia	Physiological	Blood	16 in-water & 65 nesting	*Capital*	High	Hamann et al., 2003
Loggerhead	Atlantic	Georgia, U.S.	Physiological	Stable Isotopes	25 blood & 20 yolk	*Capital*	Low	This study
		Georgia, U.S.	Physiological	Blood	31	*Capital*	High	Deem et al., 2009
		Georgia, U.S.	Behavioral	Satellite telemetry	8	*Income*	High	Stoneburner, 1982
		Florida, U.S.	Physiological	Blood	25	*Capital*	High	Perrault and Stacy, 2018
		Florida, U.S.	Physiological	Blood	18	*Capital*	High	Smith, 2010
		Alabama and Florida, U.S.	Behavioral	Satellite telemetry	39	*Income*	Low	Hart et al., 2013
		Cape Verde	Morphological	Body mass	18	*Income*	Low	Pina et al., 2020
		Cape Verde	Physiological	RNA/DNA ratio	57	*Capital*	High	Vieira et al., 2014

Species	**Ocean**	**Site**	**Evidence**	**Method**	**Number of Individuals***	**Breeding strategy**	**Level of confidence**	**Source**
Loggerhead	Atlantic	Brazil	Physiological	Blood	28	*Capital*	High	Goldberg et al., 2011
		Cyprus	Behavioral	TDRs	2	*Income*	High	Houghton et al., 2002
Loggerhead	Mediterranean	Zakynthos, Greece	Visual	Direct observation	-	*Capital*	High	Schofield et al., 2006
		Turkey	Physiological	Blood	7	*Income*	Low	Sözbilen and Kaska, 2018
Loggerhead	Pacific	Japan	Physical	T_{GT}	9	*Income*	Low	Tanaka et al., 1999
		Captivity	Physical	Blood	1	*Income*	High	Kawazu et al., 2016
Hawksbill	Atlantic	U.S. Virgin Islands	Behavioral	TDRs	5	*Capital*	Low	Hill et al., 2017
		Barbados	Behavioral	Satellite telemetry	17	*Capital*	Low	Walcott et al., 2012
		Barbados	Behavioral	TDRs	13	*Capital*	Low	Walcott et al., 2013
		Barbados	Visual	Towed camera	17	*Capital*	High	Walcott et al., 2014
		Brazil	Morphological	Body mass	36	*Capital*	Low	Santos et al., 2010
		Brazil	Physiological	Hormones	41	*Capital*	High	Goldberg et al., 2013
Hawksbill	Indian	Republic of Seychelles	Behavioral	TDRs and IMASEN	4 TDR & 1 IMASEN	*Capital*	High	Houghton et al., 2008
Olive Ridley	Atlantic	Brazil	Physical	Gut contents	10	*Income*	High	Colman et al., 2014

Species	Ocean	Site	Evidence	Method	Number of Individuals*	Breeding strategy	Level of confidence	Source
Olive Ridley	Pacific	Wessel Islands, Australia	Behavioral	Satellite telemetry (SRDLs)	2	*Income*	Low	Hamel et al., 2008

Acronyms: T_{GT}, Gastrointestinal tract temperatures; TDRs, Time-Depth Recorders; IMASEN, Inter-Mandibular Angle Sensor; SRDLs, Satellite-Relayed Data Loggers.

*Number of reproductive sea turtles analyzed did not always coincide with the number of turtles initially sampled.

4. Discussion

4.1 CASE STUDY: WASSAW ISLAND

The current study is the first to employ SIA on nesting loggerheads with the aim of addressing the *capital versus income* breeding strategy in sea turtles. Results obtained for loggerheads in this study support the *capital* breeding strategy. Values of $\Delta^{13}C$ and $\Delta^{15}N$ in plasma were positively correlated with time interval, indicating an increase in $\delta^{13}C$ and $\delta^{15}N$ values through the nesting season in most of the turtles. However, nine of the females showed a decrease in $\delta^{15}N$ and two presented a decrease in both $\delta^{13}C$ and $\delta^{15}N$. There was no relationship between $\Delta^{15}N$ values obtained from the yolk samples and time interval, maintaining stable values over time. For yolk ΔC_{LE} values, there was a significant negative correlation with time interval, indicating a progressive decrease in $\delta^{13}C$ values over the nesting season. For most of the turtles, the isotopic patterns observed in plasma through the nesting season concur with previous studies that show that the increases in $\delta^{13}C$ and $\delta^{15}N$ values are likely due to a reliance on internal N resources, where ^{14}N is primarily used and excreted (Adams and Sterner, 2000; Doi et al., 2007) and internal lipid reserves, as lipids are depleted in ^{13}C relative to protein and carbohydrates (DeNiro and Epstein, 1978; Peterson and Fry, 1987; Gaye-Siesseger et al., 2004a, 2004b). Collectively, this evidence indicates that loggerheads nesting on Wassaw decrease their food intake and rely on stored energy during the breeding season, lending support to a *capital* breeding strategy.

Organs and blood plasma of vertebrate ectotherms, such as sea turtles, present the lowest half-lives (Vander Zanden et al., 2015). Studies on metabolic rates and isotopic turnover (see section 1.3) in sea turtles are scarce. The isotopic turnover period in juvenile loggerheads is at least four months in epidermal tissue, but changes are noticeable sooner once the diet shift has taken place (Reich et al., 2008). Growth contributes significantly to the rate of isotopic incorporation, and such contribution differed among tissues. In juvenile turtles the half-life of carbon ranges from 27 to 35 days and from 11 to 31 days for nitrogen (Reich et al., 2008). For adult turtles, it is expected that these durations would increase because the growth rate is minimal. Vitellogenesis begins up to one year prior to nesting (Congdon, 1989; Miller et al., 2003); therefore, as mentioned in previous sections, plasma and yolk tissues provide information on two different time scales. Since plasma samples reflect more recent dietary changes, if nesting females were fasting, ^{13}C and ^{15}N isotopic values would increase over time because they are retained in the new proteins while ^{12}C and ^{14}N are excreted. Conversely, yolk samples reflect the energetic stores integrated over a longer period of time. Therefore, values obtained from this tissue would likely identify dietary behavior on foraging grounds, prior to the nesting season, and current fasting would not be identified. Results obtained partially support this idea, since no significant change was detected on nitrogen, suggesting that was obtained during a stable period, while feeding in the foraging grounds.

Laboratory studies that monitor isotopic changes during periods of fasting can inform field studies. Although increases in δ^{15}N values associated with fasting have been observed widely, there is no consensus that the pattern is ubiquitous. Some studies have shown increases, decreases, or lack of changes in both δ^{13}C and δ^{15}N values during fasting (Hatch, 2012). Martinez del Rio and Wolf (2005) hypothesized that δ^{15}N values should increase with fasting time duration. However, it is still unclear the degree to which δ^{15}N values may be considered a good indicator of fasting or nutritional stress, since sometimes small changes can be difficult to detect in wild populations where inter-individual variability in δ^{15}N values can be high (Stevens et al., 2006; Ugan and Coltrain, 2011). A more recent approach employing compound-specific δ^{13}C and δ^{15}N analysis of individual amino acids may more reliably quantify the reliance on stored energy and thus indicate the extent of *capital* breeding (Whiteman et al., 2020).

Yolk isotopic values, on the contrary, either remained constant over time (δ^{15}N) or decreased (δ^{13}C). Other studies suggest that yolk tissues tend to reflect the diet of the turtles at foraging grounds, prior to their migration to their breeding sites (Hatase et al., 2010; Carpentier et al., 2015). The lack of a trend in δ^{15}N over time may be attributed to the fact that vitellogenesis begins up to one year prior to breeding (Congdon, 1989; Miller et al., 2003) and its production is complete before the nesting season begins (Rostal et al., 1996, 2001; Miller et al., 1997). By allocating energy to yolk tissues prior to migration, individuals ensure some reproductive success independent of the environmental conditions at the breeding site.

The fact that δ^{13}C values of yolk decreased over the season may suggest that sea turtles use fat reserves to produce the yolk of their eggs. Similar results were obtained for leatherbacks in French Guiana (Caut et al., 2008). In Japan, no significant differences were found in δ^{13}C and δ^{15}N values in egg yolks of loggerheads over the nesting season (Hatase et al., 2002b), whereas a significant increase in δ^{15}N values of egg yolk was observed in green turtles (Hatase et al., 2006). These results could indicate different isotopic routing for C and N that may be related to dietary or species-specific traits and supports the idea that C and N incorporations should not be assumed to be equal (Hobson and Stirling 1997; Hobson and Bairlein 2003; Carleton and Martínez del Rio 2005; Reich et al., 2008).

Whether loggerheads that nest in Georgia are consistent *capital* breeders is not certain, since previous studies provided mixed support (Stoneburner, 1982; Deem et al. 2009). Although the locations of their studies were on separate islands, like Wassaw Island, both Cumberland and Blackbeard Island are located on the coast of Georgia and support nesting by loggerheads from the Northern Recovery Unit (Wallace et al. 2010). Satellite telemetry demonstrated that during inter-nesting periods, loggerheads from Cumberland Island moved directly to small, isolated areas with stable substrate, where patches of hard and soft corals, crustaceans, mollusks, and sponges are concentrated, as reported by Stoneburner (1982). The author concluded that this movement presented an opportunity for turtles to obtain food resources and suggested that loggerheads may feed during the breeding season (i.e., *income* breeders). Conversely, physiological evidence obtained through blood samples to compare the health status of foraging and nesting turtles suggested that nesting loggerheads from Blackbeard Island did not feed (Deem et al., 2009). Because the nesting turtles had lower values for glucose, potassium, and blood urea nitrogen (BUN), the authors concluded that their health condition was likely associated with a state of fasting during the breeding season (i.e., *capital* breeders).

Whether loggerheads in Georgia are strict *capital* or *income* breeders is not a simple answer based on the original definitions presented by Stearns (1989, 1992). A *capital* breeder "uses stored energy for reproduction", while an *income* breeder "uses the energy acquired during the reproductive period rather than stored energy for reproduction". While the results of this study support the idea that sea turtles use stored energy for egg production, they do not negate the possibility that turtles may feed during the breeding season and may use assimilated energy and nutrients for other reproductive activities (e.g., eggshell formation, crawling, digging, covering, and return migrations).

This idea has been partially demonstrated in green turtles. Stokes et al. (2019) compared the gut content of males, non-breeding females, and gravid females from the same area and determined that there were considerable differences between the gut contents. Gravid females presented less volume of food and different composition compared to the two other groups. Moreover, several studies identified large amounts of calcareous material in the guts of gravid sea turtles (Mortimer, 1981, 1982; Meylan, 1984; Tucker and Read, 2001; Stokes et al., 2019), supporting the hypothesis that such dietary calcium might be required for eggshell formation, since the eggs of each clutch are shelled just prior to being laid (Tucker and Read, 2001). The dichotomy between *capital* versus *income* breeding, was already presented by Stearns (1989, 1992) as a *continuum*. It is the case of poeciliid fishes, a family that presents the full spectrum from '*capital* breeders' (guppies) to '*income* breeders' (wordtails) (Turner, 1937). Therefore, the possibility that breeding turtles may simply reduce their food intake or just change their diet accordingly to their reproductive needs and environmental possibilities seems reasonable.

4.2 LITERATURE REVIEW

4.2.1 HISTORICAL CONTEXT

The idea that sea turtles are *capital* breeders has been accepted and repeated since the early literature (Hendrickson, 1958; Schulz, 1975). Some authors hypothesized that, during migration to the breeding regions or upon arrival, green turtles significantly reduced their food intake or were aphagic (Hirth, 1971; Carr et al., 1974; Bjorndal, 1985; Kwan, 1994). The idea that green turtles do not feed during their breeding season because most marine habitats adjacent to nesting beaches provided little or no food was based mainly on anecdotal observations (Carr et al., 1974; Carr, 1980).

More recently, different methodologies have demonstrated that behavioral, dietary, and physiological changes take place during reproduction. Gut content analysis of nesting or gravid females is one of the most direct lines of evidence to test whether sea turtles forage or not between nesting events and to quantify the quantity and quality of the items ingested. This methodology has been mainly conducted on green turtles, with few studies on other species, such as hawksbills.

Hematologic studies provide extensive information about numerous parameters related to an individual's health, as well as their behavior. Many hematologic variables reflect reproductive and nutritional status in sea turtles and can be used to address the question of *capital vs income* breeding. However, interpretation of these nutritional markers can be difficult because of the extent of individual variation and the many factors that affect concentrations of blood analytes such as environmental conditions, nutritional status, age, and pathogens, amongst others (Whitaker and Krum, 1999; Herbst and Jacobson, 2003). Lipid mobilization (e.g., triglyceride, cholesterol), changes in reproductive hormone concentration (e.g., leptin, ghrelin, testosterone, corticosterone), urea and other elements (e.g., calcium, phosphorus) throughout the nesting season are expected, but this review has shown that patterns are not consistent and there are many questions to be addressed. If fasting in sea turtles is physiological, as suggested by Goldberg et al. (2013), and leptin and ghrelin are related to fasting, that observation should be a universal trait. This is, all the sea turtles, or at least for example all hawksbill populations or individuals, should present the same pattern. If characteristics of reproductive physiology are phylogenetically constrained, then why is so much variation found in blood parameters among species, populations, and individuals? One explanation might be that not all individuals are behaving the same way: some fast while others do not. Similar conclusions can be taken for behavioral evidence, where different studies have shown that diving behavior of sea turtles can be linked to the bathymetric characteristics, food availability and currents of the inter-nesting areas, promoting deep or shallow dives of different time durations. Such variability complicates the description and classification of the activities.

Direct observation and video cameras may seem to be reliable sources of evidence; however, this methodology may be inaccurate, incomplete, and/or subjective, especially when the sampling time obtained from each individual may not be sufficient to answer the question that the present study is considering. That is, sampling the first 24 hours after nesting or monitoring random moments during the day may not provide accurate information. Moreover, it should be considered that direct observation data obtained while diving or snorkeling, may be biased by the possibility that the sea turtle behavior may be altered by anthropogenic factors. In conclusion, many studies have indicated that gravid females may in fact forage during the breeding season and contrary to long-standing assumptions, suggest that sea turtles may be, at least partially, *income* breeders.

Using the information summarized in the literature review, the following subsections describe the current state of knowledge with regard to *capital* versus *income* breeding in sea turtles. The information has been classified by species to simplify interpretations and avoid methodological and geographical redundancies. However, regional differences in methodology affect the strength of interpretations. This synopsis will serve as a starting point for future studies investigating the *capital-income* breeder strategies in sea turtles.

4.2.2 LEATHERBACKS

Leatherbacks are the largest extant sea turtle. These highly migratory animals have the widest distribution of any reptile and can undertake breeding migrations that exceed 15,000 kilometers per year (Plotkin, 2003). Moreover, their extraordinary diving ability allow them to reach depths of over 2,000 meters (Plotkin, 2003). Because leatherbacks have enormous energy demands and their preferred prey (jellyfish and salps) has low nutritional value, it is reasonable to assume that leatherbacks would take any opportunity to feed, even between nesting events. However, it is still not clear if leatherbacks stop feeding during the breeding season, which would imply fasting for several months every two to three years (Price et al., 2006; Stewart et al., 2014). Many studies have been conducted using different methods with the aim of understanding the feeding strategy of leatherbacks during inter-nesting periods. However, in terms of *capital versus income* breeding, there does not seem to be a consensus for the species nor any one population.

Leatherbacks, like all sea turtles, spend more than 90% of their time underwater (Renaud and Carpenter, 1994; van Dam and Diez, 1996, 1997; Lutcavage and Lutz, 1997). Their slow metabolism and extreme resistance to asphyxia distress (Berkson, 1966) allow them to spend long periods of time diving, undertaking a variety of different activities, while spending only brief periods of time at the surface. Knowing their diving behavior during inter-nesting periods, as well as the associated bathymetry in areas where diving occurs, can help researchers understand their energetic needs, their ecological roles, and their relationships with the environment, including their feeding strategies during the breeding season.

The early studies on diving behavior conducted on gravid leatherbacks nesting in the U.S. Virgin Islands (USVI) demonstrated that these pelagic animals are active divers, spending long periods of time in deep waters (Eckert et al., 1986, 1989). The diving patterns measured with time-depth recorders (TDRs) during inter-nesting periods suggested that turtles were mainly making deep dives at night within the deep scattering layer (DSL), a behavior known as diel vertical migration (Eckert et al., 1986, 1989). Because prey species (i.e., gelatinous zooplankton) migrate to shallow depths within the DSL at night, it was suspected that leatherbacks may be targeting food resources, as has been observed in some marine mammals (Kooyman, 2012). More recently, Casey et al. (2010) used time-depth data along with gastrointestinal tract temperatures (T_{GT}) to determine if USVI leatherbacks ingest prey items while diving. T_{GT} results suggested that seven of the eight turtles sampled displayed abrupt decreases in stomach temperature that were indicative of prey ingestion. The authors concluded that although leatherbacks appeared to be feeding opportunistically, the low ingestion rates indicate that the energy stored at the foraging grounds prior to breeding was essential for successful reproduction, thereby lending support for a *capital* breeding strategy.

Gravid leatherbacks nesting in Grenada performed similar inter-nesting movements and diel dive patterns as their counterparts nesting in the USVI (Myers and Hays, 2006). Using not only TDRs, but also satellite telemetry (Georges et al., 2007) and Inter-Mandibular Angle Sensors (IMASEN), the authors found that while leatherbacks may actively dive to seek out vertically migrating prey, their IMASEN data did not detect any obvious evidence of prey manipulation. Therefore, while the authors could not confirm foraging attempts, they emphasized that leatherbacks likely use gustatory cues to sense their immediate environment (Myers and Hays, 2006).

Nesting leatherbacks equipped with TDRs in French Guiana presented clear W-shaped dive patterns during inter-nesting intervals (Fossette et al., 2007). Characterized by long bottom times with numerous wiggles of several meters in amplitude (>2m), this dive pattern is commonly associated with prospecting and foraging behaviors (Wilson 1995; Shreer et al., 2001). Moreover, dives showed a progressive ascent, which the authors interpreted as behavior potentially associated with prey searching and/or capture (Fossette et al., 2007). Contrary to Eckert et al. (1989), in which USVI leatherbacks were thought to make foraging dives mainly at night, Fossette et al. (2007) recorded W-shaped dives during the daytime. This daytime foraging pattern coincides with other studies conducted on other leatherback populations (Myers and Hays, 2006) as well as other sea turtle species (hawksbill: van Dam and Diez, 1996; Storch et al., 2005; Blumenthal et al., 2009; Kemp's ridley: Gitschlag, 1996; green turtle: Hays et al., 2000; Rice and Balazs, 2008; Cheng, 2009, Blanco et al., 2013). The idea that leatherbacks in French Guiana may feed during inter-nesting intervals is not only supported by fine-scale analysis of dive shapes (Fossette et al., 2007), but also by satellite telemetry (Fossette et al., 2007; Georges et al., 2007), body mass analysis (George and Fossette, 2006), and IMASEN data (Fossette et al., 2008). As suggested by Myers and Hays (2006) for leatherbacks nesting in Grenada, isolated beak movements recorded with IMASEN indicate olfactory signatures are likely used for detecting potential prey. Unlike Myers and Hays (2006), however, Fossette et al. (2008) identified groups and series of successive beak movements that were consistent with feeding events and food processing, suggesting that leatherbacks in French Guiana may have been feeding during dives. The authors further suggested that the high productivity of the site (i.e., large blooms of gelatinous plankton) during the nesting season, which coincides with the peak of the Amazonian influence (Froidefond et al., 2002), may allow turtles in this population to feed during inter-nesting periods and attain greater body masses than leatherbacks from other regions (Georges and Fossette, 2006).

In the Pacific, TDRs were paired with animal-mounted cameras to collect data on respiratory frequency (exhalations and inhalations per minute) of Costa Rican leatherbacks during the inter-nesting period (Reina et al., 2005). Results suggested that turtles tend to exhibit U-shaped dives in order to conserve energy. U-dives are characterized by a steady descent and ascent separated by an extended period of time at a constant (or slightly variable) depth (Reina et al., 2005). In U-dives, bottom time can be interpreted as resting or foraging time. Nevertheless, the authors concluded that individuals in this nesting population do not feed during inter-nesting intervals based on the results obtained through video images. However, the data only encompassed the first 24 h after a nesting event, which is a small period of time considering the typical eight to 12-day interval between nests. In Papua Barat and Solomon Islands, nesting leatherbacks also presented deep, long dives, mainly composed by V-shaped patterns with no wiggles (Okuyama et al., 2016). Results were obtained through satellite transmitters and fine-scale archival data, offering a higher accuracy compared to other devices. The lack of wiggles was interpreted as an absence of foraging behavior.

Therefore, the authors concluded that this population follows a *capital* breeding strategy.

The bathymetric characteristics of breeding areas are a key factor affecting the diving behavior of sea turtles during inter-nesting intervals. Because managing energy use is crucial during the breeding season, turtles adapt their movements to minimize energy expenditure. Therefore, individuals may display different dive patterns in different locations when performing the same activity simply because the bathymetry is different. Leatherbacks in USVI (Eckert et al., 1986, 1989; Eckert, 2002), Grenada (Myers and Hays, 2006), and Papua Barat and Solomon Islands (Okuyama et al., 2016) show longer and deeper dives than those from South China (Eckert et al., 1996) and the Pacific Coast of Costa Rica (Southwood et al., 1999; Reina et al., 2005; Wallace et al., 2005; Shillinger et al., 2010) likely because the bathymetry in the latter areas constrained turtles to shorter and shallower dives. As these studies show, it is truly challenging to describe a universal or even species-specific dive pattern that identifies foraging, resting, or swimming. While TDRs have provided invaluable data for improving the understanding of turtle's lives underwater, variation in bathymetry and associated dive patterns provide only limited inferences with regard to whether turtles are actually feeding or not.

Morphological and physiological changes experienced by leatherbacks during the nesting season provide another means for evaluating evidence in support of a *capital* or *income* breeding strategy. In the USVI, where TDRs provided valuable but limited inferences, weight loss throughout the nesting season was lower than expected compared to egg production (Eckert et al., 1989). The authors estimated that if the follicular development at the beginning of the nesting season accounts for 50% of final clutch weight, then inter-nesting weight loss should be approximately 50% of egg production. Based on these assumptions, turtles were predicted to lose approximately 4.5 kg between two nesting events. However, this predicted amount was consistently higher than the observed weight loss (~2 kg). Although the authors suggested that it is likely that much of the egg weight added between two nesting events is water, they do not provide evidence of it. But they concluded that it would be reasonable to consider that USVI leatherback population may feed during breeding season, since water is likely to be metabolically expensive for a marine turtle.

Multiple studies based on SIA have been conducted on leatherbacks. After observing an increase in δ^{15}N values of skin tissue, Lonhton (2014) suggested the *capital* breeding strategy is used by the leatherback nesting population of Papua Barat, Indonesia. However, the decreasing $\delta^{13}C$ values over time contradict that conclusion.

Additional studies using physiological evidence from blood analyses also support the *capital* breeding strategy in leatherbacks. Various blood parameters were analyzed for USVI leatherbacks across the nesting season, and serum protein concentrations (i.e., total protein (TP), albumin and total globulin) were found to decline, which the authors attributed to fasting (Perrault et al., 2014, 2016). It has been suggested that TP concentrations are expected to be lower in nesting females due to protein loss (Harris et al., 2011), since they rely on lipids for nutrients and shift from fat metabolism to skeletal muscle catabolism (i.e., protein). TP concentration values obtained from nesting leatherbacks in Florida (Perrault et al., 2012) and Gabon (Deem et al., 2006) were only slightly lower (by 0.7 g/dL on average) than concentrations found in foraging leatherbacks (Innis et al., 2010). In contrast, an increase in TP in nesting loggerheads was attributed to protein mobilization during egg formation (Deem et al., 2009). It has been hypothesized that extrinsic factors such as environmental conditions, diet, and location may influence TP concentrations, thereby explaining variation among years, populations, and individuals in different physiological states (Osborne et al., 2010). Therefore, it is difficult to use such values as indicators of fasting, especially if those values are indicative of fat loss, which is expected when fat stores are mobilized during periods of yolk production.

Albumin concentrations in the blood of nesting leatherbacks tend to be slightly lower than those from foraging grounds (Deem et al., 2006; Innis et al., 2010; Harris et al., 2011; Honarvar et al., 2011; Perrault et al., 2012, 2014). Despite being commonly interpreted as a sign of fasting during the breeding season, it should be noted that albumin is an important component of the egg white, and therefore a loss of albumin may take place through the production of albumen during amniotic egg formation over the nesting season (Woodward, 1990).

Differences in values of total globulin (α_1-globulin, α_2-globulin, β-globulin, and γ-globulin) were observed between populations, as well as between foraging and nesting females. In most cases, concentrations obtained in foraging females tended to be higher (Innis et al., 2010) than those of nesting females (Deem et al., 2006; Perrault et al., 2012). Only the USVI nesting population had higher values than foraging females (Perrault et al., 2014). Total globulin tended to decrease during the nesting season and, although the authors indicated that acute-phase proteins, such as α_1-globulin, α_2-

globulin, and β-globulin, are expected to decrease in response to fasting, they may also make up a portion of the total albumin that is deposited into eggs (Perrault et al., 2014).

The mean body mass loss of 35 nesting females in French Guiana was 11% of their initial body mass (46.8 ± 2.6 kg of initial mass of 409.0 ± 8.9 kg) (Plot et al., 2013), which may indicate that this population does not feed during inter-nesting intervals. However, the body mass loss was smaller than total clutch mass, which could be due to water ingestion and/or by feeding on water-rich prey such as jellies (Southwood et al., 2005). The authors supported the morphological evidence with physiological evidence obtained through blood samples, where plasma metabolite levels were used to test whether jellyfish were ingested (Plot et al., 2013). Blood results showed that values of hematocrit, glucose, urea, and calcium decreased throughout the nesting season, and some of these parameters (i.e., calcium, glucose) are in fact directly correlated to reproductive consequences. For this reason, the authors stated that leatherbacks are *capital* breeders (Plot et al., 2013). Decreased values in calcium and lipids (triglyceride) are expected, since the calcium mobilization is required for egg-shelling, and triglycerides are the main source of energy to produce yolk.

Leatherbacks, despite being pelagic active divers that require large amounts of energy, especially during reproduction, feed on prey with low nutritional value. Results obtained through different methodologies support the conclusion that leatherbacks may feed during inter-nesting periods to compensate for the increase in energy expenditures to which they are subject during the breeding season. However, none of the populations studied so far has shown clear evidence to support either the *capital* or *income* breeding strategy.

4.2.3 GREEN TURTLES

The green turtle is the largest hard-shelled sea turtle (Family Cheloniidae). Considered strict herbivores for decades, their diet was thought to be comprised almost exclusively of seagrasses and algae as adults (Hirth, 1997). However, more recent studies indicate green turtles also consume animal material, including sponges, jellyfish, and other invertebrates (reviewed in Bjorndal, 1997 and Heithaus, 2013). Despite nesting in over 80 countries around the world (Seminoff et al., 2015), the two largest nesting populations are located at Tortuguero on the Caribbean coast of Costa Rica and at Raine Island on the Great Barrier Reef in Australia.

Nesting beaches are usually high energy areas that provide good conditions for females to nest but hinder the growth of marine plants. This was considered an important limitation for green turtles, as their main food items were thought to be scarce or even nonexistent at most breeding sites (Hendrickson, 1958; Carr et al., 1974; Schulz, 1975), leading to the initial assumption that they are *capital* breeders. That was the case of Ascension Island (Carr, 1974; Mortimer and Carr, 1987), where studies based on physical evidence showed that gut contents of four green turtles at Ascension Island were empty (Hays et al., 2002a). Interestingly, however, turtles were observed approaching ships to opportunistically eat dumped refuse (Carr et al., 1974), suggesting that fasting may not preferred but rather imposed by the circumstances. Further support for a *capital* breeding strategy for Ascension Island green turtles comes from morphometric and behavioral evidence using body mass changes (Hays et al., 2002a) and TDRs (Hays et al., 2000, 2002b), respectively. Turtles spent only 37% of the time in shallow waters with an average depth of 9.5 m. (Hays et al., 2000, 2002b). It was speculated that turtles do not dive below 19 m because this is the maximum depth at which individuals obtain near-neutral buoyancy after diving with full lungs. By resting at this depth with the maximal oxygen stores, sea turtles can increase their dive duration, thereby reducing the daily costs of commuting to the seafloor (Hays et al., 2002b). This neutral buoyancy dive was considered an optimal energy-saving strategy for sea turtles that inhabit inter-nesting sites with limited food availability. In cases where food availability is a limitation, the diving strategies followed by sea turtles are different than those conducted in locations where the food is abundant (see below). Collectively, these studies suggest that Ascension Island green turtles are forced to fast during the nesting season due to a lack of food resources, and therefore, by necessity, exhibit a *capital* breeding strategy.

In contrast to Ascension Island, research conducted on nesting green turtles at Tortuguero, Costa Rica, showed that four turtles sampled had food in their gut, despite the scarcity of marine plants in the area. Rather than seagrass or algae, other plants (freshwater and terrestrial plants) were found in their guts (Meylan, 1978). Further research demonstrated that not all breeding areas used by green turtles are unsuitable for their preferred food items. In Cyprus, a nesting area with abundant seagrass, two studies found substantial amounts of seagrass in the guts of four gravid females that had died during an inter-nesting period (Hays et al. 2002b; Godley and Broderick, unpubl. data). Gravid green turtles equipped with TDRs in Cyprus also displayed remarkably variable dive patterns and high activity levels (<20% of the time was resting; Hochscheid et al., 1999). Such patterns were attributed to extensive foraging, since sea turtles remained near the coast, spending 90% of the time in shallow waters (mean depth = 2.7 m), where they could take advantage of extensive seagrass beds near the nesting site (Hays et al., 2002b). Whereas green turtles in Cyprus move short distances and forage at shallow depths, larger movements between foraging and resting areas have been reported for green turtles at other locations (Bjorndal 1980; Brill et al. 1995). However, due to the local bathymetry, these long movements were not feasible in Cyprus (Hochscheid et al., 1999). Similar to leatherbacks, bathymetry plays an important role in the diving behavior of green turtles, making it challenging to decipher different underwater behaviors of turtles (resting, foraging, swimming) in different areas. All studies conducted on green turtles in Cyprus agreed that this nesting population actively feeds on seagrass, including data obtained from animal-borne cameras attached to two individuals (Fuller et al., 2009). Therefore, robust evidence obtained through multidisciplinary studies support the idea that the inter-nesting food intake rate of nesting green sea turtles in Cyprus is sufficient to be considered *income* breeders.

Multiple studies conducted in the Pacific Ocean suggested that green turtles in this region also feed during inter-nesting periods. Balazs (1980) found digested material in the digestive tracts of at least three gravid green turtles in Hawaii. Moreover, behavioral evidence obtained through TDRs indicated that the inter-nesting diving patterns recorded for green turtles in Taiwan displayed the characteristics of foraging dives (Cheng, 2009; Cheng et al., 2013). In Malaysia, data collected using radio and ultrasonic telemetry of three green turtles were interpreted as non-foraging behavior because of the restricted movements of the green turtles close to the coast, compared to other studies conducted elsewhere where sea turtles exhibited larger displacements (Liew and Chan, 1992).

Heron Island, Australia, represents an important foraging area for three of the six sea turtle species found in the Great Barrier Reef, as well as an important nesting site for green turtles (Sternberg, 1981; Limpus et al., 1984; Limpus and Reed, 1985). The presence of both nesting and non-nesting green turtles around Heron Island suggests that nesting turtles may have access to foraging opportunities throughout the season. Studies conducted on Heron Reef have reached similar but not identical conclusions.

After analyzing the stomach-lavage contents of gravid green turtles, Forbes (1996) concluded that, despite the abundant algae available, nesting females ingest only small amounts. The author suggested that additional studies were required to confirm whether or not gravid females feed during inter-nesting periods, even if the rates are low. Such studies were carried out less than a decade later. Using physical and physiological evidence (gut content and blood analysis, respectively), Hamann et al. (2002, 2003) determined that the green turtles nesting at Heron Island are *capital* breeders. This conclusion was supported by the fact that 18 out of 20 gravid turtles examined for stomach contents had empty digestive tracts, while the remaining two turtles presented only a green liquid with no signs of food boluses or identifiable material (Hamann et al., 2002). The authors concluded that for supplemental foraging to be efficient, the amount and quality of the items ingested should provide enough nutritional value to compensate for the metabolic costs associated with their respective acquisition and digestion. Blood analysis showed a decrease of plasma triglyceride concentrations towards the end of the season, while plasma protein concentration increased (Hamann et al., 2002, 2003). The authors attributed such changes to a metabolic shift towards protein catabolism, suggesting that fasting was taking place. However, no dramatic increase in corticosterone at the end of the nesting season was observed in multiple sea turtle species (Whittier et al., 1997; Rostal et al., 2001; Hamann et al., 2002), a physiological response that is commonly observed in fasting birds with depleted body reserves (Cherel et al., 1988 a, b).

Blood chemistry analyses were undertaken on 48 Caribbean green turtles nesting on Aves Island, Venezuela (Prieto-Torres et al., 2013). Whereas most of the parameters that were analyzed fell within the ranges of values for non-breeding green turtles from the Caribbean and Atlantic population, values for glucose, cholesterol and triglyceride presented different values. Glucose observation were considered low when compared to reference values of healthy males or non-breeding females, which other studies interpreted it as a reduce food intake during the nesting season (Casey et al., 2010; Anderson et al., 2011). The authors highlighted the fact that most of those reference values were obtained outside of the nesting season, which implies that the animals were captured by diving or from a boat (Aguirre et al., 1995; Aguirre and Balazs, 2000; Montilla et al., 2008), potentially generating stress and contributing to increased glucose values. Conversely, high plasma lipid values (cholesterol and triglyceride) may be attributed to egg formation. Similar explanations were given for calcium and phosphorus values because the mobilization of such elements takes place during the egg production in reproductive females. Therefore, the authors concluded that green turtles nesting on Aves Island are healthy and in good nutritional condition (Prieto-Torres et al., 2013). Although the authors did not refer to any of the inter-nesting feeding strategies specifically, it seems unlikely that the observed nutritional conditions would not concur within a fasting population subjected to nutritional stress. Despite the authors do not they provide any strong evidence to corroborate neither the *capital* or the *income* breeding strategy, they present different arguments that could suggest that these turtles may be feeding near Aves Island during the nesting season to supplement the energy and nutrients lost during egg formation and deposition.

Additional support for an *income* breeding strategy comes from the island of Guadeloupe in French West Indies, located just east of Aves Island. Delcroix et al. (2009) necropsied a gravid green turtle that was found stranded. The turtle's gastrointestinal tract was full of seagrass, indicating that she was eating prior to death and supports for the idea that an *income* breeding strategy may be feasible for the nearby nesting populations on Aves Island.

With the aim of assessing the frequency with which green turtles nesting on Raine Island, Australia, forage during the inter-nesting period, Tucker and Read (2001) analyzed the stomach contents from 101 females during two consecutive seasons. A total of 40 individuals had fresh food (boli with a minimum wet weight of 200 g) in their guts. The most common item found was a calcareous green alga (*Halimeda* sp.). Though it has a low nutritive value, *Halimeda* may provide an important source of calcium for eggshells, which are formed just prior to the eggs being laid (Miller et al., 1997). Moreover, 60 of the females with gut contents present contained either anemones or jellyfish, two taxa with high water content. Based on these results, Tucker and Read (2001) concluded that green turtles nesting on Raine Island exhibit intermittent feeding during the nesting season. That conclusion was supported by the fact that the boli found in the digestive tracts were spatially separated, instead of being continuous, as would be expected in an individual that fed constantly (Forbes, 1996). It has also been hypothesized that continuous feeding might be limited due to the space occupied by reproductive organs (maturing eggs); space for a full gut would not be available during breeding season (Bjorndal, 1997). However, intermittent feeding would necessitate less space in the body cavity, while still allowing turtles to ingest and assimilate energy and nutrients needed for reproduction and reproductive products (i.e., eggshells and contents).

More recent investigations also coincide with *income* breeding. A study performed in the Republic of Seychelles, an area with rich seagrass habitat adjacent to the nesting beach, confirmed that gravid green turtles forage during inter-nesting periods. Stokes et al. (2019) examined the gut contents of breeding and non-breeding females, as well as adult males from the same population. The authors found no significant difference between males and non-breeding females. However, gravid females presented a more restricted and poorer diet, clearly not determined by food availability. Such dietary restrictions showed a lower preference for seagrass (58 ± 8% of the diet in gravid females compared to 95 ± 2% in males and non-breeding females) and larger amounts of substrate, macroalgae, and a high presence of calcareous green algae *Halimeda* sp. (Stokes et al. 2019). Like other green turtle populations around the world, green turtles nesting in the Seychelles may restrict or change their diet, but do not fast during the nesting season and therefore should not be considered strict *capital* breeders.

The green turtle is one of the most studied sea turtle species in the world, allowing the scientific community to compare different populations and exclude the inter-specific variability. Gut content analyses have demonstrated that two different nesting populations (Cyprus and Ascension Island) can exhibit opposite behavior according to the characteristics of the environment. This demonstrates that not only should populations be considered independently, but also there is nothing physiological that prevents them from feeding during the breeding season. However, despite the evidence that some sea turtles ingest food during the inter-nesting intervals, the extent to which this feeding contributes to the reproductive process is not known.

4.2.4 LOGGERHEADS

Loggerheads are the second largest Chelonid sea turtle. They are mainly carnivorous with powerful muscles and robust jaws that enable them to feed on hard-shelled benthic invertebrates (i.e., crabs, conch, whelks), but they also frequently feed on jellyfish. Loggerheads can undertake extensive trans-oceanic migrations of over

12,000 km and, like several other species of sea turtles, they have a worldwide distribution (Dodd 1988).

In Georgia, U.S., satellite telemetry showed that after each nesting event loggerheads moved directly to isolated areas with stable, hard-bottom substrate (Stoneburner 1982). Because these areas included abundant food resources (i.e., hard and soft corals, mollusks, crustaceans, and sponges), the author suggested that such movements were likely related to foraging opportunities. Post-nesting movements of loggerheads in the northern Gulf of Mexico show different patterns but support similar inferences. Hart et al. (2013) found that nesting females satellite tagged in the Florida Panhandle and Alabama make long-distance movements between nesting events (>100 km). Because such movements are energetically expensive, the authors suggested that gravid females could be foraging during inter-nesting periods to compensate costs (Hart et al., 2013). Both studies provided a weak indication that loggerheads in the northwest Atlantic could be feeding during the nesting season (i.e., *income* strategy).

Physiological evidence obtained through blood samples suggest contradictory results. In Georgia, blood samples were used to compare the health status of foraging and nesting turtles (Deem et al., 2009). On average, the 31 nesting females had lower values for glucose, potassium, and blood urea nitrogen (BUN) than foraging turtles, leading the authors to conclude that the health condition of nesting females was likely associated with a state of fasting. In Florida, U.S., and Brazil, blood samples were also analyzed from nesting loggerheads (Smith, 2010; Goldberg er al., 2011; Perrault and Stacy, 2018). Although a number of analytes decreased or increased across the nesting season (i.e., pre-albumin, globulins, chloride), the values remained within normal reference ranges according to species and life stage. However, changes observed in hematologic, plasma biochemical, immune function, and antioxidative analytes led the authors to suggest that those nesting populations rely on fat stores obtained in their foraging grounds, prior to migration to the nesting sites. Contrary to what has been reported for leatherbacks (Plot et al., 2013) and hawksbills (Goldberg et al.,2013), no seasonal trends in BUN were observed (Perrault et al., 2014). However, as seen in previous sections, such results might not always be a conclusive indication of fasting, but a normal consequence of the high energy requirements and complexity of reproduction. Whereas blood analyses in Atlantic loggerheads indicate some degree of nutritional stress during the breeding season, the possibility that some feeding occurs cannot be ruled out.

In the northeast Atlantic, physiological evidence based on RNA/DNA ratios obtained for 57 nesting loggerheads in Cape Verde indicated that their physiological condition decreased during the nesting season (Vieira et al., 2014). The authors suggested that a considerable decrease in food intake may influence biochemical parameters such as RNA and DNA concentrations. This conclusion is contrary to a recent study on 18 nesting loggerheads at the same location that showed that reductions in mean body mass throughout the nesting season was lower than expected (only 0.53±0.33 kg in 15 days) and that 28% of the females sampled actually increased their body mass (Pina et al., 2020). Despite being a clear sign that weight lost during egg deposition is being regained, it is necessary to consider the origin of such weight gain. Possible mechanisms for weight gain include consumption of food or water ingestion (Southwood et al., 2005). Whereas at least part of the weight gain may come from food intake during the inter-nesting periods, more detailed studies are needed to confirm if and how much food is consumed.

In the Mediterranean, as in Georgia, loggerheads that were satellite tracked after nesting in Cyprus moved to areas suitable for foraging (Houghton et al., 2002). Inter-nesting habitats used by loggerheads support ecosystems where they could obtain considerable amounts of food. More recently, a comparative study of the biochemical blood parameters and hormone levels of foraging, nesting, and injured loggerheads conducted in Turkey showed that, despite the fact that parameters such as triglycerides, cholesterol, lipoprotein, magnesium, and phosphorus were higher in nesting females, urea was higher in foraging sea turtles. Lower plasma urea levels in nesting females was the only measured parameter that could be correlated to fasting (Sözbilen and Kaska, 2018). Nevertheless, the combination of these two studies provides little evidence in support of either a *capital* or *income* breeding strategy for Mediterranean loggerheads.

Nine loggerheads nesting in Japan were monitored during inter-nesting periods using T_{GT} (Tanaka et al., 1995). In all cases, T_{GT} data indicated occasional decreases in temperature. Contrary to results obtained for leatherbacks (Casey et al., 2010), the authors could not conclude if the decreases in temperature were due to foraging or drinking. Therefore, although it seems evident that some kind of ingestion takes place during inter-nesting periods, more research on the quantity of water ingested during drinking versus feeding behaviors is required to better interpret changes in gastrointestinal temperature. As the only study conducted on loggerheads in the Pacific

Ocean, the inter-nesting behavior and feeding strategy of Pacific loggerheads remains inconclusive with regard to the *capital* versus *income* breeding dichotomy.

Loggerheads, like hawksbills (see below), tend to inhabit inter-nesting areas in which their preferred food items are typically available. While gut content analyses have confirmed that green turtles sometimes feed while in their inter-nesting areas, the same evidence does not exist for loggerheads. Physiological data for loggerheads suggest nutritional stress associated with reproduction, which is not surprising, but does not provide convincing evidence that loggerheads exclusively fast during the breeding season either. New studies that test not only if turtles feed during inter-nesting intervals, but also if the amount of food obtained provides energy used for reproduction, are needed to answer the *capital-income* breeding question in loggerheads as well as other sea turtle species.

4.2.5 HAWKSBILLS

Hawksbills use the tropical areas of the world for both foraging and nesting (Witzel, 1983). They inhabit nearshore foraging grounds, especially coral reef and mangrove habitats, where their narrow beaks allow them to reach food in cracks and crevices. Despite being omnivorous, their diet is mainly comprised of sponges (Meylan, 1998).

Behavioral evidence has shown that hawksbills nesting in both Barbados and USVI have specific resting sites and remain in those sites during the inter-nesting period (Starbird et al., 1999; Hill et al., 2017). Moreover, individuals show fidelity to certain resting sites during subsequent inter-nesting periods (Walcott et al., 2012). Satellite telemetry of gravid hawksbills in Barbados showed that between nesting events most individuals moved parallel to the coastline where hard coral habitat is located, but they were rarely recorded swimming offshore (Walcott et al., 2012). All routes between nesting beaches and resting sites were reef habitat, a suitable ecosystem for hawksbills to forage. Especially in resting areas, where females spent the majority of dives (90%) traveling to the bottom (Walcott et al., 2013), the habitat was comprised of completely or partially hard coral cover. Similar results were obtained for hawksbills nesting in the Republic of Seychelles, where four TDRs and one IMASEN were attached to nesting females (Houghton et al., 2008). Despite the availability of food, most authors assumed turtles were fasting, interpreting bottom time as resting instead of foraging (Houghton et al., 2008; Walcott et al., 2012; Hill et al., 2017). These assumptions are difficult to reconcile when studies on immature individuals suggested that similar dive profiles created by foraging turtles across a region of seagrass could just as easily be interpreted as resting on the bottom (Hazel et al., 2009). Dive profiles alone can neither confirm nor deny the possibility that hawksbills feed during the breeding season.

Visual, morphological, and physiological evidence suggests that hawksbills do not eat between nesting events. Cameras attached to 17 nesting females in Barbados confirmed that turtles in this population preferred to remain in shallow habitats with high relief structures covered with dense biotic assemblages, especially with hard corals, during their inter-nesting intervals (Walcott et al., 2014). However, the authors concluded that such habitats offered opportunities for resting but not for foraging, arguing that females did not show any preference for sites with higher sponge abundance. The authors also suggested that females exhibit a behavioral tradeoff between the quality of a site (i.e., relief, biota) and the energy expenditures needed to get there. Because the priority during the breeding season is not feeding, females tend to seek out areas that are relatively close and that are more conducive to resting and egg production (i.e., areas with water temperatures and places to hide from males and predators). For this reason, authors suggested that gravid females may prefer inter-nesting sites that are more structured and richer in biota, but low in sponges, rather than sites with abundant sponges, therefore, to assume fasting. However, more research is encouraged since lower density of the preferred item (sponges) may not imply strict fasting.

Sea turtles exhibit a significant difference between pre-oviposition and post-oviposition body mass. Body mass changes were analyzed for 36 nesting hawksbills in Brazil (Santos et al., 2010), with a mean decrease of 1.6 kg between two nesting events. The study used 79.6 kg as the average mass of a nesting hawksbill (first oviposition mass) and assumed that if no mass recovery took place during inter-nesting intervals a turtle would lose from 20.7-34.5% of the initial pre-oviposition mass after 3-5 clutches (1,183 $kJ \cdot d^{-1}$ per clutch). The overall energy expenditures (OEE), which includes total daily energy consumption (egg production plus maintenance), were calculated based on theoretical minimum (2,413 $kJ \cdot d^{-1}$), maximum (5,663 $kJ \cdot d^{-1}$), and mean (4,053 $kJ \cdot d^{-1}$) estimated energy requirements. The result obtained for the OEE average value was similar to the estimated energy consumption required during the inter-nesting interval

(4,213 kJ · d^{-1}). The authors indicated that food was available nearby, but they concluded that if the average value obtained in their study is correct, the mass recovery observed between nesting events was likely due to rehydration rather than energy obtained through feeding (Santos et al., 2010), thereby supporting a capital breeding strategy.

Physiological evidence obtained by analyzing hormone concentrations (leptin and ghrelin) of 41 nesting hawksbills in Brazil also indicated that hawksbills do not feed during inter-nesting periods (Goldberg et al., 2013). Leptin is an appetite-suppressing protein and ghrelin is a hunger-stimulating peptide, and both hormones influence energy intake and body mass in vertebrates. Nesting hawksbills in Brazil showed a decrease in leptin and an increase in ghrelin concentrations over the nesting season, suggesting that females were fasting during the breeding season, and the changes in leptin and ghrelin would stimulate foraging during or after the post-nesting migration (Goldberg et al., 2013). However, complementary studies seem to indicate that leptin and ghrelin also have an important role in reproduction, possibly influencing hormone levels such testosterone and follicle-stimulating hormones (El-Eshmawy et al., 2010). More work is needed to understand the physiological roles of these hormones in sea turtles before conclusive interpretations can be made from such analyses.

Globally, there seems to be some consensus that hawksbills do not feed during inter-nesting periods despite available food resources in their inter-nesting habitats. This lies in contrast to green turtles, which tend to feed (at least to some degree) during inter-nesting periods when foraging opportunities are available. Why green turtles would feed opportunistically while hawksbills would not is difficult to reconcile. This apparent difference may be the result of differences in methodology of the published studies. The strongest inferences for green turtles come from gut content analyses, which provided direct evidence of feeding. However, no gut content analyses exist for hawksbills and inferences come mostly from indirect methods (TDRs, body mass changes, and hormones). For hawksbills, more research is required to test the assumption that they fast during their reproductive stage.

4.2.6 OLIVE RIDLEYS

Olive ridleys are one of the smallest and most numerous sea turtles in the world, and they are primarily found in tropical regions. They are omnivorous, feeding on a wide variety of items such as mollusks, crabs, lobsters, tunicates, and algae. Large, synchronized nesting events, called arribadas, occur on some beaches in Costa Rica, Mexico, and India, where tens of thousands of nesting females emerge from the ocean to nest over the course of several days. However, many olive ridley populations also nest solitarily. Unlike other species of sea turtles, female olive ridleys can nest every year.

Little is known about the inter-nesting behavior of olive ridleys, and only two studies addressed their feeding strategies. Physical and behavioral evidence both suggest that this omnivorous species may feed between nesting events. Gut contents of 10 gravid females stranded in Brazil were analyzed, and four of them had food in their stomachs, mainly composed of benthic prey (i.e., crabs, mollusks, and cephalopods; Colman et al., 2014). Because more than half of the turtles did not present food in their digestive tracts, it can be concluded that only some turtles in this olive ridley population feed during inter-nesting events. However, it should be considered when in the inter-nesting interval the female stranded. Eggs in an early development stage take up less space and the female may tend to feed more. Conversely, later in the inter-nesting interval, when the eggs are almost or totally developed, they take more space and the turtle may decrease or even stop feeding (Bjorndal, 1997). The study also showed that males and females differed in the proportion with food in their guts (four of 10 females or 40% vs. three of four males or 75%) (Colman et al., 2014), but the authors did not mention if the stranded turtles were ill or injured, which could have affected their feeding behavior. However, the ability to conclude that these patterns are representative of true intake differences is limited by the small sample size.

Satellite transmitters attached to two nesting olive ridley females in the Wessel Islands, Australia, revealed that both individuals travelled long distances during the inter-nesting intervals (125 and 200 km), which is behavior that can either be associated with foraging, searching for alternative nesting sites or avoiding predators (Hamel et al., 2008). The authors suggested that foraging behavior was more common prior to the day they nested, since more time spent on the surface and erratic movements were recorded. Moreover, dive durations decreased several days prior to nesting, leading to the interpretation that sea turtles were saving energy in preparation for egg laying (Hamel et al., 2008).

With so little data, it is difficult to determine whether olive ridleys tend to be *capital* or *income* breeders. Current data, however, suggest that olive ridleys may exhibit a mixed or opportunistic foraging strategy during inter-nesting intervals. There is evidence that some populations and/or individuals may eat during the nesting season, while also trying to conserve energy by reducing dive time. Future satellite tracking studies should consider comparing the times spent in distinct activities between breeding females, non-breeding females, and males according to the environmental traits of their habitats. Moreover, studies on olive ridleys would benefit from the application of new technologies, such IMASEN and animal-mounted camera systems.

5. Conclusions and Future Directions

5.1 CONCLUSIONS

The idea that sea turtles are strict *capital* breeders has been accepted as a conventional wisdom for decades. The high energy demands of their reproduction, large bodies, low metabolic rates, and long migrations away from productive foraging areas to distant breeding grounds may all have led the scientific community to assume that female sea turtles use only "stored energy for reproduction" (Stearns 1989, 1992). This assumption has repeatedly been presented as fact in the literature. Consequently, many studies refer to sea turtles as *capital* breeders without presenting direct scientific evidence, and instead cite convenient sources or give more emphasis on results that support a *capital* breeding strategy.

It is reasonable to assume that most energy used to produce lipid-rich egg yolks comes from fat stores obtained at foraging grounds. Female sea turtles sequester considerable fat stores during the months and years prior to breeding migrations presumably because breeding areas do not provide opportunities to acquire additional dietary lipids. However, producing egg yolks is only one requirement of reproduction, and there is a relatively poor understanding of the energetic and nutrient requirements of sea turtles during the other components of reproduction, including migration, nesting, and inter-nesting periods. As identified in this study, evidence that individuals in some populations do in fact ingest food during the breeding season highlights an important question with regard to Stearns' original definitions: do all *capital* breeders fast? Presumably, as Sterns (1989) already suggested, individuals could use stored energy for reproduction (a *capital* breeding strategy), but also feed occasionally or opportunistically to acquire supplemental energy or required nutrients (e.g., calcium) used in reproduction (an *income* breeding strategy). Therefore, according to the definitions provided by Stearns (1989, 1992), sea turtles would fall somewhere in between *capital* and *income* breeders, as part of a *continuum*.

For now, data seem to indicate that this inter-nesting feeding strategy *continuum* is used for sea turtles. It may be considered that the nesting population of Ascension Island could be at one edge of the *continuum*, since all the evidence showed that gravid females nesting there are forced to fast because of the extreme environmental circumstances. On the other end of the *continuum*, gut content analysis of green turtles nesting in Cyprus demonstrate they feed in the nearby abundant seagrass meadows. Other sea turtle populations are at different positions along the *continuum* according to their level of ingestion and energy use. For example, loggerheads nesting on Wassaw Island, appear to fall closer to *capital* breeders because SIA (this study) and previous studies carried out on blood analysis indicate that this nesting population relies mainly on fat stores obtained prior migration.

During the breeding season, sea turtles employ many strategies to minimize energy expenditure. Therefore, the question remains why turtles would not feed when food is available, assuming the intake would compensate reproductive costs and/or complement stored energy. For some populations the energy stored prior migration could be enough to support vitellogenesis, round-trip migrations between foraging grounds and breeding areas, mating, and nesting activities without endangering the individual's survival. Also, as ectotherms, sea turtles have metabolic rates low enough to allow them to fast for long periods of time, and in some cases decreases in body mass during the nesting season seems to indicate that females are consuming internal energy stores. However, even if all those statements are correct, they are not universal. For this reason, it is imperative to acknowledge each population, if not each individual, as different, since the factors that might promote feeding or fasting could be determined not only by the characteristics of the nesting site, but the initial conditions presented by the sea turtle at the beginning of the breeding season.

Results obtained from blood samples of loggerheads nesting on Wassaw suggest that they decrease food intake and rely on stored energy during the breeding season, lending support to a *capital* breeding strategy. Conversely, values obtained from yolk would likely identify dietary behavior on foraging grounds, prior to the nesting season, and current fasting would not be identified since no significant change was detected on nitrogen. Moreover, the fact that δ^{13}C values of yolk decreased over the season may suggest that sea turtles use fat reserves to produce the yolk of their eggs.

In conclusion, a thorough review of the literature has revealed that the question of *capital* vs *income* breeding strategies in sea turtles should not be viewed as a simple dichotomy of one or the other. Rather, sea turtles exhibit a range of strategies that fall along the *continuum* between the two extremes. The energetic and nutritional benefits to sea turtles from feeding during inter-nesting periods remain to be quantified.

Knowledge of the extent of such benefits will guide efforts to protect inter-nesting habitats and improve understanding of reproductive cycles of sea turtles.

5.2 FUTURE DIRECTIONS

Sea turtles have a worldwide distribution, resulting in vast areas where there is little or no information. The inter-nesting feeding strategy remains unknown for some of the world's largest nesting populations (e.g., loggerheads in Oman, green turtles in Hawaii, olive ridleys in Mexico, and leatherbacks in New Guinea). Moreover, research on the inter-nesting behavior of flatbacks and Kemp's ridley is needed, as there are no studies on this topic in either species. Additionally, studies that attempt to quantify the differences in inter-nesting food intake amongst populations are recommended. For those populations (or individuals) that demonstrated evidence of food intake during the inter-nesting period, it would be useful to further study whether the additional energy is used during the reproductive period or not.

Studies on energetic dynamics based on energy budgets (Sousa et al., 2008, 2010; Kooijman, 2010; Jusup et al., 2016; Marn et al., 2017) that accurately determine energy intake and expenditure of specific individuals would be a step forward to strengthen conclusions, since knowledge obtained so far do not provide accurate information on whether sea turtles actually use the energy acquired during breeding for reproductive products (i.e., eggs) or reproductive activities (i.e., nesting or diving). Models based on physiological energetics, would consider not only the sea turtle energy budget, but also important parameters such as temperature and food availability, providing population or even individual-specific perspectives.

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