

Investigating Potential for Depensation in Marine Turtles: How Low Can You Go?

C. D. BELL,*† J. M. BLUMENTHAL,*‡ A. C. BRODERICK,* AND B. J. GODLEY*§

*Marine Turtle Research Group, Centre for Ecology and Conservation, University of Exeter, Cornwall Campus, Penryn TR10 9E2, United Kingdom

†Pendoley Environmental, P.O. Box 98, Leederville, WA 6902, Australia

‡Department of Environment, P.O. Box 486, George Town, Grand Cayman, Cayman Islands

Abstract: *Where mechanisms inherent within the biology of a species affect individual fitness at low density, demographic-scale depensation may occur, hastening further decline and leading ultimately to population extirpation and species extinction. Reduction in fertility at low population densities has been identified in marine and terrestrial species. Using data on hatch success and hatchling-emergence success as proxies for fertilization success, we conducted a global meta-analysis of data from breeding aggregations of green turtles (*Chelonia mydas*) and loggerhead turtles (*Caretta caretta*). We found that there has been no reduction in fertility in small nesting aggregations in either of these species worldwide. We considered mechanisms within the mating strategies and reproductive biology of marine turtles that may allow for novel genetic input and facilitate enhanced gene flow among rookeries. Behavioral reproductive mechanisms, such as natal philopatry and polyandry, may mitigate potential impacts of depensation and contribute to the resilience of these species.*

Keywords: Allee effects, depensation, exploitation, marine turtles, population recovery

Investigando el Potencial de Anticompensación en Tortugas Marinas: ¿Qué Tan Bajo Se Puede Llegar?

Resumen: *Cuando los mecanismos inherentes a la biología de una especie afectan la eficacia individual a baja densidad, puede ocurrir la anticompensación, que acelera la declinación y en última instancia conduce a la extirpación de la población y a la extinción de la especie. La reducción de fertilidad en poblaciones con baja densidad se ha identificado en especies marinas y terrestres. Utilizando datos de éxito de eclosión y emergencia de crías como indicadores del éxito de fertilización, realizamos un meta-análisis global de datos de agregaciones de tortugas verdes (*Chelonia mydas*) y tortugas caguama (*Caretta caretta*). Encontramos que no ha habido reducción en la fertilidad en agregaciones pequeñas de estas dos especies. Consideramos los mecanismos en las estrategias de apareamiento y de la biología reproductiva de tortugas marinas que pueden permitir el ingreso de material genético nuevo y facilitar el flujo de genes entre colonias. Mecanismos de la conducta reproductiva, como la filopatría natal y la poliandria, pueden mitigar impactos potenciales de la anticompensación y contribuir a la resiliencia de estas especies.*

Palabras Clave: anticompensación, efectos Allee, explotación, recuperación de la población, tortugas marinas

Introduction

A critical aspect of conservation biology is an understanding of the factors that inhibit recovery of small populations (reviewed in Berec et al. 2007). Causal mechanisms influencing population dynamics where rarity is increas-

ing are of particular concern and have critical implications for meta-population management (Amarasekare 1998). The term *depensation* (Neave 1953) refers to a decreased per capita population growth rate at low density and is also known as the Allee effect (Allee et al. 1949). Depensation may result from any number of mechanisms

§email b.j.godley@exeter.ac.uk

Paper submitted August 21, 2008; revised manuscript accepted April 22, 2009.

that affect individual fitness, although demographic and environmental variability make these mechanisms difficult to detect (Liermann & Hilborn 2001). Where present, they can ultimately lead a population to a point of critical depensation, where populations are unable to recover and dwindle inexorably toward extinction (Clark 1985).

Due to overexploitation, recovery potential in marine taxa has been of particular concern (Liermann & Hilborn 2001). Recovery from low numbers is variable among marine taxa and is influenced by the fundamental biology of the species (Rowe & Hutchings 2003) and interactions with anthropogenic influences, such as exploitation patterns (Hutchings 2001) and habitat loss (Roberts & Hawkins 1999). Although demonstrated widely in terrestrial species (reviewed in Berec et al. 2007), there is little empirical evidence in the literature for widespread depensation in marine species, particularly in nonbroadcast spawners (Gascoigne & Lipcius 2004).

Marine turtles are colonial breeders, exhibit natal philopatry, and deposit multiple clutches in the sand adjacent to the offshore mating area within one reproductive season (Miller 1997). Marine turtles are polyandrous and may engage in multiple matings prior to oviposition (Pearse & Avise 2001; Ireland et al. 2003). They exhibit temperature-dependent sex determination, and primary sex ratios are therefore determined by environmental variables (Ackerman 1997). Fertility, as indicated by assessing hatching success, is typically high (>80%) (Miller 1997).

Intensive historical exploitation has focused on marine turtle assemblages worldwide, which has caused massive declines (reviewed in McClenachan et al. [2006]). In some areas where exploitation has been halted or severely restricted and comprehensive monitoring and conservation programs implemented, numbers have increased: for example, green turtles (*Chelonia mydas*) of Ascension Island (Broderick et al. 2006), Costa Rica (Tortuguero) (Troëng & Rankin 2005), Hawaii (East Island) (Balazs & Chaloupka 2004), Japan (Chichi-jima) (Chaloupka et al. 2008), and Florida (Archie Carr National Wildlife Reserve, U.S.A.) (Chaloupka et al. 2008); loggerhead turtles (*Caretta caretta*) of Brazil (Marcovaldi & Chaloupka 2007); leatherback turtles (*Dermochelys coriacea*) of U.S. Virgin Islands (Dutton et al. 2005); hawksbill turtles (*Eretmochelys imbricata*) of Antigua (Richardson et al. 2006), Barbados (Beggs et al. 2007), Mexico (Yucatan) (Garduno-Andrade et al. 1999), and Puerto Rico (Mona Island) (Mortimer & Donnelly 2007; van Dam & Diez 2007); and Kemps' ridley (*Lepidochelys kempii*) of Mexico (Márquez et al. 1999). All these populations now number in the hundreds or thousands of females nesting each year.

That a critical density may exist below which populations cannot recover (Courchamp et al. 1999) has been suggested via modeling (Liermann & Hilborn 2001). Reduction in fertility at low densities, evident as depressed

breeding success, has been identified in other species in the marine and terrestrial realms (Liermann & Hilborn 2001; Berec et al. 2007). Although considered for other marine taxa (Hutchings 2001; Jennings 2001) such models have been applied to marine turtle stocks only recently (Chaloupka & Balazs 2007) and suggest that depensation may occur when a population drops below 5% of historical biomass.

In the Cayman Islands, although historical rookery size for green turtles has been estimated in the millions, by 1900 this breeding aggregation was deemed extirpated (Groombridge 1982; Aiken et al. 2001). Today fewer than 10 females each of two species (green turtles and loggerhead turtles) nest per year in the Cayman Islands (Bell et al. 2007). Although some degree of recovery may have occurred during the last century, it has not been substantial. Many rookeries, although massively reduced, have not been entirely extirpated (McClenachan et al. 2006); however, the viability of these breeding aggregations has not been assessed. Perhaps there is a threshold below which recovery cannot occur or, conversely, marine turtles are more resilient than previously thought.

Our hypothesis was that a depensatory lowering of individual breeding success as a result of increased rarity and consequent reduced or inferior mating opportunities is evident in very small breeding aggregations of marine turtles. This is known as a component Allee effect and is related to density. It describes the positive relationship between individual fitness and population size and is a mechanism for depensation where the population growth rate is influenced by population size (Berec et al. 2007). We tested our hypotheses through a detailed analysis of reproductive success at the Cayman Islands rookery and a meta-analysis of global conspecific breeding success.

Methods

Beach monitoring for marine turtle nesting in the Cayman Islands has been conducted since 1998 (Bell et al. 2007). After hatching we excavated all clutches and collected data on all standard parameters, including clutch size, hatch success, emergence success, and fertilization success. We opened all unhatched eggs to determine fertilization and development status (Miller 1999). Early embryonic death was distinguished from nonfertilization by the presence of blood in the yolk (Miller 1997).

For reproductive aggregations of green and loggerhead turtles outside of the Cayman Islands, we defined demographic units when possible on the basis of either clear geographic discreteness or molecular data (Lahanas et al. 1994; Schroth et al. 1996; Dethmers et al. 2006). Some data represent multiple samples from rookeries of the same stock. We used total number of clutches per

season as an index of rookery size. Due to natal homing and site fidelity in these species, the number of clutches and hence females at a nesting site can be attributed reliably to a single rookery (Seminoff 2004). Where possible, we avoided point estimates and used data collected and averaged over a number of years to minimize potential variance bias in estimated rookery size caused by interannual variability of breeding numbers (Broderick et al. 2001; Heppell et al. 2003). For the few cases in which only number of females was given, we used a mean clutch frequency of three females per reproductive season (Seminoff 2004). Hatching success or, in some cases, hatchling emergence success were used as proxies for fertilization success (Miller 1997).

Results

Hatching and fertilization success were highly correlated for both species in the Cayman Islands (linear regression: green turtle, $R = 0.91$, $p < 0.005$, $n = 90$ [Fig. 1a]; loggerhead turtle, $R = 0.84$, $p < 0.005$, $n = 99$ [Fig. 1b]). Emergence and fertilization successes were also highly correlated (green turtle, $R = 0.77$, $p < 0.005$, $n = 84$ [Fig. 1c]; loggerhead turtle, $R = 0.59$, $p < 0.005$, $n = 80$ [Fig. 1d]). Our data therefore suggest that either of these parameters (hatching success or emergence success) serve as reasonable proxies for fertilization success. Estimates of fertility made at clutch excavation may un-

derestimate actual fertility because of egg decomposition (Bell et al. 2003); thus, we present hatching or emergence success as minimum indicators of fertility. This opens up the potential for meta-analysis across a number of different projects in which data were collected on either of these commonly measured parameters because data are rarely collected on fertilization success.

In the small rookery in the Cayman Islands, some clutches had low levels of fertilization success (18% of total number of clutches demonstrated fertilization success $\leq 60\%$ in green turtles; 10% of total number of clutches showed fertilization success $\leq 60\%$ in loggerhead turtles). Nevertheless, when we incorporated overall mean values of fertilization success in the Cayman Islands of 81% and 78% for green and loggerhead turtles, respectively, into a global overview (Figs. 2 & 3; green turtles $n = 25$ rookeries; loggerhead turtles $n = 18$ rookeries [Table 1]), proxies of fertilization success did not vary systematically with rookery size. Furthermore, there was clearly no pronounced reduction in fertility in either species at low numbers, even in rookeries yielding as few as 10 clutches per year.

Discussion

We were unable to identify depensation as indicated by depressed fertility in either loggerhead or green turtle rookeries in the Cayman Islands. Nor was a trend identified among conspecific rookeries when global fertility data were investigated. Our primary finding is that depensation may not be important in green and loggerhead turtles. The capacity to maintain functional levels of fertilization success in the face of high levels of exploitation may help in part to explain why total extirpations have been few and recoveries have been possible. This information does not, however, explain why in some cases recovery has not occurred. It is therefore imperative to identify and explore mechanisms preventing decline and other signals of depensatory reduction in these rookeries. Clarity regarding these mechanisms may have implications for a wide range of terrestrial and marine species exhibiting similar life-history characteristics.

The absence of conspecific facilitation within mating systems is perhaps the most common mechanism by which depensation occurs when numbers are reduced (Stephens & Sutherland 1999; Gardmark et al. 2003). Among other things, this may hinder mate-finding ability and thus result in lower overall fertilization success. Like many marine vertebrates, marine turtles are colonial breeders (Danchin & Wagner 1997), both males and females show a degree of natal philopatry (Fitzsimmons 1997a, 1997b), and mating is thought to be largely carried out near breeding areas (Limpus 1993; Godley et al. 2002). These characteristics have the potential to

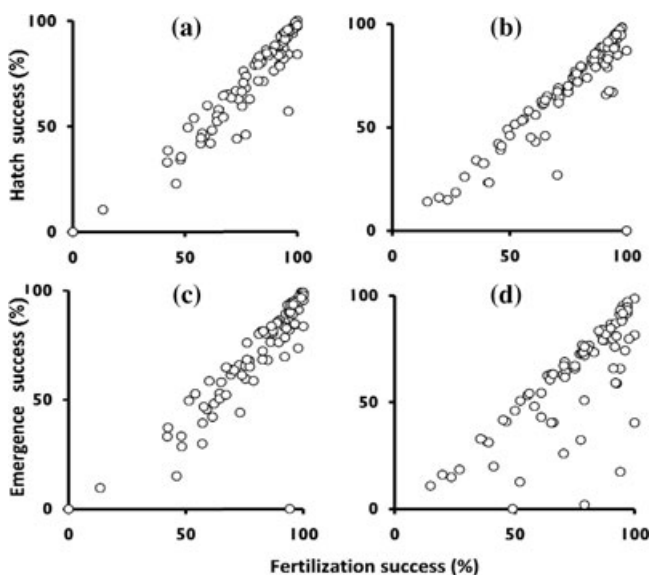


Figure 1. Correlation of hatch success and fertilization success in the Cayman Islands populations of (a) green and (b) loggerhead turtles (1998–2003) and correlation of emergence success and fertilization success for (c) green and (d) loggerhead turtles (2000–2003).



Figure 2. Geographical origin of data on proxies for fertilization success and rookery size as indicated by number of clutches per year for green and loggerhead turtles (white circles, origin of green turtle population data; black circles, origin of loggerhead turtle data; double circles, origin of data for both species; numbers, literature source [see Table 1]).

enhance mate finding (Danchin & Wagner 1997) and buffer Allee effects (Soutullo et al. 2006). The presence of male green turtles peaks with arrival of new females to the breeding site (Godley et al. 2002). During the breeding season, male loggerhead turtles are located primarily in areas where female density is highest, presumably to maximize mating opportunities (Schofield et al. 2009). If all these behavioral mechanisms are maintained where numbers are reduced, they may play a key role in maintenance of functional levels of fertilization.

Inbreeding may occur where fewer individuals are present; this can cause decreased fertilization success in some species (Tregenza & Wedell 2002). Where multiple compensatory mechanisms are present, demographic-scale impacts can be more severe (Berec et al. 2007). Species-specific behavioral elements may minimize this impact in marine turtles. It is understood that opportunistic mating occurs during migration in non-natal areas (Fitzsim-

mons et al. 1997a,b; Roberts et al. 2004) and therefore may occur with individuals from alternate breeding aggregations. Natal fidelity is not absolute, and a proportion of each aggregation is continually interchanging among rookeries within a single breeding season and between breeding seasons (Limpus et al. 2003; Dethmers et al. 2006). This interchange is of particular value to individuals recruiting to small aggregations in which genetic diversity may be limited, which facilitates gene flow and enhances reproductive viability.

Marine turtles are often polyandrous (Limpus 1993; Hoekert et al. 2002; Hamman et al. 2003), which can create higher egg or offspring viability via postcopulatory sperm competition and selection (Jennions & Petrie 2000; Hosken & Stockley 2003). Sperm competition facilitates higher fertility assurance, increased hatchling viability, and good gene acquisition (reviewed in Fitzsimmons [1998] and Hosken et al. [2003]). Furthermore, multiple

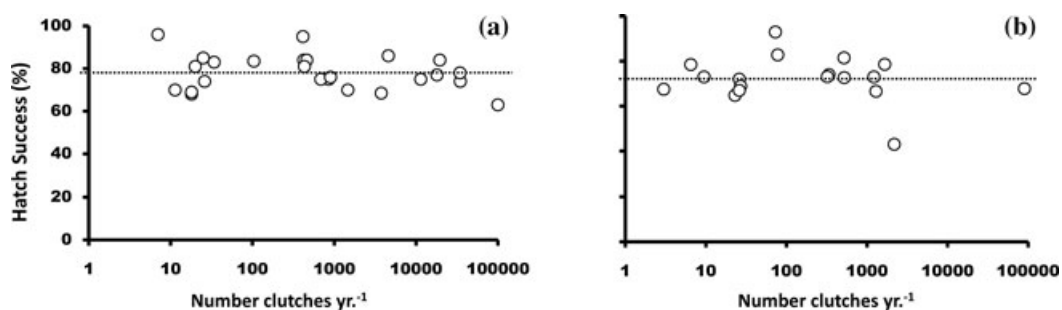


Figure 3. Mean number of clutches per year and fertility for (a) green and (b) loggerhead turtles (broken line, global average hatch/emergence success [%] for each species).

Table 1. Mean hatching success (HS), mean emergence success (ES) or mean reproductive success (RS) presented as fertilization proxies followed by estimate of number of clutches per year and the period during which these data were gathered.

<i>Location</i>	<i>Fertilization success proxy</i>	<i>Value (%)</i>	<i>Value derivation process^a</i>	<i>Number of clutches/year</i>	<i>Study period</i>	<i>Value derivation process^a</i>	<i>Reference (ID no. in Fig. 2)</i>
<i>C. mydas</i>							
Ascension Island	HS	75	*	11,400	1999–2004	†	Broderick, A. unpublished data (1) Broderick et al. 2006 (2) ^b
Australia, Bramble Cay	ES	69	*	3,753	1979	*	Limpus et al. 2001 (3)
Australia, Raine Island	HS	74	*	34,695	1979	†	Limpus et al. 2003 (4)
Australia, Raine Island	HS	78	*	34,401	1984	†	Limpus et al. 2003 (5)
Brazil, Atol das Rocas	HS	75	*	853	1990–1994	‡	Claudio et al. 1995 (6)
Cayman Islands	HS	71	*	26	2000–2003	*	C. Bell., unpublished (7)
Costa Rica, Tortuguero	HS	63	*	104,411	1999–2003	*	deHaro et al. 2008 (8); Troeng & Rankin 2005 (9) ^b
Cuba, Guanahacabi-bes Peninsula	HS	84	*	423	2000	*	Martin et al. 2002 (10)
Equatorial Guinea, Bioko Island	HS	70	‡	1,464	1996–1997	‡	Tomás, J. personal communication (11)
Hawaii, French Frigate Shoals, Tern Island	HS	81	*	432	1986–1991	*	Niethammer et al. 1997 (12)
Indonesia, Enu Island	HS	85	*	25	1997	*	Dethmers 2000 (13)
Japan, Ryukyu Islands	ES	69	§	18	1993–1996	§	Abe et al. 1998 (14)
Kenya	HS	75	‡	171	1997–2000	*	Okemwa et al. 2004 (15)
La Reunion, St. Leu	HS	96	*	7	2004–2006	*	Ciccione & Bourjea 2006 (16)
Mexico, X'caret	HS	95	*	415	1997	*	Arenas et al. 2000 (17)
Northern Cyprus	HS	84	*	462	1994	*	Broderick & Godley 1996 (18); Broderick et al. 2003 (19) ^b
Oman, Ras al Had	HS	77	*	18,000	1978	†	Ross 1979 (20)
Philippines, Baguan Island	HS	87	*	4,576	1984–1989	‡	Trono 1991 (21)
South Africa, Europa Island	HS	84	‡	19,500	1969–1972	§/†	Hughes 1974b (22)
South Africa, Tromelin Island	HS	76	*	900	1969–1972	§/†	Hughes 1974b (24)
Syria, Latakia Beach	HS	84	*	104	2004	*	Rees et al. 2008 (26)
Taiwan, Wan-an Island	HS	70	*	11	1992–1994	‡	Cheng & Chen 1996 (28)
Turkey, Alata	ES	81	*	20	2005	*	Ergene 2006 (29)
U.S.A., Florida, P.A.F.B.	RS ^c	68	‡	18	1987–1994	‡	Bagley et al. 1996 (30)
U.S.A., North Carolina	HS	83	*	34	1980–1994	*	Woodson et al. 1998 (31)
<i>C. caretta</i>							
Brazil, Praia do Forte	HS	73	*	322	1987–1993	‡	Marcovaldi & Laurent 1996 (32)
Brazil, Praia do Forte	HS	74	*	338	1994–1998	*	Santos et al. 2000 (33)
Cape Verde Is., Boa Vista	HS	43	*	2,178	2003–2004	*	Varo-Cruz, unpublished (34)
Cayman Islands	HS	67	*	26	1999–2003	*	C. Bell., unpublished (35)
Cuba, Guanahacabi-bes Peninsula	HS	65	*	23	2000	*	Martin et al. 2002 (36)
Egypt, Sinai Peninsula	HS	69	*	27	1999	*	Clarke et al. 2002 (37)
Greece, Kyparissia Bay	HS	73	*	522	2001	*	Rees et al. 2002 (38)
Greece, Zakynthos	ES	67	*	1,294	1984–2002	*	Margaritoulis 2005 (39)
Japan, Ryukyu Islands	ES	80	§	6.5	1993–1996	§	Abe et al. 1998 (40)
Libya, Sirte	HS	93	‡	73	2005	*	Hamza et al. 2006 (41)
Northern Cyprus	HS	82	*	519	1994	*	Broderick & Godley 1996 (42)
Oman, Masirah Island	HS	68	*	90,000	1978	†	Ross 1979 (43)
South Africa, Tongaland	HS	79	*	1,660	1969–1972	*	Hughes 1974a (44)
Tunisia, Kuriat Islands	HS	71	*	13	2000	*	Jribi et al. 2002 (45)
Turkey, Alata	ES	66	*	26	2005	*	Ergene et al. 2006 (46)

continued

Table 1. (continued)

Location	Fertilization success proxy	Value (%)	Value derivation process ^a	Number of clutches/year	Study period	Value derivation process ^a	Reference (ID no. in Fig. 2)
U.S.A., Florida, P.A.F.B.	RS ^c	73	‡	1,219	1987–1994	‡	Bagely et al. 1996 (47)
U.S.A., North Carolina, Bald Head Island	ES	83	*	108	1999–2003	*	Hawkes et al. 2005 (48)
Venezuela, Laguna de Tacarigua	HS	68	‡	3	1998	*	Gomez et al. 2002

^aKey: *, number presented as in text or publication; †, author-calculated annual clutch estimate from number of nesting females as per Seminoff (2004); ‡, author-calculated annual mean of multiple data sets (>1 year or >1 site within one project); §, author-calculated median of range of data.

^bReferences are listed for hatch success and number of clutches respectively.

^cReproductive success defined as total nest output (Bagley et al. 1996).

matings provide the foundation for multiple paternity within clutches (Bollmer et al. 1999; Moore & Ball 2002) and therefore increased genetic diversity. Multiple paternity raises the effective male population size and ensures that in the case of nest or individual reproductive failure, the male genetic contribution is represented in more than one instance (Galbraith 1993). Polyandry may therefore be a critical factor in the maintenance of functional levels of fertilization and, ultimately, in hatching success, particularly in the Cayman Islands, where there are few individuals. It is worth exploring whether marine turtles have the facility to store significant amounts of viable sperm across seasons (Sanz et al. 2008). This function holds potential to greatly enhance effective male population size.

Populations with temperature-dependent sex determination may be more susceptible to depensation because inherently biased primary sex ratios reduce mate-finding ability (Berec et al. 2001). The majority of primary sex ratios have been estimated as female dominated, but data on sex ratios in older cohorts are still few (Hawkes et al. 2009), and female-dominated populations may experience increased productivity (Girondot et al. 2004). The paucity of data quantifying adult sex ratios, precise male reproductive contribution, and the interaction between mating success and nesting frequency constrains the predictive power of present modeling efforts assessing demographic-scale responses to changes in population size. At small population sizes, adult sex ratio will become vital. Current adult sex ratios within Cayman Islands rookeries are unknown, although our findings indicate that this ratio remains productive. This is another area worthy of further investigation.

Understanding density dependence is a key to prediction of population dynamics where exploitation has occurred (reviewed in Sutherland and Norris [2003]). Green turtle stocks take a long time to recover from extensive harvesting (Chaloupka 2001). Chaloupka (2002) suggested that it could be >100 years if no density-dependent compensatory process occurs; however, re-

cent evidence suggests that compensation does occur and may facilitate rebound capacity and more-rapid recovery (Chaloupka et al. 2008). In Ascension Island (Broderrick et al. 2006), Hawaii (Balazs & Chaloupka 2004), and Costa Rica (Troëng & Rankin 2005), increases have been seen in <40 years. Under the right conditions therefore, recovery time may be short, and there may be compensatory mechanisms in operation.

Despite successes elsewhere, the Cayman Islands breeding aggregation of green and loggerhead turtles has failed to recover since cessation of large-scale exploitation over 200 years ago (Aiken et al. 2001). Lack of close geographic proximity to adjacent nesting areas may inhibit gene flow (Heppell et al. 2003), or these animals may not be remnants of a heavily exploited rookery. Rather, they may represent the slow recolonization of the Cayman Islands from other stocks in the region. If so, there may be depensatory mechanisms specific to recolonizing populations, or rookeries, that inhibit growth. There may also be alternate depensatory mechanisms present that we have not identified. In addition, low-level legal harvest of adults in the Cayman Islands (Bell et al. 2006) and take outside the Cayman Islands (Blumenthal et al. 2006) have likely played a significant role in preventing recovery and have important management and policy implications for this region.

We recognize that our approach is not without limitations. It is intrinsically complex to define the precise spatial extent of discrete marine turtle rookeries. We did use data from multiple rookeries within the same metapopulations and believe that given the substructuring shown in green and loggerhead turtle populations (Schroth et al. 1996; Dethmers et al. 2006), these comparisons are valid. Use of emergence success data as a proxy for fertilization success may provide a small degree of error because emergence success depends on both physical conditions at the nest site and fertilization success. Some researchers examined only emerged nests in clutch investigations and therefore may have slightly overestimated hatching success. Although point measurements are

inferior to long-term data sets for each rookery, long-term data are rarely available, and we used averaged multianual data when it was available. In a minority of cases, where only number of females was given, we used a standard clutch frequency of three to assess rookery size. We recognize that this will add some variance to our proxy population estimates, but given that these estimates range over five orders of magnitude versus less than one order of magnitude for clutch frequency, this should not be cause for concern. This study does, however, represent a benchmark for the beginning of critical analysis of such factors in marine turtles.

Fertility proxies in highly reduced rookeries in the Cayman Islands and elsewhere were comparable to those in other, larger aggregations worldwide. It seems that density-dependent reduction in hatching success is not a constraint to recovery in these species. Other factors, aside from magnitude, must be driving hatching success. Clearly, in addition to the inherent conservation value of monitoring reduced rookeries, there is heuristic value in identifying the mechanisms present within the reproductive strategies of these species that facilitate continued viability at low numbers and that may or may not provide foundation for resurgence. We reiterate here the call of McClenachan et al. (2006) for renewed focus on small, highly reduced marine turtle rookeries.

Acknowledgments

We recognize the support of all staff at the Cayman Islands Department of Environment for their contributions and commitment to the Cayman Islands Marine Turtle Research Project. In addition, we heartily thank all those around the world who shared their data for this analysis. This study was initially inspired by the interaction with M. Chaloupka, whose modeling of marine turtle populations provided the kernel for this project. This manuscript benefited from the review of T. Tregenza and D. Hosken and that of an additional four anonymous reviewers. C.D.B. and J.M.B. were supported by postgraduate scholarships from the University of Exeter. A. Broderick and B. Godley acknowledge the additional support of the Darwin Initiative, European Social Fund, Foreign and Commonwealth Office Overseas Territory Environment Programme, INTERREG and the Natural Environment Research Council.

Literature Cited

- Abe, O., Y. Takanda, T. Shibuno, K. Hashimoto, and S. Tanizaki. 1998. Nesting activity of sea turtles on Ishigaki Island, Ryukyu Islands, Japan. Technical memorandum NMFS-SEFSC-415. Page 115 in S. P. Epperly and J. Braun, editors. Proceedings of the 17th annual symposium on sea turtle biology and conservation. National Oceanic and Atmospheric Administration, Washington, D.C.
- Ackerman, R. A. 1997. The nest environment and embryonic development of sea turtles. Pages 83–107 in P. Lutz and J. Musick, editors. The biology of sea turtles. CRC Press, Boca Raton, Florida.
- Aiken, J. J., B. J. Godley, A. C. Broderick, T. J. Austin, G. Ebanks-Petrie, and G. C. Hays. 2001. Two hundred years after a commercial marine turtle fishery: the current status of marine turtles nesting in the Cayman Islands. *Oryx* 35:145–151.
- Allee, W. C., A. E. Emerson, O. Park, T. Park, and K. P. Schmidt. 1949. Principles of animal ecology. Saunders, Philadelphia, Pennsylvania.
- Amarasekare, P. 1998. Allee effects in metapopulation dynamics. *The American Naturalist* 152:298–302.
- Arenas, A., R. Villavicencio, A. D'Amiano, L. Gomez, and R. Raigoza. 2000. The sea turtle program of X'caret, '97 nesting's season results. Technical memorandum NMFS-SEFSC-436. Pages 172–174 in F. A. Abreu-Grobois, R. Briseno-Duenas, R. Marquez, and L. Sarti, compilers. Proceedings of the 18th annual symposium on sea turtle biology and conservation. National Oceanic and Atmospheric Administration, Washington, D.C.
- Bagley, D. A., L. T. Uong, W. J. Porte, W. B. Blihoude, R. D. Owen, and L. M. Ehrhart. 1996. Marine turtle nesting at Patrick Air Force Base, Florida in 1994. Technical memorandum NMFS-SEFSC-387. Pages 10–15 in J. A. Keinath, D. E. Barnard, and J. A. Musick, compilers. Proceedings of the 15th annual symposium sea turtle biology and conservation. National Oceanic and Atmospheric Administration, Washington, D.C.
- Balazs, G. H., and M. Chaloupka. 2004. Thirty-year recovery trend in the once depleted Hawaiian green sea turtle stock. *Biological Conservation* 117:491–498.
- Beggs, J. A., J. A. Horrocks, and B. H. Krueger. 2007. Increase in hawksbill sea turtle, *Eretmochelys imbricata*, nesting in Barbados, West Indies. *Endangered Species Research* 3:159–168.
- Bell, B. A., J. R. Spotila, F. V. Paladino, and R. D. Reina. 2003. Low reproductive success of leatherback turtles, *Dermochelys coriacea*, is due to high embryonic mortality. *Biological Conservation* 115:131–138.
- Bell, C. D., J. M. Blumenthal, T. J. Austin, G. Ebanks-Petrie, A. C. Broderick, and B. J. Godley. 2006. Traditional Caymanian fishery may impede local marine turtle population recovery. *Endangered Species Research* 2:63–69.
- Bell, C. D., J. Solomon, J. M. Blumenthal, T. J. Austin, G. Ebanks-Petrie, A. C. Broderick, and B. J. Godley. 2007. Monitoring and conservation of critically reduced marine turtle nesting populations: lessons from the Cayman Islands. *Animal Conservation* 10:39–47.
- Berec, L., D. S. Boukal, and M. Berec. 2001. Linking the Allee effect sexual reproduction and temperature-dependent sex determination via spatial dynamics. *The American Naturalist* 157:217–230.
- Berec, L., E. Angulo, and F. Courchamp. 2007. Multiple Allee effects and population management. *Trends in Ecology & Evolution* 22:185–191.
- Blumenthal, J. M., J. L. Solomon, C. D. Bell, T. J. Austin, G. Ebanks-Petrie, M. S. Coyne, A. C. Broderick, and B. J. Godley. 2006. Satellite tracking highlights the need for international cooperation in marine turtle management. *Endangered Species Research* 2:51–61.
- Broderick, A. C. and B. J. Godley. 1996. Population and nesting ecology of the green turtle, *Chelonia mydas*, and loggerhead turtle, *Caretta caretta*, in Northern Cyprus. *Zoology in the Middle East* 13:27–46.
- Broderick, A. C., B. J. Godley, and G. C. Hays. 2001. Trophic status drives interannual variability in nesting numbers of marine turtles. *Proceedings of the Royal Society of London* 268:1481–1487.
- Broderick, A. C., F. Glen, B. J. Godley, and G. C. Hays. 2003. Variation in reproductive output of marine turtles. *Journal of Experimental Marine Biology & Ecology* 288:95–109.
- Broderick, A. C., R. Frauenstein, F. Glen, G. H. Hays, A. L. Jackson, T. Pelembe, G. D. Ruxton, and B. J. Godley. 2006. Are green turtles globally endangered? *Global Ecology & Biogeography* 15:21–26.
- Bollmer, J. L., M. E. Irwin, J. P. Reider, P. G., and P. Parker. 1999. Multiple paternity in loggerhead turtle clutches. *Copeia* 1999:475–478.
- Chaloupka, M. 2001. Historical trends, seasonality and spatial synchrony in green turtle egg production. *Biological Conservation* 101:263–279.

- Chaloupka, M. 2002. Stochastic simulation modeling of southern Great Barrier Reef green turtle population dynamics. *Ecological Modeling* **148**:79–109.
- Chaloupka, M., and G. Balazs. 2007. Using Bayesian state-space modeling to assess the recovery and harvest potential of the Hawaiian green sea turtle stock. *Ecological Modeling* **205**:93–109.
- Chaloupka, M., K. Bjørndal, G. Balazs, A. Bolten, L. Erhart, C. J. Limpus, H. Suganuma, S. Tröeng, and M. Yamaguchi. 2008. Encouraging outlook for recovery of a once severely exploited marine megaherbivore. *Global Ecology and Biogeography* **17**:297–304.
- Cheng, I., and T. Chen. 1996. Green turtle research in Taiwan. Technical memorandum NMFS-SEFSC-387. Page 70 in J. A. Keinath, D. E. Barnard, and J. A. Musick, compilers. Proceedings of the 15th annual symposium on sea turtle biology and conservation. National Oceanic and Atmospheric Administration, Washington, D.C.
- Ciccione, S., and J. Bourjea. 2006. Nesting of green turtles in Saint Leu, Reunion Island. *Marine Turtle Newsletter* **112**:1–3.
- Clark, C. W. 1985. Bioeconomic modelling and fisheries management. John Wiley and Sons, New York.
- Clarke, M., A. C. Campbell, C. Simms, W. Salama Hameid. 2002. Observation on the ecology of marine turtles nesting on the Mediterranean coast of Egypt. Technical memorandum NMFS-SEFSC-447. Pages 257–258 in A. Mosier, A. Foley, and B. Bros, compilers. Proceedings of the 20th annual symposium on sea turtle biology and conservation. National Oceanic and Atmospheric Administration, Washington, D.C.
- Claudio, B., M. A. Marcovaldi, T. M. Sanches, A. Grossman, and G. Sales. 1995. Atol das Rocas biological reserve: second largest Chelonia rookery in Brazil. *Marine Turtle Newsletter* **72**:1–2.
- Courchamp, F., T. Clutton-Brock, and B. Grenfell. 1999. Inverse density dependence and the Allee effect. *Trends in Ecology & Evolution* **14**:405–410.
- Danchin, E., and R. H. Wagner. 1997. The evolution of coloniality: the emergence of new perspectives. *Trends in Ecology & Evolution* **12**:342–347.
- deHaro, A., S. Tröeng, and E. Harrison. 2008. How can monitoring of hatching success guide sea turtle management? Technical memorandum NMFS-SEFSC-569. Page 262 in A. F. Rees, M. Frick, A. Panagopolou, and K. Williams, compilers. Proceedings of the 27th annual symposium on sea turtle biology and conservation. National Oceanic and Atmospheric Administration, Washington, D.C.
- Dethmers, K. E. M. 2000. Demography of a green turtle nesting population on Enu Island, Aru, Indonesia. Technical memorandum NMFS-SEFSC-443. Page 291 in Kalb and T. Wibbels, compilers. Proceedings of the 19th annual symposium on sea turtle biology and conservation. National Oceanic and Atmospheric Administration, Washington, D.C.
- Dethmers, K. E. M., D. Broderick, C. Moritz, N. N. Fitzsimmons, C. J. Limpus, S. Levery, S. Whiting, M. Guinea, R. I. T. Prince, and R. Kennett. 2006. The Genetic structure of Australasian green turtles (*Chelonia mydas*): exploring the Geographical scale of genetic exchange. *Molecular Ecology* **15**:3931–3946.
- Dutton, P. H., M. Chaloupka, and R. H. Boulon. 2005. Increase of a Caribbean leatherback turtle *Dermochelys coriacea* nesting population linked to long-term nest protection. *Biological Conservation* **126**:186–194.
- Ergene, S., C. Aymak, and A. Ucar. 2006. Nesting activity of the marine turtles (*Chelonia mydas* and *Caretta caretta*) during 2005 in Alata, Mersin-Turkey. Page 368 in Frick, A. Panagopolou, A. Rees, and K. Williams, compilers. Book of abstracts. Proceedings of the 26th annual symposium on sea turtle biology and conservation. International Sea Turtle Society, Athens.
- FitzSimmons, N. N. 1998. Single paternity of clutches and sperm storage in the promiscuous green turtle (*Chelonia mydas*). *Molecular Ecology* **7**:575–584.
- FitzSimmons, N. N., A. R. Goldizen, J. A. Norman, C. Moritz, J. D. Miller, and C. J. Limpus. 1997a. Philopatry of male marine turtles inferred from mitochondrial markers. *Proceedings of the National Academy of Sciences* **94**:8912–8917.
- Fitzsimmons, N. N., C. Moritz, C. J. Limpus, L. Pope, and R. Prince. 1997b. Geographic structure of mitochondrial and nuclear gene polymorphisms in Australian green turtle populations and male-biased gene flow. *Genetics* **147**:1843–1854.
- Gardmark, A., K. Enberg, J. Ripa, J. Laasko, and V. Kaitala. 2003. The ecology of recovery. *Annals Zoological Fennici* **40**:131–144.
- Galbraith, D. A. 1993. Review: multiple paternity and sperm storage in turtles. *Journal of Herpetology* **3**:117–123.
- Garduno-Andrade, M., V. Guzman, E. Miranda, R. Briseno-Duenas, and A. Abreu-Grobois. 1999. Increases in Hawksbill turtle (*Eretmochelys imbricata*) nestings in the Yucatán Peninsula, Mexico, 1977–1996: data in support of successful conservation. *Chelonian Conservation Biology* **3**:286–295.
- Gascoigne, J., and R. N. Lipcius. 2004. Conserving populations at low abundance: delayed functional maturity and Allee effects in reproductive behaviour of the queen conch *Strombus gigas*. *Marine Ecological Progress Series* **284**:185–194.
- Girondot, M., V. Delmas, P. Rivalan, F. Courchamp, A. C. Prevot-Juliard, and M. H. Godfrey. 2004. Implications of temperature dependent sex determination for population dynamics. Page 194 in N. Valenzuela and V. Lance, Temperature dependent sex determination in vertebrates. Smithsonian Books, in Washington, D.C.
- Godley, B. J., A. C. Broderick, R. Frauenstein, F. Glen, and G. C. Hays. 2002. Reproductive seasonality and sexual dimorphism in green turtles. *Marine Ecological Progress Series* **226**:125–133.
- Gomez, F., A. Arteaga, D. J. Alvarez, and H. J. Guada. 2002. Results of the 1998 and 1999 sea turtle monitoring activities in the Launa De Tacarigua National Park, Veneuela. Technical memorandum NMFS-SEFSC-477. Pages 248–249 in A. Mosier, A. Foley, and B. Brost, compilers. Proceedings of the 20th annual symposium on sea turtle biology and conservation. National Oceanic and Atmospheric Administration, Washington, D.C.
- Groombridge, B. 1982. The IUCN amphibia—reptilia red data book. IUCN, Gland, Switzerland.
- Hamman, M., C. J. Limpus, and D. W. Owens. 2003. Reproductive cycles of males and females. Pages 135–162 in P. L. Lutz, J. A. Musick, and J. Wyneken, The biology of sea turtles II. CRC Press, Boca Raton, Florida.
- Hamza, A., et al. 2006. Marine turtles conservation at three nesting sites in Sirte, Libya. Page 138 in M. Frick, A. Panagopolou, A. Rees, and K. Williams, compilers. Book of abstracts. Proceedings of the 26th annual symposium on sea turtle biology and conservation. International Sea Turtle Society, Athens.
- Hawkes, L., A. C. Broderick, M. H. Godfrey, and B. J. Godley. 2005. Status of nesting loggerhead turtles *Caretta caretta* at Bald Head Island (North Carolina U.S.A.) after 24 years of intensive monitoring and conservation. *Oryx* **39**:65–72.
- Hawkes, L. A., A. C. Broderick, M. H. Godfrey, and B. J. Godley. 2009. REVIEW: Climate change and marine turtles. *Endangered Species Research* **7**:137–154.
- Heppell, S. S., M. L. Snover, and L. B. Crowder. 2003. Sea turtle population ecology. Pages 279–306 in P. L. Lutz, J. Musick, and J. Wyneken, editors. Biology of Sea Turtles II. CRC Press, Boca Raton, Florida.
- Hoekert, W. E. J., H. Neuféglise, A. D. Schouten, and S. B. J. Menken. 2002. Multiple paternity and female-biased mutation at a microsatellite locus in the olive ridley sea turtle (*Lepidochelys olivacea*). *Journal of Heredity* **8**:107–113.
- Hosken, D. J., T. W. J. Garner, T. Tragenza, N. Wedell, and P. I. Ward. 2003. Superior sperm competitors sire higher quality offspring. *Proceedings of the Royal Society of London* **B270**:1933–1938.
- Hosken, D., and P. Stockley. 2003. Benefits of polyandry: a life-history perspective. *Evolutionary Biology* **33**:173–194.
- Hughes, G. R. 1974a. The sea turtles of South East Africa II. Page 93 in Investigational report 36. South African Association of Marine Biological Research, Durban.

- Hughes, G. R. 1974b. The sea turtles of South East Africa I. Page 143 in Investigational report 35. South African Association of Marine Biological Research, Durban.
- Hutchings, J. A. 2001. Influence of population decline, fishing, and spawner variability on the recovery of marine fishes. *Journal of Fisheries Biology* 59:306–322.
- Ireland, J. S., A. C. Broderick, F. Glen, B. J. Godley, G. C. Hays, P. L. M. Lee, and D. O. F. Skibinski. 2003. Multiple paternity assessed using microsatellite markers in the green turtle, *Chelonia mydas* (Linnaeus, 1758) of Ascension Island, South Atlantic. *Journal of Experimental Ecology and Biology* 29:149–160.
- Jennings, S. 2001. Patterns and prediction of population recovery in marine reserves. *Reviews in Fish Biology and Fisheries* 10:209–231.
- Jennions, M. D., and M. Petrie. 2000. Why do females mate multiply? A review of the genetic benefits. *Biological Reviews* 75:21–64.
- Jribi, I., M. N. Bradai, and A. Bouain. 2002. Marine turtle nesting in Kuriat Islands, Tunisia, 2000. *Marine Turtle Newsletter* 96:4–6.
- Lahanas, P. N., M. M. Miyamoto, K. A. Bjørndal, and A. B. Bolten. 1994. Molecular evolution and population genetics and biology of Greater Caribbean green turtles (*Chelonia mydas*) as determined by mtDNA control region sequences. *Genetica* 94:57–67.
- Liermann, K., and R. Hilborn. 2001. Depensation: evidence, models and implications. *Fish and Fisheries* 2:33–58.
- Limpus, C. J. 1993. The green turtle, *Chelonia mydas*, in Queensland: breeding males in the Southern Great Barrier reef. *Wildlife Research* 20:513.
- Limpus, C. J., D. Carter, and M. Hamann. 2001. The green turtle, *Chelonia mydas*, in Queensland, Australia: the Bramble Cay rookery in the 1979–1980 breeding season. *Chelonian Conservation Biology* 4:34–46.
- Limpus, C., J. Miller, C. Parmenter, and D. Limpus. 2003. The green turtle, *Chelonia mydas*, population of Raine island and the northern Great Barrier Reef 1843–2001. *Memoirs of the Queensland Museum* 49:349–440.
- Marcovaldi, M. A., and A. Laurent. 1996. A six-season study of marine turtle nesting at Praia do Forte, Bahia, Brasil with implications for conservation and management. *Chelonian Conservation Biology* 2:55–59.
- Marcovaldi, M. A., and M. Chaloupka. 2007. Conservation status of the loggerhead sea turtle in Brazil: an encouraging outlook. *Endangered Species Research* 3:133–143.
- Margaritoulis, D. 2005. Nesting activity and reproductive output of loggerhead sea turtles, *Caretta caretta*, over 19 seasons (1984–2002) at Laganas Bay, Zakynthos, Greece: the largest rookery in the Mediterranean. *Chelonian Conservation Biology* 4:916–929.
- Márquez, R., J. Díaz, M. Sánchez, P. Burchfield, A. Leo, M. Carrasco, J. Peña, C. Jiménez, and R. Bravo. 1999. Results of the Kemp's ridley nesting beach conservation efforts in México. *Marine Turtle Newsletter* 85:2–4.
- Martin, M. E. I., R. Diaz-Fernandez, A. N. Konnorov, J. A. Rocardo, J. A. Valdes, G. E. Lopez, and J. P. Roberto. 2002. Project Update: University project for the study and conservation of Cuban sea turtles—completion of year three. *Marine Turtle Newsletter* 95:18–20.
- McClenachan, L., J. B. C. Jackson, and M. J. H. Newman. 2006. Conservation implications of historic sea turtle nesting beach loss. *Frontiers in Ecology and Evolution* 4:290–296.
- Miller, J. D. 1999. Determining clutch size and hatching success. Pages 124–139 in K. L. Eckert, K. A. Bjørndal, A. Abreu-Grobois, and M. Donnelly, editors. *Research and management techniques for the conservation of sea turtles*. IUCN/SSC Marine Turtle Specialist Group Publication No. 4.
- Miller, J. D. 1997. Reproduction in Sea Turtles. Pages 51–82 in P. Lutz and J. Musick, editors. *The biology of sea turtles*. CRC Press, Boca Raton, Florida.
- Moore, K. M., and R. M. Ball. 2002. Multiple paternity in loggerhead turtle (*Caretta caretta*) nests on Melbourne Beach, Florida: a microsatellite analysis. *Molecular Evolution* 11:281–288.
- Mortimer, J., and M. Donnelly. 2007. IUCN Red List Assessment: *Eretmochelys imbricata*. IUCN, Gland, Switzerland.
- Neave, F. 1953. Principles affecting the size of pink and chum salmon population in British Columbia. *Journals of the Fisheries and Resources Board Canada* 9:450–491.
- Niethammer, K. R., G. H. Balazs, J. S. Hatfield, G. L. Nakai, and J. L. Megyesi. 1997. Reproductive Biology of the green turtle (*Chelonia mydas*) at Tern Island, French Frigate Shoals. *Hawaiian Pacific Science* 51:36–47.
- Okemwa, G. M., S. Nzuki, and E. M. Mueni. 2004. The status and conservation of sea turtles in Kenya. *Marine Turtle Newsletter* 105:1–6.
- Pearse, D. E., and J. C. Avise. 2001. Turtle mating systems: behaviour, sperm storage and genetic paternity. *American Genetic Association* 92:206–211.
- Rees, A. F., E. Tzovani, and D. Margaritoulis. 2002. Conservation activities for protection of the loggerhead sea turtle (*Caretta caretta*) in Kyparissia Bay, Greece, during 2001. *Testudo* 5:45–54.
- Rees, A. F., A. Saad, and M. Jony. 2008. Discovery of a regionally important green turtle *Chelonia mydas* rookery in Syria. *Oryx* 42:456–359.
- Richardson, J. I., D. B. Hall, P. A. Mason, K. M. Andrews, R. Bjorkland, Y. Cai, and R. Bell. 2006. Eighteen years of saturation tagging data reveal a significant increase in nesting hawksbill sea turtles (*Eretmochelys imbricata*) on Long Island, Antigua. *Animal Conservation* 9:302–307.
- Roberts, C. M., and J. P. Hawkins. 1999. Extinction risk in the sea. *Trends in Ecology & Evolution* 14:241–246.
- Roberts, M. A., T. S. Schwartz, and S. A. Karl. 2004. Global population genetic structure and male-mediated gene flow in the green sea turtle (*Chelonia mydas*): Analysis of microsatellite loci. *Genetics* 166:1857–1870.
- Ross, J. P. 1979. Sea turtles in the sultanate of Oman. Project 1320. World Wildlife Fund, Washington, D.C.
- Rowe, S., and J. A. Hutchings. 2003. Mating systems and the conservation of commercially exploited marine fish. *Trends in Ecology and Evolution* 18:567–572.
- Santos, A. S., M. A. Marcovaldi, and M. H. Godfrey. 2000. Update on the nesting population of loggerhead sea turtles in Praia do Forte, Bahia, Brasil. *Marine Turtle Newsletter* 89:8–11.
- Sanz, P., S. Roques, A. Marco, and L. F. Lopez-Jurado. 2008. Fine-scale paternity of a loggerhead from Cape-Verde: within and between seasons. Technical memorandum NMFS-SEFSC-569. Page 138 in M. Frick, A. Panagopolou, A. Rees, and K. Williams, compilers. *Proceedings of the 27th annual symposium on sea turtle biology and conservation*. National Oceanic and Atmospheric Administration, Washington, D.C.
- Schofield, G., M. K. S. Lilley, C. M. Bishop, P. Brown, K. A. Katselidis, P. Dimopoulos, J. D. Pantis, and G. C. Hays. 2009. Conservation hotspots: implications of intense spatial area use by breeding male and female loggerheads at the Mediterranean's largest rookery. *Endangered Species Research* in press.
- Schroth, W., B. Streit, and B. Schierwater. 1996. Evolutionary handicap for turtles. *Nature* 7:521–522.
- Seminoff, J. A. 2004. 2004 IUCN Red List status assessment green turtle (*Chelonia mydas*). Marine Turtle Specialist Group, Gland, Switzerland, and Cambridge, United Kingdom.
- Soutullo, A., R. Liminana, V. Urios, M. Surroca, and J. A. Gill. 2006. Density-dependent regulation of population size in colonial breeders: Allee and buffer effects in the migratory Montagu's harrier. *Oecologia* 149:1432–1939.
- Stephens, P. A., and J. W. Sutherland. 1999. Consequences of the Allee effects for behaviour, ecology and conservation. *Trends in Ecology & Evolution* 14:401–404.

- Sutherland, W. J., and K. Norris. 2003. Behavioural models of population growth rates: implications for conservation and prediction. Pages 225–248 in R. M. Sibly, J. Hone, and T. H. Clutton-Brock, editors. *Wildlife Population Growth Rates*. Cambridge University Press, Cambridge, United Kingdom.
- Tregenza, T., and N. Wedell. 2002. Polyandrous females avoid costs of inbreeding. *Nature* **415**:71–73.
- Troëng, S., and E. Rankin. 2005. Long-term conservation efforts contribute to positive green turtle *Chelonia mydas* nesting trend at Tortuguero, Costa Rica. *Biological Conservation* **121**:111–116.
- Trono, R. B. 1991. Philippine Marine Turtle Conservation Program. *Marine Turtle Newsletter* **53**:5.
- van Dam, R. P., and C. E. Diez. 2007. Hawksbill nesting activity on Mona Island, Puerto Rico. *Proceedings of the 29th annual symposium on sea turtle biology and conservation*, in press.
- Woodson, H. M., D. W. Webster, and L. Creech. 1998. The nesting green sea turtles of North Carolina. Technical memorandum NMFS-SEFSC-412. Pages 152–154 in R. Byles and Y. Fernandez, compilers. *Proceedings of the 16th annual symposium on sea turtle biology and conservation*. National Oceanic and Atmospheric Administration, Washington, D.C.

