REVIEW

Growth rates of adult sea turtles

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ABSTRACT: Indeterminate growth, i.e. growth that persists throughout life, is common in long-lived reptiles. Because fecundity and body size tend to be correlated in such species, individuals face a life-history trade-off at sexual maturity. Saturation tagging and intensive monitoring at nesting grounds can potentially provide opportunities to accumulate data on individual measurements and reproductive output. Until recently, however, shortcomings from these methods have prevented the testing of theories on resource allocation between growth and reproduction at sexual maturity in wild populations of sea turtles. Here, we review the state of knowledge of growth rates in adult sea turtles and potential life-history trade-offs. We found that post-maturity growth rates varied among ocean basins. They appeared highest in the Atlantic Ocean for both green turtles *Chelonia mydas* and hawksbill turtles *Eretmochelys imbricata*, and highest in the Mediterranean Sea for loggerhead turtles *Caretta caretta*. For other species, there are too few studies at present to allow for intraspecific comparison. Additionally, we found no significant difference in mean female compound annual growth rates among species and ocean basins. Although captive studies have provided great insight into changes in energy allocation at sexual maturity and life-history trade-offs, this review highlights the lack of data on wild animals regarding changes in post-maturity growth rates and reproductive output over time. Such data are desirable to further our understanding of energy allocation, growth and ageing in wild sea turtles. They are further required to assess the status of species and to understand population dynamics for both conservation and management.

KEY WORDS: Somatic growth rates · Indeterminate growth · Size at sexual maturity · Age at sexual maturity · Life-history trade-off · Energy allocation · Sea turtle

INTRODUCTION

Organisms need to partition finite resources among competing needs, such as somatic maintenance, growth and reproduction throughout life (Gadgil & Bossert 1970). Trade-offs occur so that fitness of any one trait cannot be maximised without leading to a cost in others (Stearns 1989). Sexual maturity represents the age, size or stage at which individuals can reproduce (Bernardo 1993). As somatic maintenance has priority over competing needs (Zera & Harshman 2001), maturation requires a change in resource allocation from growth to reproduction (Bernardo 1993). In contrast to species with determinate growth, where growth halts at sexual maturity, growth persists throughout life in species with indeterminate growth (Kozłowski 1996), as demonstrated in fish (Charnov & Berrigan 1991), clams (Heino & Kaitala 1996), freshwater turtles (Congdon et al. 2013) and desert tortoises (Nafus 2015). The Von Bertalanffy growth curve (von Bertalanffy 1957) is believed to be the best approximation of growth, defined as the increase in skeletal size, in indeterminate growers. It assumes that no maximum size exists and that growth rates decay with age.

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Because fecundity and body size tend to be correlated in indeterminate growers (Olsson & Shine 1996), individuals face a life-history trade-off at sexual maturity (Heino & Kaitala 1999). Indeed, sexual maturity represents a balance between the benefits and costs associated with early versus late age at maturation and is influenced by growth rates during development (Stearns 1989). The most common maturation norm is one in which, when growth is rapid, organisms mature early at a large size, whereas when growth is slow, sexual maturity is delayed and a smaller size at sexual maturity (SSM) is reached (Stearns & Koella 1986). In contrast, a less common maturation norm describes an inverse relationship between growth rates during development and age at sexual maturity (ASM; Stearns & Koella 1986, Day & Rowe 2002), such that either: (1) when growth is rapid, organisms mature early, benefit from increased survival to first reproduction and decreased generation time, at the cost of a smaller body size (Bernardo 1993), which is likely to lead to a reduction of lifetime reproductive output (Shine 1980), or (2) when growth is slow, individuals mature late, benefit from increased body size and competitive ability (Bernardo 1993), at the cost of a decrease in survival probability to first reproduction (Gadgil & Bossert 1970). Finally, a rare maturation norm is one in which maturation is the result of a genetically determined size or age threshold (Bernardo 1993).

Carry-over effects are considered drivers of fitness differences (reviewed in Harrison et al. 2011). They occur as a result of changes in extrinsic factors between 2 time periods affecting an individual's body condition and therefore its fitness. Capital breeders, such as species that undergo long migrations to breed or species that provide parental care, fuel reproduction using resources accumulated during non-breeding years (Jönsson 1997, Price 2017). In such species, the cost of reproduction is high and individuals can skip reproduction in a given year in order to increase future reproduction (Harris & Ludwig 2004, Rivalan et al. 2005, Rideout & Tomkiewicz 2011). Kozłowski (1996) proposed that, in seasonal environments, indeterminate growth is the optimal strategy, allowing individuals to alternate allocation of resources in excess of somatic maintenance between growth and reproduction, such that reproduction is maximised over time. Thus, post-maturity growth phases are expected to vary temporally (e.g. Harris & Ludwig 2004, Baron et al. 2013, Folkvord et al. 2014), declining with age and occurring straight after breeding events in order to increase future reproduction (Heino & Kaitala 1996, Kozłowski 1996).

ASM and SSM inherently result from the interaction of intrinsic and extrinsic factors influencing somatic growth prior to sexual maturity (Bernardo 1993). Although empirical evidence (e.g. Choat et al. 2006, Armstrong & Brooks 2013, Tucek et al. 2014) suggests that sexual maturity is frequently the result of a genetically determined size threshold (Roff 2000), differences in growth curves, SSM and ASM are likely to arise between individuals (Bernardo 1993). Indeed, enormous variation in both ASM and SSM can be observed within and among species (e.g. Miaud et al. 1999, Madsen & Shine 2006, Bjorndal et al. 2013a, 2014, Campos et al. 2013, Folkvord et al. 2014, Avens et al. 2015, 2017). As males are less readily accessible to study, knowledge of reproductive biology in sea turtles remains highly female-biased (Rees et al. 2016). Whilst little is known about the maturation process of males (Blanvillain et al. 2008, Ishihara & Kamezaki 2011, Arendt et al. 2012, Avens et al. 2015), post-maturity growth rates (Avens et al. 2015), estimates of ASM (Schwanz et al. 2016; however, see Avens et al. 2017 for absence of a difference in ASM) and life-history trade-offs, as a consequence of sexual selection (Adler & Bonduriansky 2014), are likely to be sex specific.

ASM and SSM are fundamental life-history parameters needed to assess the status of species and to understand population dynamics for both conservation and management (Chaloupka & Musick 1997, Heppell et al. 2003). Sea turtles are an excellent study system in which to investigate post-maturity growth rates and life-history trade-offs, being slow-growing with a 'bet-hedging' life-history strategy (Avens et al. 2015) and delaying sexual maturity for decades (Van Houtan et al. 2014, 2016). However, most work investigating growth rates in sea turtles has focused on early life stages prior to sexual maturity (Bjorndal et al. 2000b, 2016, Casale et al. 2009, Kubis et al. 2009, Sampson et al. 2015). Estimates of ASM have been generated by parametric growth curves (e.g. von Bertalanffy, logistic and Gompertz) using juvenile and sub-adult somatic growth data and estimates of SSM derived from mean female size at nesting grounds (reviewed in Avens & Snover 2013). Sea turtles, however, exhibit sex-specific growth functions as a result of sexual dimorphism, with males showing slower growth rates than females, resulting in differences in SSM, with mature males being on average smaller (Chaloupka & Limpus 1997, Limpus & Chaloupka 1997, Diez & van Dam 2002, Godley et al. 2002a, Chaloupka et al. 2004; Table 1; but see Dodd 1988 and Kamezaki 2003 for larger SSM of males; see Avens et al. 2015 for

Table 1. Summary of published studies of wild male and female post-maturity growth rates per species and ocean basin. No data available for Kemp's ridley and olive ridley turtles. Curved carapace length (CCL): mean ± SD (range). Estimated clutch frequency: mean ± SD (range; n). CMR: capture-mark-recapture. Interbreeding interval: mean ± SD (range; n). CCL growth rates: mean ± SD (range; n). N/A: not applicable. Numbers refer to these references: [1]Broderick et al. (2003); [2*]oceanic foragers, Hatase et al. (2013); [2**]neritic foragers, Hatase et al. (2013); [3]Hatase et al. (2004); [4]Goshe et al. (2010); [5]Bjorndal et al. (1999); [6]Troëng & Chaloupka (2007); [7]Carr & Goodman (1970); [8]Chaloupka & Limpus (1997); [9]Limpus (1993); [10]Limpus (1979); [11]Santidrián Tomillo et al. (2009); [12]Santidrián Tomillo et al. (2007); [13]Price et al. (2004); [14]Dobbs et al. (1999); [15]Bell & Pike (2012); [16]Bjorndal et al. (1985); [17]Snover et al. (2013); [18]Pilcher & Ali (1999); [19]Limpus (2007); [20]Limpus et al. (1984); [21]Parmenter & Limpus (1995)

Species	Ocean basin and study area	Year of study	CCL (cm)	Method	Estimated clutch frequency	Interbreeding interval (yr)	CCL growth rates (cm yr^{-1})
Caretta caretta	Mediterranean Sea						
	♀ E Mediterranean (N Cyprus)	1992–2000	73.6 ± 4.6 (63–87)	CMR nesting beach	1.9 ± 1.2 (168)	2 (median) (1–6; 44)	0.36 ± 0.57 (−1.0 to 1.8; 38)[1]
	Pacific Ocean						
	♀ NW (Minabe, Japan)	1992–2001	(79.3–102.3)[a]	CMR nesting beach	3.6 ± 1.0 (1–5; 31)[2*] 4.3 ± 1.2 (1–6; 229)[2**]	2.7 ± 1.0 (1–6; 78)	0.27 (−1.89 to 1.57; 78)[3,9]
Chelonia mydas	Atlantic Ocean						
	♀ NW (Virginia to Florida, USA)	N/A	(106.1–110.0)[b,c]	Skeletochronology	N/A	N/A	0.30 (0–1.75; 9)[4,9]
	♀ Caribbean Sea (Limón, Costa Rica)	1956–1968	106.1 ± 5.3 (76.9–126.7)[d]	CMR nesting beach	2.8 (1–6)[5]	2.95 ± 0.88 (1–6)[6]	0.42 (179)[7,9]
	Mediterranean Sea						
	♀ E Mediterranean (N Cyprus)	1992–2000	91.5 ± 6.3 (77–106)	CMR nesting beach	3.0 ± 1.4 (97)	3 (median) (2–6; 46)	0.11 ± 0.46 (−1.0 to 1.3; 51)[1]
	Pacific Ocean						
	♀ Coral Sea (Qld, Australia)	1974–1991	(100–105)	CMR, laparoscopy at foraging grounds	N/A	N/A	0.12 ± 0.04 (±SE)[8]
	♂	1974–1991	(95–99)	CMR foraging grounds	N/A	N/A	0.07 ± 0.02 (±SE)[8]
	♂ Coral Sea (Heron Island and Wistari Reefs, Qld, Australia)	N/A	(90–102)	CMR foraging grounds	N/A	2.08 ± 1.14 (1–5; 24)[9]	0.14 ± 0.11 (−0.3 to 2.6; 12)[10]
Dermochelys coriacea	Pacific Ocean						
	♀ NE (Guanacaste, Costa Rica)	1993–2002	147.0 ± 5.9 (133–165)	CMR nesting beach	9.45 ± 1.63 (61)[11]	3.7 ± 0.2 (1–9)[12]	0.2 ± 0.05 (−1.5 to 2.0; 152)[13]
Eretmochelys imbricata	Atlantic Ocean						
	♀ Caribbean Sea (Limón, Costa Rica)	1955–1977	82.0 ± 3.9 (72.4–94.0)	CMR nesting beach	2.1	3.0 (3–6; 4)	0.3 ± 0.3 (−0.9 to 2.7; 4)[16]
	Pacific Ocean						
	♀ SW (Milman Island, Qld, Australia)	1991–1995	81.6 (63.5–91.9)	CMR nesting beach	2.54 ± 1.44 (1–7; 1525)	3.4 ± 0.62 (22)	0.27 ± 0.19 (0–0.7; 22)[14]
	♀ Coral Sea (Qld, Australia)	1997–2008	>80	CMR, laparoscopy at foraging grounds	N/A	N/A	0.17 (−0.9 to 2.7; 45)[15]
	♀ N (Hawaii, USA)	N/A	>86.5[d,e]	Skeletochronology	N/A	N/A	0.30 (9)[17,9]
	♀ NW (Sabah, Malaysia)	1985–1997	82.1[d]	CMR nesting beach	2.7	1.84	0.24[18,9]
Natator depressus	Pacific Ocean						
	♀ SW (Peak Island, Qld, Australia)	1980–1991	94.0 ± 2.60 (85.5–100.0)[19]	CMR nesting beach	2.84 ± 0.78 (1–4; 43)[20]	2.2 ± 0.44 (1–5; 215)	0.012 ± 0.009 (±SE; 440)[21]

[a]Converted from straight carapace length (SCL) using equation in Peckham et al. (2011). [b]Converted using equation in Goshe (2009). [c]Adult green turtles nesting at an average of 99.1 cm SCL (105.2 cm CCL) (Van Buskirk & Crowder 1994). [d]Converted using equation in Bjorndal et al. (2008). [e]Adult hawksbill turtles nesting at an average of 82.3 cm SCL (89 cm CCL) (Seitz et al. 2012). [f]Three females and 6 individuals of unknown sex. [g]Converted from original SCL growth values

faster growth in sub-adult and adult male logger-head turtles and larger SSM; see Avens et al. 2017 for absence of a difference in SSM).

Sea turtle research has primarily been focused at nesting beaches (Schroeder & Murphy 1999). Although saturation tagging and intensive monitoring at nesting grounds provide the perfect opportunity to accumulate data on individual measurements and reproductive output, such methods have shortcomings which, until recently, have prevented testing, for example, of theories on resource allocation between growth and reproduction at the onset of sexual maturity in wild populations of sea turtles (Bjorndal et al. 2013a, Avens et al. 2015, 2017). Indeed, despite being relatively inexpensive compared to in-water surveys, such programmes remain costly, labour intensive, logistically challenging and difficult to maintain for sufficiently long periods of time to be able to follow individuals throughout their reproductive lifespans (Sims et al. 2008). In addition, their effectiveness decreases as population size increases unless the study area ranges widely (Witt et al. 2009) to encompass flexibility in natal homing (Lee et al. 2007, Nishizawa et al. 2011, Lohmann et al. 2013, Brothers & Lohmann 2015) and nest site fidelity (Tucker 2010, Weber et al. 2013). Although some populations are recovering (da Silva et al. 2007, Bellini et al. 2013, Weber et al. 2014, García-cruz et al. 2015), sea turtles remain conservation-dependent and require intensive management (Wallace et al. 2011, Casale & Heppell 2016). Hamann et al. (2010) highlight that reproductive biology and population ecology are 2 priority research categories for sea turtles, and these require methods to accurately age individuals and determine ASM. Additionally, Rees et al. (2016) reiterate that there is still much to be done in this regard.

This comprehensive review explores the state of knowledge of growth rates in adult sea turtles from the onset of sexual maturity as well as potential life-history trade-offs. Although some researchers consider ASM, age at first mating and age at first reproduction identical, it is possible for females to start reproducing 2–4 yr after reaching sexual maturity (Limpus 1990, Rostal 2005, Caillouet et al. 2011; some individuals in Bjorndal et al. 2013a, 2014). However, for the purpose of this review, ASM and age at first observed nesting are considered to be the same.

We searched for peer-reviewed literature on ISI Web of Knowledge and Google Scholar for the terms growth, growth rates, maturity, age, adult, survival, survivorship, nesting, reproductive output and trade-off. Along with each search term was included the word 'turtle'. Additionally, we searched for publications in the Marine Turtle Newsletter (www.seaturtle.org/mtn/, last accessed January 2016), Synopses of Biological Data for marine turtles (www.fao.org/fishery/org/fishfinder/3, 5/en) and Proceedings of the Annual Symposia on Sea Turtle Biology and Conservation (www.internationalseaturtlesociety.org/#/Proceedings, last accessed January 2016). This review is structured in 6 major sections: life-history dichotomies, age–size trade-off, energy allocation shift, post-maturity growth rates, breeding frequency and population recovery.

LIFE-HISTORY DICHOTOMIES

Sea turtles are highly mobile and juveniles may move among multiple foraging habitats before reaching sexual maturity (Bolten 2003b, McClellan & Read 2007, Fukuoka et al. 2015). Environmental differences between foraging habitats will influence habitat use and foraging strategies of individuals and may, in turn, result in differential growth, survival, SSM and ASM (Peckham et al. 2011). While movement between alternative habitats may incur physiological, morphological and behavioural costs as individuals adapt to their new environment, these may be outweighed by the benefits associated with more suitable environmental conditions (Werner & Gilliam 1984, Bolten 2003b). Juveniles that move between habitats might benefit from higher growth rates due to higher food availability and quality and thus larger SSM (Werner & Gilliam 1984, Bolten 2003a, Snover et al. 2010). Although Gross (1984) argued that, for evolutionary strategies to be stable, fitness of alternative strategies should be equivalent, with reproductive output being positively correlated with SSM in sea turtles (Van Buskirk & Crowder 1994), life-history dichotomies may ultimately result in differential fecundity both within and between populations and species (Hatase et al. 2013, Ceriani et al. 2015).

Inter-specific differences in developmental life-history patterns exist within the sea turtles (reviewed in Bolten 2003b). Whereas flatback turtles (*Natator depressus*) develop entirely in neritic waters (Walker & Parmenter 1990), leatherback (*Dermochelys coriacea*) and many populations of olive ridley (*Lepidochelys olivacea*) turtles complete their development entirely in oceanic waters (Bolten 2003b). In contrast, green (*Chelonia mydas*), loggerhead (*Caretta caretta*), hawksbill (*Eretmochelys imbricata*), Kemp's ridley (*Lepidochelys kempii*) and remaining populations of olive ridley turtles generally exhibit

an intermediate life-history pattern (Bolten 2003b). Hatchlings and small juveniles from the latter species inhabit oceanic waters for an undetermined period of time, feeding on nutrient-poor epipelagic prey and experiencing relatively slow growth (Bjorndal et al. 2000b, Bolten 2003a). Upon reaching a size threshold (Bjorndal et al. 2000b, Bolten 2003b), large juveniles undergo what was long thought to be a marked, non-reversible ontogenetic shift to neritic waters, feeding on more abundant, nutrient-rich benthic prey (Hawkes et al. 2006, Snover et al. 2010). Although this change of environment may come at the cost of an increase in predation risk (Bolten 2003b), it could result in as much as a 30% increase in juvenile growth rates (Snover et al. 2010), thus appearing highly advantageous. Recent studies, however, suggest that the ontogenetic shift is both facultative, with some individuals remaining in oceanic waters throughout their life cycle (Hatase et al. 2002, Hawkes et al. 2006, Ramirez et al. 2015), and reversible, with some individuals returning to oceanic waters (McClellan & Read 2007, McClellan et al. 2010, Ramirez et al. 2015).

The decision to transition from oceanic to neritic waters is likely to result from a combination of body size, metabolic rate and density-dependent effects on food availability and growth rates (Olsson et al. 2006). Smaller individuals experiencing higher growth rates in oceanic waters are believed to remain there until they reach sexual maturity, whereas larger individuals with higher metabolic rates and low growth rates would disperse to neritic water in search of better growth conditions (Bjorndal et al. 2000a, Hawkes et al. 2006, Hatase et al. 2010). In turn, these individuals would compensate for previously low growth conditions by performing catch-up growth (Bjorndal et al. 2003, Roark et al. 2009, Bjorndal & Bolten 2010; but see Snover et al. 2007b for absence of compensatory growth). Smaller individuals, however, are potentially constrained to oceanic waters due to their size, which limits their diving capacity (Mori 2002, Hawkes et al. 2006). Thus, life-history dichotomies are maintained through differences in body size, which, in turn, influence habitat use and foraging strategy, leading to differences in SSM (e.g. Hatase et al. 2010, 2013, Peckham et al. 2011).

AGE–SIZE TRADE-OFF

Rare are the studies that observe wild individuals of known age due to the challenges associated with studying sea turtles throughout their life cycle and ageing individuals (e.g. Bell et al. 2005, Caillouet et al. 2011, Tucek et al. 2014, Rees et al. 2016). To overcome this problem, a number of studies have investigated growth rates using captive individuals of known age (e.g. Jones et al. 2011, Bjorndal et al. 2013a, 2014). Unlike wild individuals, captive individuals can be measured at regular time intervals both before and after sexual maturity. Such studies have investigated how growth rates vary over the course of an individual's lifetime, providing great insight into life-history trade-offs and the shape of growth curves (e.g. Bjorndal et al. 2013a, 2014).

Captive individuals reared under similar conditions exhibit a wide range of age, size, mass and body condition at sexual maturity (Bjorndal et al. 2013a, 2014). Whilst a study of 47 captive green turtles *Chelonia mydas* found no evidence for an age–size trade-off, as the 2 individuals that matured at the greatest age had both the largest and second to smallest SSM (Bjorndal et al. 2013a), this trade-off was observed in a study of 14 captive Kemp's ridley turtles *Lepidochelys kempii*, potentially as a result of a greater variation in ASM in the latter species (Bjorndal et al. 2014). Additionally, the detection of an age–size trade-off in green turtles could have been hampered by the mixed genetic origin of individuals (Bjorndal et al. 2013a) and group feeding of a high quality diet (Bjorndal et al. 2013a, 2014).

Within-species variation in SSM in wild individuals is greater than that observed in captive species (Witzell 1983, Dodd 1988, Marquez 1994, Hirth 1997, Tiwari & Bjorndal 2000, Caillouet et al. 2011, Avens et al. 2015, 2017; see Table 2), potentially due to greater variation in juvenile growth rates within and between populations and species (Chaloupka & Limpus 1997, Kubis et al. 2009, Bell & Pike 2012, Avens et al. 2017). Carry-over effects resulting from early environmental conditions, such as those associated with differences in habitat use or productivity at foraging grounds, have been speculated to be linked to differences in juvenile growth rates within and among populations and thus differences in SSM (Eder et al. 2012).

In contrast, data on variation in ASM in wild populations are scarce (Caillouet et al. 2011, Avens et al. 2015, 2017) and whether an age–size trade-off would be observed remains to be shown. The authors are aware of only one study in a wild population of loggerhead turtles *Caretta caretta* (Tucek et al. 2014) which found no evidence for such a trade-off. Variation in juvenile growth rates could be dampened if individuals performed compensa-

Table 2. Summary of captive studies of female post-maturity growth rates per species and ocean basin. No data available for loggerhead, leatherback, olive ridley and flatback turtles. Curved carapace length (CCL): mean ± SD (range; n). CCL growth rates: mean ± SD (range; n). CMR: capture-mark-recapture. Numbers refer to these references: [1]Bjorndal et al. (2013a); [2]Kawazu et al. (2015); [3]Bjorndal et al. (2014); [4]Marquez (1994)

Species	Ocean basin and study area	Origin of individuals	CCL (cm)	Method	CCL growth rates (cm yr^{-1})
Chelonia mydas	Atlantic Ocean Caribbean Sea (Grand Cayman, UK)[1]	Derived from eggs collected at Ascension Island, Suriname and Tortuguero, Costa Rica between 1968 and 1972	101.8 ± 7.1 (87.6–119.4; 33)	CMR	0.94 ± 0.73 (0–3.81; 33)[a]; 0.38 ± 0.21 (0.13–0.95; 31)[b]
Eretmochelys imbricata	Pacific Ocean NW (Okinawa, Japan)[2]	Derived from eggs collected at Zamami Island between 1993 and 1994	84.0 ± 3.3 (79.2–90.3; 23)[c]	Ultrasonography	1.08 (23)[d,i]
Lepidochelys kempii	Atlantic Ocean Caribbean Sea (Grand Cayman, UK)[3]	Derived from eggs collected at Tamaulipas, Mexico in 1979	55.2 ± 3.7 (47.0–61.0; 12)	CMR	0.4 ± 0.4 (0–1.3; 12)[e]; 0.3 ± 0.2 (0–0.5; 10)[f]
	Gulf of Mexico (Mexico)[4,g]	Unknown	66.6 ± 2.4 (63.7–71.1; 11)[h]	CMR	0.96 (−2.35 to 6.32; 11)[i]

[a]Four-year duration after first nesting. [b]Average across ages (9–20 yr duration after first nesting). [c]Three-year duration after the onset of follicular development. [d]Converted from straight carapace length using equation in Bjorndal et al. (2008). [e]Three-year duration after first nesting. [f]Average across ages (6–11 yr duration after first nesting). [g]Extracted from Table 15 in Marquez (1994), excluding females with recapture interval of <11 mo (n = 2). [h]Converted using equation in Snover et al. (2007b). [i]Converted from original straight carapace length growth values

tory growth — which in some cases they appear to do (e.g. Bjorndal et al. 2003, Roark et al. 2009, but see Snover et al. 2007b) — or if slow-growing individuals experienced increased mortality pressures as they remain in the vulnerable size classes for longer (Bjorndal et al. 2013a, 2014). This, in turn, would reduce the variation in ASM and SSM, which could hamper the detection of an age–size trade-off in wild populations.

ENERGY ALLOCATION SHIFT

The onset of vitellogenesis occurs a few years prior to reaching sexual maturity (Saka et al. 2014) and requires some energy to be diverted away from somatic growth towards follicular development until breeding occurs (Kawazu et al. 2015). Using ultrasonography, Kawazu et al. (2015) observed a reduction of growth just after the onset of vitellogenesis in captive hawksbill turtles *Eretmochelys imbricata*. Similarly, pre-maturity growth rates were negatively correlated with ASM in both captive green (*Chelonia mydas*) and Kemp's ridley (*Lepidochelys kempii*) turtles (Bjorndal et al. 2013a, 2014). In both species, whereas one group of individuals shifted to negligible growth the same year as they reached sexual maturity, the other group shifted to negligible growth at least 2 yr prior to laying their first clutch (Bjorndal et al. 2013a, 2014). This, coupled with changes in pre-maturity growth rates, suggests that the shift in energy allocation occurs a few years prior to reaching sexual maturity.

The delay observed when captive individuals shift to negligible growth and first reproduction could result from turtles being less efficient at shifting resources away from skeletal and mass growth towards reproduction (Bjorndal et al. 2013a) or could result from individuals in poorer condition delaying reproduction to accumulate sufficient resources to exceed a certain threshold (Kwan 1994). The decision to nest in a given year is likely to result from the combination of an assessment of body condition and favourable environmental conditions (e.g. Baron et al. 2013). For example, annual breeding probability is correlated with sea surface temperatures (Chaloupka 2001, Saba et al. 2007, Mazaris et al. 2009, del Monte-Luna et al. 2012), which may correlate with favourable conditions.

Whilst the shift in energy allocation starts a few years prior to sexual maturity, it persists for an unknown number of years after. Changes in energy allocation can be inferred from changes in post-

maturity growth rates. In both Bjorndal et al. studies (2013a, 2014), growth rates in the first 3 to 4 yr after sexual maturity were higher than those averaged throughout post-maturity years, regardless of SSM. This, coupled with the abrupt decrease in spacing of lines of arrested growth (LAG) in bone cross-sections in females of known history (Avens et al. 2015), supports the idea that, once females reach sexual maturity, resources are gradually diverted from growth towards reproduction (Hatase et al. 2004).

POST-MATURITY GROWTH

Skeletochronology and capture-mark-recapture (CMR) studies have provided estimates of post-maturity growth rates for wild populations, which are summarised in Table 1. Although skeletochronology derives growth rates from estimates of female length from humerus diameter (reviewed in Avens & Snover 2013), comparison of lengths and growth rates obtained from such a technique and those collected and calculated at nesting beaches proves skeletochronology to be a powerful technique to estimate growth rates (Snover et al. 2007a, Goshe et al. 2010, Avens et al. 2015, 2017).

Growth rates (Table 1) ranged from 0.20 to 0.42 cm yr^{-1} for green turtles *Chelonia mydas* and appeared higher in the Atlantic Ocean than in the Mediterranean Sea and Pacific Ocean. Similarly, growth rates appeared higher in the Atlantic Ocean than in the Pacific Ocean for hawksbill turtles *Eretmochelys imbricata*, ranging from 0.17 to 0.30 cm yr^{-1}. For loggerhead turtles *Caretta caretta*, growth rates ranged from 0.20 to 0.47 cm yr^{-1} and appeared higher in the Mediterranean Sea than in the Atlantic Ocean and Pacific Ocean. It should be noted, however, that growth rates for the Atlantic Ocean (0.20 cm yr^{-1} in Bjorndal et al. 2013b; 0.47 cm yr^{-1} in Avens et al. 2015) are not included in Table 1 and Fig. 1 because they are averages from 10 cm bins which can include both large juveniles and adults, assuming that females are sexually mature at >80 cm straight carapace length (SCL). Data are lacking altogether for olive ridley turtles *Lepidochelys olivacea* and only one growth measurement was available for leatherback (*Dermochelys coriacea*; 0.20 cm yr^{-1}), flatback (*Natator depressus*; 0.012 cm yr^{-1}) and Kemp's ridley turtles (*Lepidochelys kempii*; 0.6 cm yr^{-1}; Avens et al. 2017). Again, it should be noted that the value for Kemp's ridley turtles is not included in Table 1 and Fig. 1 as it is an average from 10 cm bins, which can include both large juveniles and adults, assuming
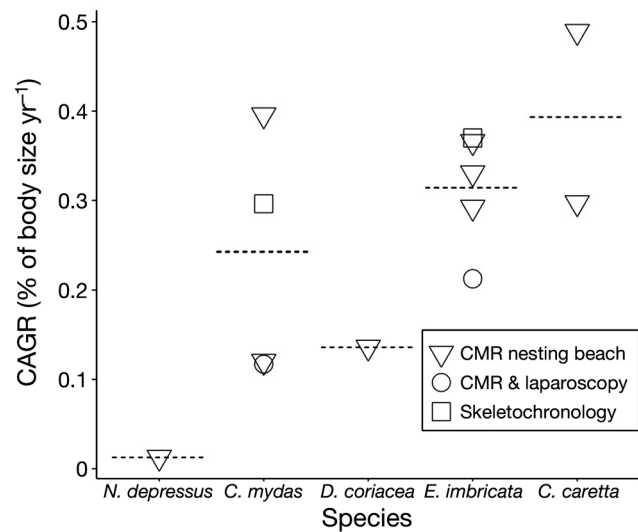

Fig. 1. Female compound annual growth rates (CAGR) for wild populations. Dashed lines represent the mean for each species. CAGR were calculated from values presented in Table 1. The arithmetic mean of range values was used when mean CCL was not available. CMR: capture-mark-recapture. See Table 1 for genus names

that females are sexually mature at >60 cm SCL (Caillouet et al. 2011).

Post-maturity growth rates in sea turtles are low regardless of ocean basin or species in both captive and wild populations (Table 1) and were correlated with neither SSM, ASM nor body condition in captive species (Bjorndal et al. 2013a, 2014). As expected under indeterminate growth, in the first 3 to 4 yr following sexual maturity, individuals grew more rapidly before growth decreased and became negligible (Bjorndal et al. 2013a, 2014; Table 1). Similar temporal analyses of post-maturity growth rates are needed in wild populations, as all studies reporting post-maturity growth rates have averaged values across years without taking into account factors such as years since first reproduction. Additionally, differences in resource use between oceanic and neritic foragers are likely to lead to foraging-ground-specific growth curves and post-maturity growth rates.

In order to be better able to compare growth rates across populations and species and to account for individuals maturing at different sizes, female compound annual growth rates were calculated from Table 1 for wild populations and for each species as a percentage of body size per year. When comparing hawksbill, green and loggerhead turtles for which there are more than one data point, there is no significant difference in mean female compound annual growth rates among species (Kruskal-Wallis, H_{10} =

10, p > 0.05) or ocean basins (Kruskal-Wallis, H_2 = 1.35, p > 0.05). Regardless of the large variation in SSM at nesting beaches, post-maturity growth rates appear to follow a similar pattern among species (Fig. 1). This would support findings from both captive and wild studies that suggest that post-maturity growth rates are correlated neither with SSM, ASM nor body condition (Bjorndal et al. 2013a, 2014, Avens et al. 2015). However, Avens et al. (2015) found lifetime mean growth rates to be correlated with both ASM and SSM in wild loggerhead turtles. Additionally, although sample size is very small, like juvenile growth rates, post-maturity growth rates appear to be sex specific in green turtles, with males exhibiting lower growth rates than females (Table 1; but see Avens et al. 2015 for faster growth in sub-adult and adult male loggerhead turtles). More data for wild individuals, however, are needed, across both species and sex, to further investigate both of these emerging trends.

Inter-individual differences in responses to seasonality play a role in the duration of both nesting seasons and time spent at foraging grounds (Chaloupka 2001). Vitellogenesis and follicular development are seasonal, occurring around 8–10 mo prior to the breeding season (Rostal et al. 1998) and happen in parallel with lipid deposition (reviewed in Hamann et al. 2003). With reproduction occurring every 2–4 yr (Miller 1997), individuals that remigrate sooner would have a shorter interval to partition resources between growth and restoring body condition. Although delaying reproduction in a given year to invest in growth should be advantageous and individuals with longer remigration intervals should exhibit higher growth rates, data from leatherback turtles *Dermochelys coriacea* show no such trade-off (Price et al. 2004). Changes in energy allocation appear independent of reproduction.

Seasonality might also help explain some of the variation in post-maturity growth rates. Whereas some individuals remain in colder waters throughout colder months, others migrate into warmer waters (Hawkes et al. 2007). At temperatures below 15°C, individuals in some populations have been observed to rest on the sea floor for extended periods of time, increasing their dive duration as sea surface temperatures decrease (Godley et al. 2002b, Hochscheid et al. 2005, Broderick et al. 2007). Resting dives allow individuals to conserve large amounts of energy (Hays et al. 2000), which could then be partitioned between growth and restoring body condition. In contrast, individuals that migrate out of colder waters might incur greater energetic costs, which could lead to reduced energy available for growth and restoring body condition. However, Hawkes et al. (2007) suggest that those individuals acquire sufficient energy to counteract such costs and that neither strategy confers a significant advantage with regards to reproduction. Nevertheless, as growth and temperature are inversely correlated (Balazs & Chaloupka 2004, Richard et al. 2014), individuals that do not migrate during colder months and reside in highly seasonal environments would be expected to exhibit lower post-maturity growth rates.

BREEDING FREQUENCY

The amount of resources invested in post-maturity growth decreases over time after sexual maturity, freeing increasing proportions of surplus energy available to maximise lifetime reproductive output (Kozłowski 1996, Rideout & Tomkiewicz 2011, Bjorndal et al. 2013a, 2014). Changes in reproductive efficiency or capacity with age have often been used to explain the difference in reproductive output between new and returning females (Stokes et al. 2014) and have been reported in multiple populations (e.g. Tucker & Frazer 1991, Hawkes et al. 2005, Beggs et al. 2007). Satellite tracking of both new and returning females, however, suggests that low site fidelity of new females is more likely to explain this pattern (Tucker 2010).

With migration being costly, females that delay reproduction should accumulate larger fat stores than females that remigrate sooner. In turn, those females would use a smaller proportion of their fat stores while migrating, which could result in increased clutch size or frequency (number of clutches per season) (Price et al. 2004). While data from leatherback turtles *Dermochelys coriacea* showed that females with longer remigration intervals do not have a greater reproductive output in a given season (Price et al. 2004), Stokes et al. (2014) found that female green turtles *Chelonia mydas* in Cyprus with remigration intervals of less than 3 yr laid 25% fewer clutches in a given season. These contradictory findings could result from variation in how clutch frequency was estimated or from geographical differences in resource availability (Tucker 2010, Weber et al. 2013). Indeed, the Mediterranean Sea is characterised by low levels of nutrients (Sarà 1985), which may constrain clutch frequencies when remigration intervals are shorter. Similarly, climatic variability is likely to dramatically change resources availability from year to year (Barber et al. 1996, Hays et al.

2005), resulting in changes in both remigration interval and clutch frequency (Broderick et al. 2001, Saba et al. 2007, Neeman et al. 2015).

While changes in energy allocation could help explain the variation in reproductive output over time, individual physiological differences and environmental factors might play a larger role. Indeed, increased energy assimilation efficiency, coupled with increased food availability and quality at foraging grounds, should result in a decrease in remigration interval (Hays 2000, Price et al. 2004, Ceriani et al. 2015). Similarly, should all foraging grounds be of equal quality, females with a shorter migration between foraging and breeding grounds will require shorter periods to acquire sufficient energy (Price et al. 2004).

Body size can influence foraging habitat use, which in turn influences remigration intervals and breeding frequency (Hawkes et al. 2006, Ceriani et al. 2015; Fig. 2). Adult female loggerhead turtles in Japan exhibit size-related differences in foraging habitat use, with smaller females foraging on nutrient-poor planktonic items in oceanic waters, requiring more

time to accumulate sufficient resources (Hatase et al. 2004). In contrast, not only do larger females have a shorter interbreeding interval, they also lay a greater number of larger clutches (Hatase et al. 2013). Although similar foraging dichotomies have been documented in other populations and species (Hawkes et al. 2006, Hatase et al. 2006, Seminoff et al. 2008, Reich et al. 2010, Watanabe et al. 2011), they appear to be facultative. For example, telemetry studies in Cyprus showed that nearly all loggerhead turtles are neritic foragers despite their unusual small size (Snape et al. 2016).

Exactly why life-history dichotomies have evolved in sea turtles remains unclear, as they do not appear to be evolutionary stable. Indeed, settling in oceanic, rather than in neritic, waters appears to be suboptimal for reproducing females as explained above. Eder et al. (2012) speculated that life-history dichotomies have arisen because of immature juveniles settling opportunistically in previously encountered foraging grounds close to their natal beaches (Bowen et al. 2005, Casale et al. 2008), rather than in the best available ones, maturing there and returning to these
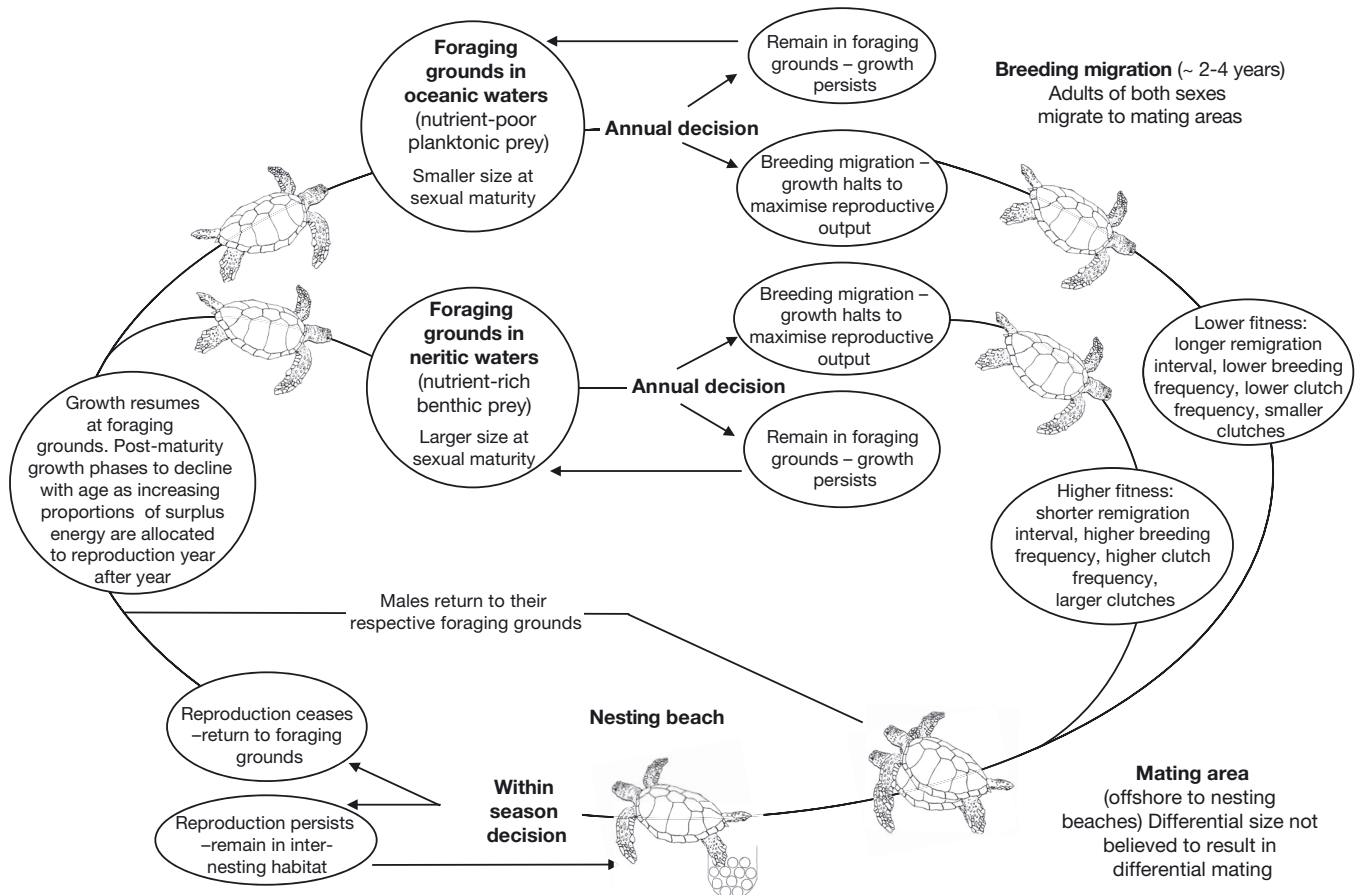

Fig. 2. Dichotomous adult life cycle for loggerhead, green, hawksbill, Kemp's ridley and olive ridley turtles

same foraging grounds with high fidelity as adults (Broderick et al. 2007, Marcovaldi et al. 2010). In turn, differences in settlement locations would lead to differences in growth rates and thus differences in SSM and, ultimately, fitness between oceanic and neritic foragers.

POPULATION RECOVERY

Many maturity threshold studies have focused on exploited fish stocks where both ASM and SSM were observed to vary with fisheries intensity and ASM and SSM of targeted fish (e.g. Ernande et al. 2004, Dieckmann & Heino 2007). As fish stocks were exploited, ASM and/or SSM decreased (Folkvord et al. 2014). Overexploitation of sea turtles likely resulted in the release of intraspecific competition pressures, which allowed individuals to exhibit higher growth rates and thus to mature at a larger size and potentially younger age if sexual maturity resulted from a size threshold (Bernardo 1993). However, it is unlikely that individuals matured at a younger age, as currently available data suggest that sexual maturity is not the result of a size threshold (Caillouet et al. 2011, Bjorndal et al. 2013a, 2014, Avens et al. 2015, 2017).

In contrast, population recovery and its associated density-dependent effects are likely to influence ASM and SSM through increased intraspecific competition for limited resources and habitat availability at foraging grounds. This, in turn, would lead to slower growth rates (Bjorndal et al. 2000a, Balazs & Chaloupka 2004), thus decreasing both SSM and mass at sexual maturity and increasing ASM (Heppell et al. 2007, Chaloupka et al. 2008), potentially explaining the observed decrease in mean female size at nesting grounds in a number of recovering populations (e.g. da Silva et al. 2007, Bellini et al. 2013, Weber et al. 2014).

Additionally, the reduction in mean SSM observed at nesting beaches could result from selection pressures on larger individuals as a result of fisheries interactions. For example, survival probabilities of loggerhead turtles *Caretta caretta* worldwide are higher for oceanic than for neritic juveniles (Casale et al. 2015, Casale & Heppell 2016). This, coupled with the higher levels of predation in neritic habitats (Bolten 2003b), could help explain the decrease in mean SSM observed at nesting beaches (e.g. da Silva et al. 2007, Bellini et al. 2013, Weber et al. 2014) and is likely to lead to a temporal variation in mean SSM. Whether ASM would follow a similar pattern seems

unlikely as oceanic and neritic foragers appear to reach sexual maturity at similar ages (Hatase et al. 2010).

CONCLUSIONS

Despite the need to refine population models and the long-term emphasis on obtaining life-history parameters for wild populations in order to assess the conservation status of sea turtles (Rees et al. 2016), unanswered questions remain. The cryptic life-history of sea turtles makes the necessary data difficult to obtain and most studies have therefore relied on indirect methods to estimate these parameters.

Captive studies (e.g. Bjorndal et al. 2013a, 2014) have provided great insight into life-history trade-offs and the shape of growth curves of some, but not all, individuals. They have shown changes in energy allocation to occur a few years prior to sexual maturity and to persist for an unknown number of years after. As expected under indeterminate growth, regardless of size at sexual maturity, captive individuals grow more rapidly in the first few years following sexual maturity before growth decreases and becomes negligible. Similar temporal analyses of post-maturity growth rates for wild populations and for both sexes are needed to refine existing growth curves, estimates of ASM and population dynamic models.

Furthermore, life-history dichotomies have been linked to differences in SSM as well as fitness differences in wild populations. However, it is yet to be demonstrated why these have evolved as they do not appear to be evolutionary stable. Additionally, mean SSM has decreased in recovering populations potentially as a result of a combination of selection pressures imposed by fisheries interaction as well as density-dependent effects associated with population recovery and habitat loss. Whether the observed decrease in mean SSM is due to younger and smaller females entering an older, stable nesting female size distribution due to population protection and recovery over several decades remains to be shown.

Finally, theories on resource allocation and life-history trade-offs from the onset of sexual maturity need to be tested in wild populations. Indeed, it is unclear whether captive species exhibit an age–size trade-off and whether such a trade-off would be observed in wild populations. We have yet to find a non-lethal method that can be used to accurately age all species of sea turtles and determine ASM. Such data are desirable to further our understanding of

energy allocation, growth and ageing in wild sea turtles. Furthermore, they are required to assess the status of species and to understand population dynamics for both conservation and management.

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