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Variation in reproductive output of marine turtles

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Abstract

Most marine turtle species are non-annual breeders and show variation in both the number of eggs laid per clutch and the number of clutches laid in a season. Large levels of inter-annual variation in the number of nesting females have been well documented in green turtle nesting populations and may be linked to environmental conditions. Other species of marine turtle exhibit less variation in nesting numbers. This inter-specific difference is thought to be linked to trophic status. To examine whether individual reproductive output is more variable in the herbivorous green turtle (*Chelonia mydas* Linneaeus 1758) than the carnivorous loggerhead (*Caretta caretta* Linneaeus 1758), we examined the nesting of both species in Cyprus over nine seasons. Green turtles showed slower annual growth rates (0.11 cm $year^{-1}$ curved carapace length (CCL) and 0.27 cm $year^{-1}$ curved carapace width (CCW)) than loggerhead turtles (0.36 cm $year^{-1}$ CCL, 0.51 cm $year^{-1}$ CCW). CCL was highly correlated to mean clutch size in both green ($R^2 = 0.51$) and loggerhead turtles ($R^2 = 0.61$) and maximal clutch size of green turtles ($R^2 = 0.58$). Larger females did not lay a greater number of clutches or have a shorter remigration interval than smaller females of either species. On average, the size of green turtle clutches increased and that of loggerhead turtles decreased as the season progressed. Individual green turtles, however, produced more eggs per clutch through the season to a maximum in the third or fourth clutch. In loggerhead turtles, clutches 1–4 were very similar in size but the fifth clutch was 38% smaller than the first. No individuals of either species were recorded laying more than five clutches. Green turtles may not be able to achieve their maximum reproductive output with respect to clutch size throughout the season, whereas only loggerhead turtles laying five clutches ($n = 5$) appear to become resource depleted. Green turtles nesting in years when large numbers of nests were recorded laid a greater number of clutches than females nesting in years with lower levels of nesting.

Keywords: *Caretta caretta*; *Chelonia mydas*; Clutch size; Green turtle; Loggerhead turtle; Mediterranean

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1. Introduction

Knowledge of the age, size, growth rate and relative reproductive output of individuals is fundamental in understanding the demography of a population. In reptiles, with indeterminate growth as adults, variation in reproductive output between individuals may be explained in part by adult body size (Olsson and Shine, 1996). Body size may set the upper limit to the number of eggs/clutch but this limit may not be reached if conditions are sub-optimal (Shine, 1992). In addition, high costs of reproduction may limit the reproductive output of individuals in some years thus delaying breeding may actually increase the life-time reproductive output of an individual should it survive until the next breeding season (reviewed by Shine, 1980).

Unlike most species of bird and mammal, marine turtles show no parental care of their eggs. Future breeding is not dependent on the survival of past clutches and it is unlikely that learned behaviour can contribute to any increase in reproductive success with age. Most species of marine turtle do not nest annually, but typically deposit two to four clutches of 50–150 eggs every 2 to 4 years (see reviews: Ehrhart, 1982; Hirth, 1997; Miller, 1997). Turtles have been shown to undertake long migrations to nesting grounds where optimal feeding areas may not always be found (Miller, 1997). Although many studies of marine turtles have shown a strong relationship between female body size and the number of eggs laid in a clutch (Ehrhart, 1982; Frazer and Richardson, 1986; Bjorndal and Carr, 1989; Pinckney, 1990; Hays and Speakman, 1991, 1992; Hirth, 1997; Van Buskirk and Crowder, 1994), few have examined the number of clutches laid by females in relation to their size (Frazer and Richardson, 1986; Johnson and Ehrhart, 1996), and fewer still have examined how these indices vary (Bjorndal and Carr, 1989).

Among species or populations, behavioural, morphological, physiological or dietary variations may all contribute to variation in reproductive output. In some species, such as the loggerhead turtle (*Caretta caretta*), levels of nesting numbers at a given rookery are usually similar from year to year (Ehrhart et al., 1996). In the green turtle (*Chelonia mydas*), numbers of nests fluctuate dramatically and are likely to be related to inter-annual variations in quantity and quality of forage driven by prevailing weather patterns (Limpus and Nicholas, 1987; Broderick et al., 2001).

To allow us to understand the within- and between-species variation in breeding startegies in marine turtles, more holistic studies are needed that examine not only the relationship between size of adults and clutches, but also the within- and between- season variation in individual reproductive output as well as the effects of size and time on these variables. Our 9-year study in Cyprus helps to fill some of these gaps by investigating the reproductive output of individual green and loggerhead turtles at the same nesting site.

2. Methods

2.1. Study site

We collected information on green and loggerhead turtles nesting on Alagadi Beach, Northern Cyprus (35°33′N, 33°47′E) between 1992 and 2000. The beach consists of two coves of 0.8-and 1.2-km length.

2.2. Data collection

The beach was monitored from 21:00 to 06:00 each night throughout the nesting seasons (late May until mid-August) of 1993–2000 by three to five groups of two observers (in 1992, the beach was monitored sporadically from early July). Females were externally tagged with plastic flipper tags from 1992 to 1998 and titanium flipper tags from 1998 to 2000. In addition, since 1997, females have been injected with passive integrated transponders (PIT tags; Godley et al., 1999). At each laying, curved carapace length (CCL) and curved carapace width (CCW) of females were measured three times and means were calculated for each female to use in analyses. For females laying more than one clutch in a season, overall mean of measurements was used, assuming no detectable growth would occur during the 10–12-week season. After laying, positions of nests were determined by triangulation from marker posts. Numbered markers were placed inside nests and external markers placed on screens above the nests. When turtles hatched, the contents of nests were excavated and hatched and unhatched eggs counted. Nests were not routinely excavated in 1992, thus data on clutch size were only collected 1993–2000.

2.3. Data analysis

To examine the reliability of our estimate of the number of eggs laid from counts of hatched fragments, 15 nests of each species were excavated immediately after laying and the eggs counted. These counts were compared with numbers of eggs estimated from these remaining nests after hatchlings had emerged. These nests were being moved to safer sites on the beach, because they were situated in sub-optimal sites.

Through mark and recapture of females within and between years, we were able to estimate the number of clutches laid by an individual in a season and calculate the remigration interval of the female (number of years between successive breeding seasons for an individual). Where a missed nesting was apparent (e.g. when an internesting interval (number of days between successive clutches being laid by an individual within a breeding season) of >18 days was recorded Broderick, 1997; Broderick et al., 2002), we corrected

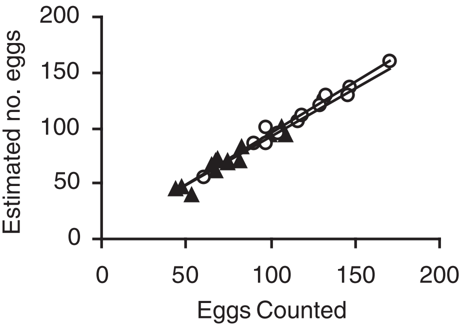

Fig. 1. The relationship between the number of eggs counted and the estimated number of eggs obtained by counting hatched fragments and unhatched eggs in 15 green turtle nests (open circles; $y=1.05x+1.04$, $R^2=0.98$) and 15 loggerhead turtle nests (shaded triangles; $y=1.06x+0.06$, $R^2=0.91$).

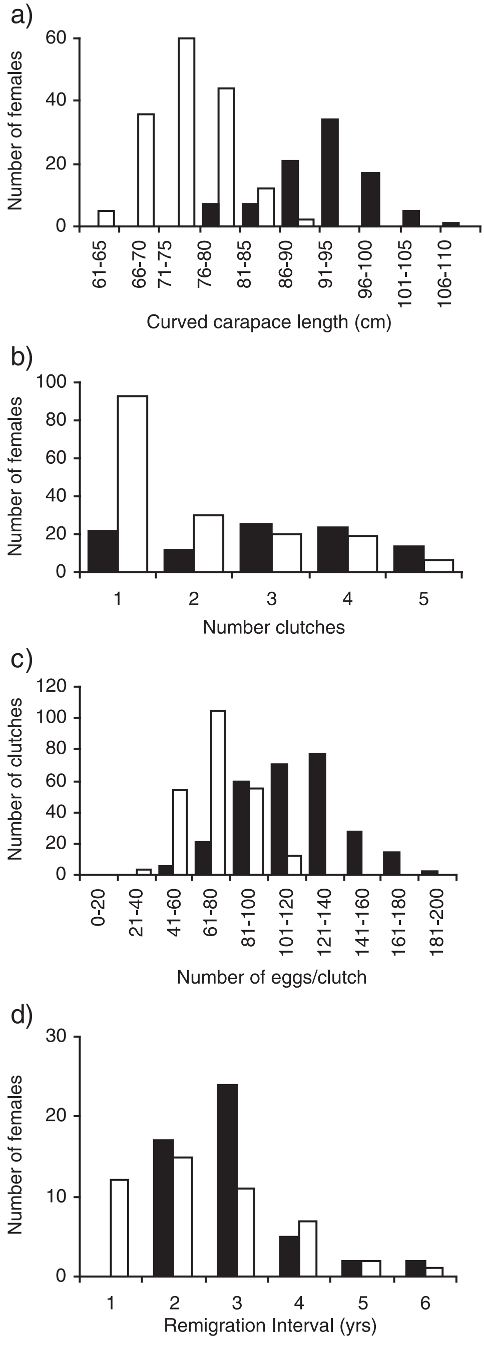

Fig. 2. Frequency distributions of (a) curved carapace length of females, (b) number of clutches laid, (c) clutch size, (d) remigration intervals. Shaded: green turtles; unshaded: loggerhead turtles.

the number of clutches laid accordingly and used these corrected numbers in analyses. The day of the season was calculated with day 1 being the day on which the first nest of that species was laid in a given year.

3. Results

3.1. Validation of methodology

We compared the counts of eggs at laying with counts of shell fragments from 30 clutches (15 of each species) which had been relocated and then subsequently hatched. The counts were highly correlated (green turtles: Regression $F_{1,15} = 485$, $P < 0.001$, $R^2 = 0.91$; loggerhead turtles $F_{1,15} = 130$, $P < 0.001$, $R^2 = 0.98$; Fig. 1) and the difference between the two measures was not related to clutch size ($F_{1,30} = 2.9$, $P > 0.05$, $n = 30$, $R^2 = 0.07$).

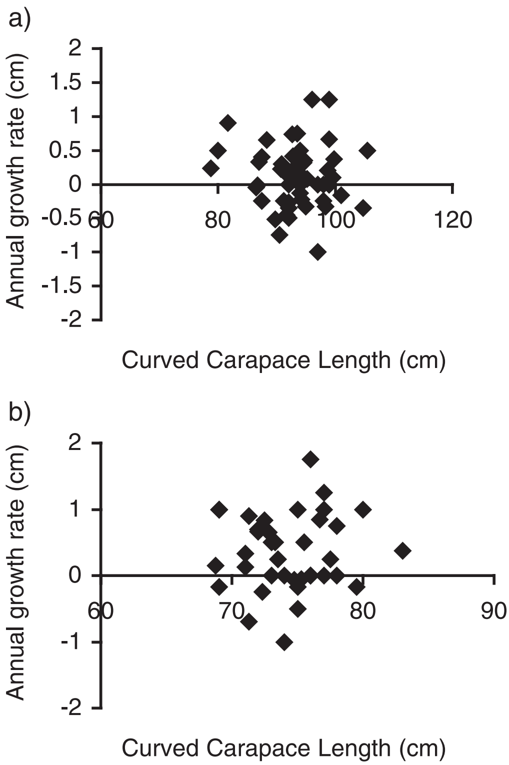

Fig. 3. Annual growth rate (cm) as measured by curved carapace length (CCL) for (a) green turtles and (b) loggerhead turtles.

3.2. Basic parameters

In Fig. 2, we present the data collected on female size, reproductive output (clutch size and number of clutches) and remigration intervals. Female green turtles ranged from 77 to 106 cm in CCL (mean ± S.D.; 91.5 ± 6.3 cm, $n=92$ females; Fig. 2a) and loggerhead females ranged from 63 to 87 cm CCL (73.6 ± 4.6 cm, $n=159$ females; Fig. 2a). High levels of variation were recorded in the reproductive output of females with green turtles laying on average 3.0 clutches (± 1.4, $n=97$; 1995–2000; Fig. 2b) of 115 eggs (± 27, range 51–199, $n=277$ clutches; Fig. 2c) and loggerhead females 1.9 clutches (± 1.2, $n=168$; 1995–2000; Fig. 2b) of 73 eggs (± 16, range 28–144, $n=229$ clutches; Fig. 2c). Greater variation in clutch size was recorded in green turtles with mean coefficient of variation for females laying three or more clutches of 0.17 (± 0.09, range 0.06–0.38 for 46 females) compared to 0.14 for loggerhead turtles (± 0.08, range 0.04–0.42 for 26 females). Variance in clutch size was not related to CCL (green turtles: $F_{1,38}=0.45$, $P>0.05$, $R^2=0.01$; loggerhead turtles $F_{1,18}=0.01$, $P>0.05$, $R^2=0.0$). The median remigration interval for green turtles was 3 years (Inter-quartile range (IQ) = 2–3, range 2–6, $n=46$; Fig. 2d) and for loggerhead females, the median remigration interval was 2 years (IQ = 2–3, range 1–6, $n=44$; Fig. 2d).

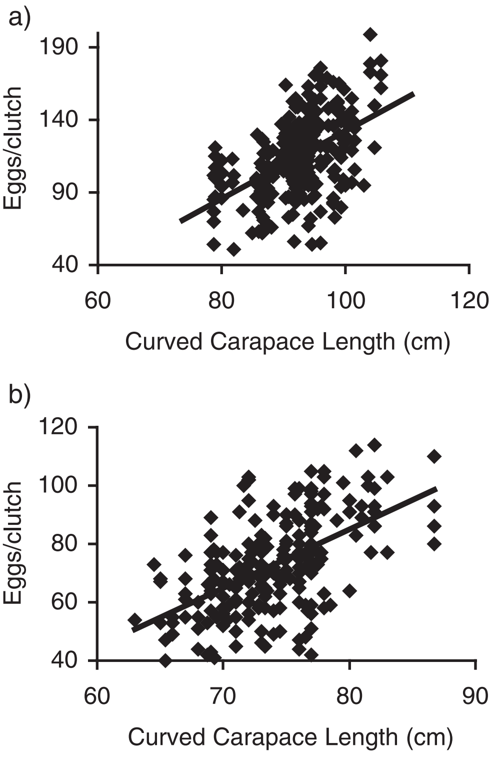

Fig. 4. Curved carapace length and number of eggs laid for (a) green turtles ($y=2.3x-100.95$, $R^2=0.25$) and (b) loggerhead turtles ($y=2.01x-75.7$, $R^2=0.29$). All raw data are included.

3.3. Growth of females

We examined the change in female size (curved carapace length and width) over time as a proportion of the original measurement. Negative values were included. The annual growth rate of females for green turtles at this site was 0.11 cm year^{-1} CCL ($\pm$ 0.46, $n=51$, range -1.0–1.3 cm year^{-1}) and 0.27 cm year^{-1} CCW ($\pm$ 0.77, $n=49$, range -0.9–2.9 cm year^{-1}). The annual growth rate for loggerhead turtles was 0.36 cm year^{-1} CCL ($\pm$ 0.57, $n=39$, range -1.0–1.8 cm year^{-1}) and for 0.51 cm year^{-1} CCW ($\pm$ 0.62, $n=38$, range -1.0–2.0 cm year^{-1}). We found no relationship between female CCL or CCW and annual growth rate for green (CCL: Regression, $F_{1,51}=0.26$, $P>0.05$, $R^2=0.0$; Fig. 3a; CCW $F_{1,49}=0.07$, $R^2=0.0$, $P>0.05$) or loggerhead turtles (CCL: $F_{1,39}=0.08$, $R^2=0.0$, $P>0.05$; Fig. 3b; CCW $F_{1,38}=0.0$, $R^2=0.0$, $P>0.05$). However, it should be noted that our sample sizes are small for this type of comparison.

3.4. Female size and reproductive output

To compare the reproductive output of females among years, it was first necessary to examine the relationship with adult size and correct for any variation resulting from this factor. Initially we examined the raw data set including all values. For green turtles 25% ($F_{1,277}=86.7$, $P<0.05$, $R^2=0.25$; Fig. 4a) and for loggerhead turtles 29% of the variation in clutch size was explained by CCL ($F_{1,229}=94.9$, $P<0.001$, $n=229$, $R^2=0.29$; Fig. 4b).

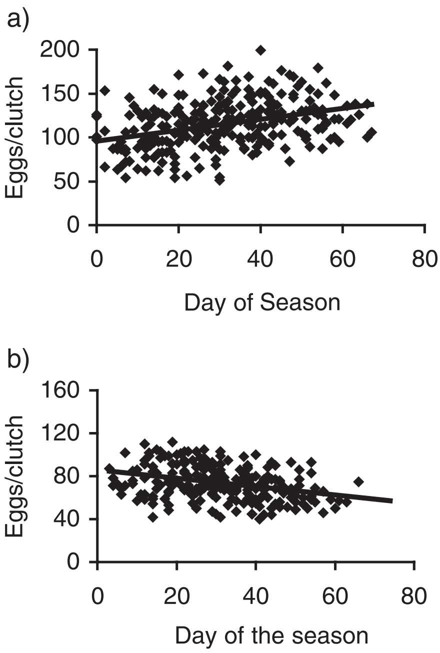

Fig. 5. The relationship between the day of the season on which a clutch was laid and the number of eggs in the clutch for (a) green turtles; $y=0.62x+95.9$, and (b) loggerhead turtles, $y=-0.4x+85.7$.

There was no significant difference in the size (CCL) of green turtles that laid three, four or five clutches (ANOVA $F_{2,62}=0.8$, $P>0.05$) or loggerhead turtles that laid two, three, four or five clutches;: $F_{3,74}=1.0$, $P>0.05$;). There was no significant difference in CCL among groups of either species remigrating at different intervals (green turtles: Kruskal–Wallis $H_{4,100}=6.0$, $p>0.05$; loggerhead turtles: $H_{5,43}=2.5$, $p>0.05$).

3.5. Within-season variation in reproductive output

At a population level, as the season progressed, clutch size of green turtles increased (Regression: $F_{1,227}=41.2$, $P<0.001$, $R^2=0.13$; Fig. 5a) and that of loggerhead turtles decreased ($F_{1,217}=28.1$, $P<0.001$, $R^2=0.11$, $n=217$; Fig. 5b). However, as females commonly lay multiple clutches in a breeding year, we calculated the percentage change in clutch size over the season for females laying three or more clutches in one season. In the green turtle, a gradual increase in clutch size was recorded with clutch order (Fig. 6a). For loggerheads, clutches 1–4 were very similar in size with clutch 5 ($n=5$) being on average 38% smaller than the first clutch of the season (Fig. 6b). We compared CCL with mean clutch size of green turtles that laid three or more clutches. In addition, we compared CCL

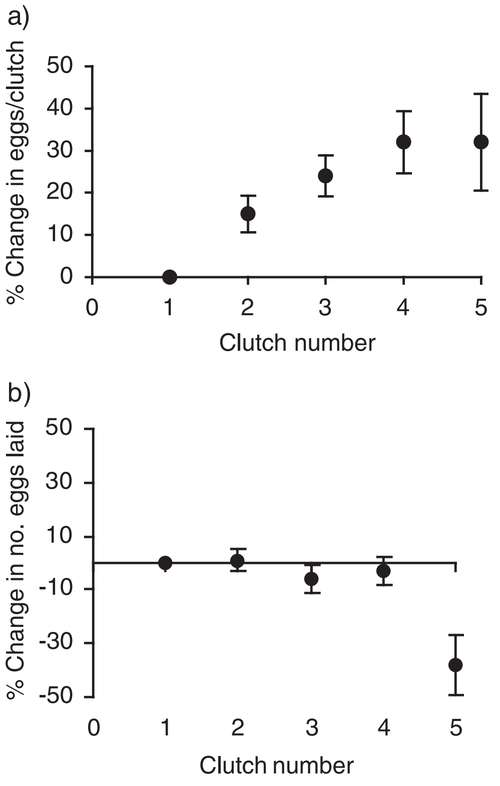

Fig. 6. For females laying three or more clutches, we examined the proportional change in number of eggs laid/clutch with clutch order for (a) green turtles and (b) loggerhead turtles. Error bars represent ± one standard error.

with mean clutch size of loggerhead turtles that laid two or more clutches within a season. If a female was recorded nesting in more than one season, we used her overall mean clutch size and CCL. For green turtles, the amount of variation in clutch size explained by CCL rose to 51% (Regression $F_{1,41} = 41.6$, $P < 0.001$, $R^2 = 0.51$) and for loggerhead turtles, this rose to 61% ($F_{1,29} = 40.5$, $P < 0.001$, $R^2 = 0.61$; Fig. 7b). As it appeared from our data that green turtles often laid smaller clutches at the start of their season and maximum clutch size was only reached by clutch 3 or 4 (Fig. 6b), we examined maximum clutch size of these females. If the same female was represented more than once, we included only her overall maximum clutch size. For green turtles 58% ($F_{1,41} = 57.6$, $P < 0.001$, $R^2 = 0.58$; Fig. 7a) and for loggerhead turtles 51% of the variation was explained ($F_{1,22} = 22.7$, $P < 0.001$, $R^2 = 0.51$) by mean CCL.

3.6. Between-season variation in reproductive output

It might be argued that in some years the same female will be more productive than in other years as a result of resource availability. After correcting for female size, we found no significant differences in the mean clutch size (green turtles: $F_{5,119} = 1.7$, $P > 0.05$;

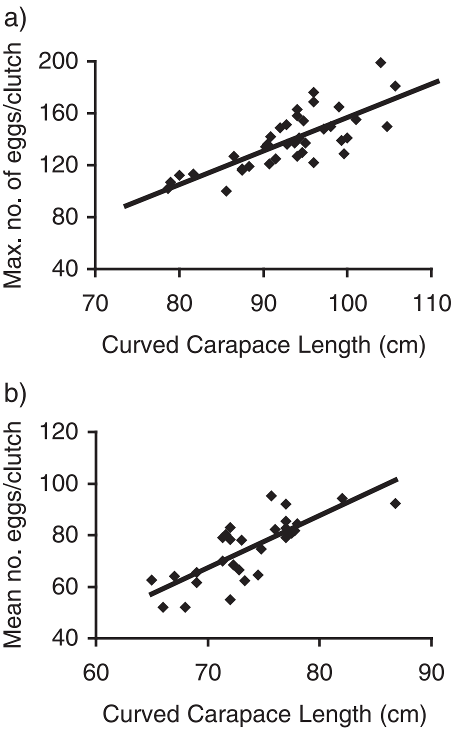

Fig. 7. The relationship between curved carapace length (cm) and (a) the maximum number of eggs laid by green turtles ($y = 2.58x - 101.3$, $R^2 = 0.58$) and (b) the mean number of eggs laid by loggerhead turtles ($y = 2.03x - 74.9$, $R^2 = 0.6$).

loggerhead turtles: $F_{5,48}=1.2$, P>0.05) or maximum clutch size (green turtles: $F_{5,119}=1.7$, P>0.05; loggerhead turtles: $F_{5,48}=1.5$, P>0.05) recorded in the different years of the study. However, the median number of clutches laid by green turtles was significantly greater in 1995 and 1998 (4 clutches) than in 1996 and 1999 (1.5 clutches; Kruskal–Wallis: $H_{5,96}=12.1$, $P<0.05$). Years with high levels of nesting correspond to those when individual females laid a greater number of clutches (Fig. 8a). No significant inter-annual variation in the median number of clutches laid by loggerhead turtles was recorded ($H_{5,48}=1.44$, P>0.05; Fig. 8b).

We found no difference in either the maximum or the mean clutch size (Kruskal–Wallis: Maximum clutch size: $H_{4,32}=0.7$, P>0.05; Mean clutch size: $H_{4,32}=0.3$, P>0.05,) or the number of clutches laid ($H_{4,32}=8.1$, P>0.05) for green turtles returning after different remigration intervals. Loggerheads returning after a 1-year interval however laid a greater number of eggs than those returning after longer remigration intervals (Mean clutch size: $H_{3,19}=9.7$, $P<0.05$). There was no difference in the number of clutches laid by loggerhead turtles returning after different remigration intervals ($H_{3,19}=5.7$, P>0.05).

We compared females laying ≥ 2 clutches in two or more successive breeding seasons and found that green turtles laid larger clutches (mean clutch size $F=5.43$ and maximum clutch size $F=3.53$, $df=3$, $P<0.05$), but not a greater number of clutches ($H=3.18$, $df=3$, P>0.05) in subsequent seasons. Loggerhead females however, laying ≥ 2 clutches in two

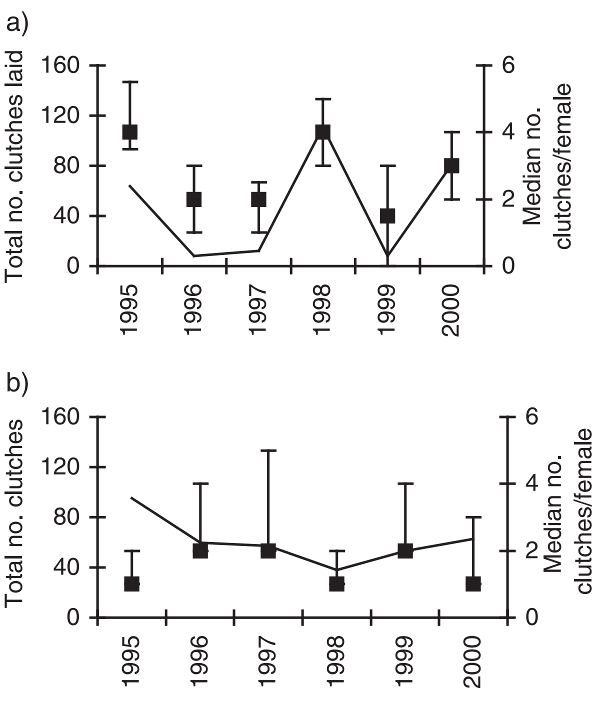

Fig. 8. Number of clutches laid in each survey year: (a) green turtles and (b) loggerhead turtles together with median number of clutches laid by individual females with inter-quartile ranges. Solid line represents total number of clutches recorded in each season 1995–2000.

or more successive breeding seasons, did not lay larger clutches (mean: $F = 1.21$, Maximum: $F = 1.8$, $df = 6$, $P > 0.05$) or a greater number of clutches ($H = 0.34$, $df = 4$, $P > 0.05$) in subsequent seasons. In both cases, we corrected for any effects of an increase in female size (CCL) over time.

4. Discussion

In this study, we have clearly shown that clutch size increases with body size in both green and loggerhead turtles nesting in Cyprus. Many previous studies have only explained 10–40% of the variation in clutch size by curved carapace length (Bjorndal and Carr, 1989; Hays and Speakman, 1991; Hays et al., 1993). Here we have shown that a large proportion of the variation in clutch size is a result of within individual variation and by using mean or maximum clutch size, we can explain 58–61% of the variation in clutch size. Larger females did not lay more clutches; this variable appears to be independent of female size. This result is in keeping with findings elsewhere (Frazer and Richardson, 1986; Johnson and Ehrhart, 1996).

Upon examination of clutch size and clutch order, it appears that the small number of loggerhead females laying five clutches ($n = 5$) may become resource limited by the fifth clutch, this being the significantly smaller clutch. Resource depletion may be the factor which causes the within-season decrease in clutch size of loggerhead turtles at a population level (Fig. 5). Green turtles however lay smaller clutches at the start of their laying season which may result from a gradual increase in efficiency or capacity in the process related to vitellogenesis (see Solomon, 1991 for description of similar phenomenon in domestic fowl). The space available in the coelomic cavity of female turtles will dictate the maximum physical carrying capacity of a female with respect to clutch size. We have compelling evidence that green turtles nesting in Cyprus, unlike most conspecific populations studied to date undertake at least some degree of foraging in the internesting interval (Hochscheid et al., 1999; Hays et al., 2000). It may be that as the season progresses, the turtles feed less, thus liberating space in the body cavity.

Growth rates of adult females of both species in this study were negligible, as has been found in other nesting populations (Carr and Goodman, 1970; Limpus and Chaloupka, 1997). However, loggerhead turtles, although smaller, appeared to grow faster than green turtles. Although working on individuals of all age classes, Kennett (1996) recorded a greater growth rate in a carnivorous species of freshwater turtle in relation to a herbivorous species, thus differing diet may explain our result. The size at which females reach maturity varies greatly and will affect the life-time reproductive output of an individual (Tiwari and Bjorndal, 2000). Whether size at maturity is genetic or a result of developmental conditions, smaller females will lay smaller clutches. They may however mature at an earlier age and we have no evidence to suggest that they lay fewer clutches or breed more infrequently than larger females. However, loggerhead turtles nesting in Cyprus are the smallest breeding females of this species reported in the literature and in turn lay the smallest clutches (Broderick and Godley, 1996; Margaritoulis et al., in press). The frequency of 1-year remigrants is the highest that we have found evidence of in this species. This might indicate a reproductive trade off with small females laying smaller clutches in a season but with a shorter interval between seasons. One loggerhead female, for example, has been recorded breeding in six of a possible seven seasons.

In non-annual breeders, the decision to reproduce in a given year is likely to be based upon an assessment of body condition of the individual in addition to environmental conditions at that time. Between breeding seasons, marine turtles must feed and accumulate energy stores for reproduction and the associated energetic costs of migration and, where present, fasting. If these reserves exceed a threshold, and the environmental conditions are suitable, then successful breeding will occur. In this study, we found that in a poor nesting year when very few green turtles bred, they also laid fewer clutches. This may signify that although these females were presumably in better body condition than those females who did not breed that they were still not in optimal body condition. There is clearly greater annual variation in the number of clutches laid by individual green turtles in comparison to loggerhead turtles. The fact that the degree of variation mirrors the level of nesting suggests that both of these factors are under the control of the same variables, most likely weather conditions affecting food availability (Broderick et al., 2001). In other animal species, fluctuations in food availability have been shown to affect reproductive output (Harvey et al., 1988; Wikelski and Thom, 2000). In particular, Madsen and Shine (1999) found that water pythons (*Liasis fuscus*) adjusted their reproductive thresholds in response to annual variation in prey abundance and reduced their clutch size in a poor year. Marine turtles are very vulnerable on land and may face the threat of predation on the beach or in shallow coastal waters. Thus, it may be a better strategy to lay fewer clutches rather than smaller clutches in these species and may explain why the females in our study did not lay smaller clutches in years of low levels of nesting but instead laid fewer clutches.

Although females did not lay larger clutches after returning after a longer remigration interval, green turtles did lay larger clutches in subsequent nesting seasons than those recorded in their previous breeding season. A similar finding was reported by Bjorndal and Carr (1989) in Costa Rica. This finding was not a result of an increase in size, and thus some of the variation in clutch sizes recorded may be a result of an increase in efficiency in the breeder with time. Longer studies may reveal the duration over which a female can reproduce, which we know to be at least 9 years at this site. They may also reveal any decrease in reproductive output as females enter senescence.

In this study, we chose to examine reproductive output as measured by the number of eggs and clutches laid. We have shown curved carapace length to be a good indicator of mean and maximum clutch size in both species. In might, however, be suggested that body mass may have been a better index to use. The practicality of weighing individuals was not deemed appropriate at this nesting site where minimum disturbance is a conservation priority. Similarly, weighing and measuring of eggs was not routinely undertaken in this study as the disturbance of natural nest conditions was not justified. In instances where clutches are relocated to safer sites, handling of eggs was necessary and in these cases eggs were measured. We found no relationship between either CCL or clutch size and egg diameter or weight for either species ($n = 20$ loggerhead clutches; $n = 11$ green clutches). In some studies, relationships have been recorded between CCL or clutch size and egg size (e.g. Bjorndal and Carr, 1989; Hays et al., 1993) while in others no such relationship has been found (Hays and Speakman, 1991). Thus, we cannot thus rule out egg size as an important variable in the reproductive output of our population.

In enigmatic taxa such as sea turtles, much of the information gathered on life history is dependent on chance recapture, and with such long lived species, this is further confounded by the errors that arise from tag loss. In addition, the majority of marine turtle species are classified by the IUCN as endangered and indeed the Mediterranean sub-population of the green turtle is listed as critically endangered (Hilton-Taylor, 2000). Manipulation of individuals and controlled experiments are thus not an option to unravel the intricacies of the life histories of these species. The advent of improved methods of marking individuals to reduce the effects of tag loss, more accurate assessments of fidelity to nesting beaches, and the development of more reliable ageing techniques will help to answer some of the unsolved questions concerning sea turtle biology and these studies will unquestionably be long-term efforts over several decades.

Many population estimates of marine turtles are based upon estimates of remigration intervals and the number of clutches laid, and are made over short periods of time. In this study, we have clearly illustrated that the number of clutches laid, in addition to the number of nesting green turtles, is highly variable among years. These findings highlight the importance of long-term monitoring of both number of nesting females and reproductive output of individuals in order to fully understand and assess the status of nesting populations.

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