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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

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Abstract. – **Nesting data for the loggerhead sea turtle (*Caretta caretta*) are presented over a 19-year period (1984–2002) from Laganas Bay, Zakynthos Island, Greece. The nesting habitat is comprised of six beaches, totaling 5.5 km, which differ in physical features and human pressures. An average of 1293.7 nests were laid per season over the available nesting habitat, giving an overall nesting density of 235.2 nests/km, by far the highest in the Mediterranean. Mean nesting density was unevenly distributed per beach, ranging from 53.7 nests/km to 1062.8 nests/km. Despite the 19-year standardized work, no linear trend in the annual number of nests was detected. An overall 79.3% of laid nests were hatched, with an average clutch size of 116.5 eggs and a hatchling emergence success of 66.6%, yielding a mean annual output of 81,128 viable hatchlings. Spatial variability in incubation durations indicated production of hatchlings with different sex ratios on different beaches, with one producing almost entirely male hatchlings. Conservation measures for this important habitat, hosting 25.7% of the documented total loggerhead nesting effort in the Mediterranean, are in conflict with local economic interests and poorly enforced. However, the recent creation of a National Marine Park and associated Management Agency, comprising government, local communities, and environmental organizations, provides hope for a more balanced situation in the future.**

Key Words. – **Reptilia; Testudines; Cheloniidae; *Caretta caretta*; sea turtle; long-term nesting data; nesting season; incubation duration; reproductive output; Zakynthos; Mediterranean; Greece**

Loggerhead sea turtles (*Caretta caretta*) (Fig. 1) were first reported to nest in Laganas Bay, Zakynthos Island, Greece, in 1977, and preliminary data from 1977 through 1979 provided evidence that a substantial turtle population uses this area for nesting (Margaritoulis, 1982).

The loggerhead turtle is considered a threatened species by IUCN; it was listed initially as Vulnerable (Groombridge, 1982) and later, under the new Red List categories and criteria, as Endangered (Baille and Groombridge, 1996). The loggerhead is also included as a protected species in several international conventions which Greece has ratified (e.g., Barcelona Convention, Bern Convention, CITES). Soon after the nesting habitat's discovery in Laganas Bay, it was realized that parts of the habitat were seriously threatened by the onset of mass tourism, which was causing intensive and unplanned trends in development. The Greek government, by way of the National Council of Physical Planning and Environment, in 1980 passed a Directive for the protection of nesting areas in the bay. In compliance with the above Directive, since 1983 various building and land use regulations have been issued for the wider area. However, imposed regulations were poorly enforced as they were met with strong opposition by land owners who consider them as a hindrance to their expectations for easy and swift economic gain from tourism.

In order to provide scientific support for the upcoming legislation, a long-term beach monitoring and tagging project, with its main objectives to assess the nesting effort and other baseline data, was designed by the author and initiated in 1982 by the Ministry of Environment. During preliminary field work, in 1982 and 1983, standardized protocols were developed, biology students were trained as field observers, and logistical support was secured. A core of those students in 1983 formed the Sea Turtle Protection Society of Greece (STPS, now ARCHELON), which gradually undertook the task of recruitment and training of field workers during subsequent years. From 1984 onwards, the beach monitoring work covered systematically, and without interruption, the entire nesting habitat in Laganas Bay. Since 1988, the project, enriched with a public awareness component, was fully undertaken by STPS.

Although some of the collected data have been presented for conservation purposes to national authorities and/or to international agencies, the overall results of the beach monitoring work have not appeared in the scientific literature. This paper is an attempt to fill this gap with the hope that the published data will provide a substantial base for assisting in further planning of protection measures and management priorities, especially after the recent establishment of the National Marine Park of Zakynthos and the associated Management Agency (Dimopoulos, 2001).

STUDY SITE

The Island of Zakynthos, Greece, is located in the Ionian Sea, from 37°38' to 37°56' N and from 20°37' to

Figure 1. Loggerhead sea turtle (*Caretta caretta*) resting at the bottom of Laganas Bay, Zakynthos Island, Greece. Photo by Alan Rees/ARCHELON.

21°00' E, about 20 km from the western Peloponnesus coast. The island features a mild climate (mean annual air temperature 18.9°C) with a strong seasonality (mean monthly air temperatures range from 11.8°C in January to 27.5°C in August with little or no rain from June to August (Fig. 2)). Predominant winds blow from May through October from the northeast, while in November and December they change to southerlies (Andreakos, 1978).

Laganas Bay, on the south coast of Zakynthos, has a southeastern orientation with a coastline exceeding 20 km and an opening of about 12 km (Fig. 3). The waters inside the bay are rather shallow; the 20 and 50 m isobaths are found at distances of about 3.5 km and 6.0 km, respectively, from the coast at the center of the bay (Fig. 3). The bottom is generally sandy, with occasional submerged rocks along the sides and around the two islets inside the bay. Extensive sea grass (*Posidonia oceanica*) meadows start growing from the shallows along the sides of the bay, but at the center, due to wave action, they start at depths of about 20 m and reach depths of 40 m (P. Panagiotides, *pers. comm.*). Tourist development is now well established mainly in and around the villages of Laganas and Kalamaki, the boundaries of which have been expanded considerably during the last decade (Fig. 3).

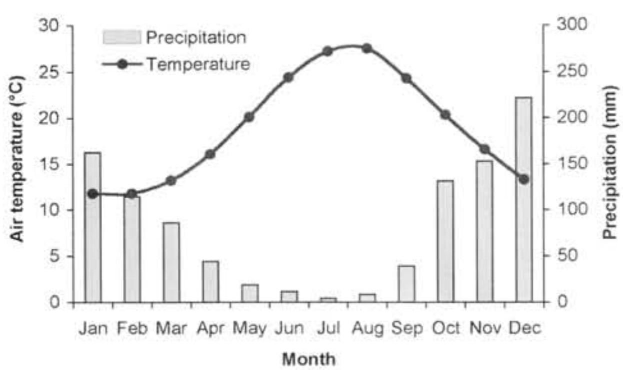

Figure 2. Monthly mean values of air temperature and precipitation on Zakynthos Island for the period 1930–75 (data adapted from Andreakos, 1978).

The suitable nesting habitat has a beach length of 5.5 km, consisting of a system of six discernible beaches with the following names (and lengths, measured along the water's edge in 1995): Marathonissi (370 m), East Laganas (2780 m), Kalamaki (500 m), Sekania (650 m), Daphni (600 m), and Gerakas (600 m) (Fig. 3). The beaches vary greatly in the degree of development, accessibility, human use, orientation, and substrate composition and color. A description of the beaches and the major problems they face appear in the Appendix. Further, Arianoutsou (1988) has described human perturbations affecting the beaches during 1985.

METHODS

Beach surveys and collection of data were mostly done by volunteer field observers, trained on site and supervised by project personnel. During the nesting season female loggerhead turtles emerge on their nesting beaches, mostly at night, to dig an egg-chamber where they lay a clutch of eggs. However, not all emergences result in nests; the percentage of emergences resulting in nests is defined as "nesting success". Although female turtles may not nest every year and a portion of females may nest repeatedly in a nesting season, counting of nests in a nesting area is an established way of estimating the abundance (and, thereby, possible trends) of the nesting population (Meylan, 1982; Bjorndal et al., 1999). After successful incubation of the eggs, hatchlings exit the nest and crawl to the sea, usually at night.

The emergence of mature females from the sea, and the emergence of hatchlings from nests, was determined by walking the beaches early in the morning and searching for tracks. The main aim of the beach surveys was twofold: (1) to record and count all adult female emergences and classify them, by the morphology of the track, as "nesting" or "non-nesting", and (2) to locate hatching nests by following tracks of emerged hatchlings. The second task was done systematically for all hatching nests from 1988 onwards. Hatching nests were marked and monitored with the aim to excavate them after termination of hatchlings' emergence in order to determine various parameters (e.g., clutch size). After recording, all tracks of females and hatchlings were obliterated to avoid confusion with the next count and possible interference from unauthorized persons.

Depending on logistics and manpower, beach surveys started annually from the middle of May through the beginning of June and terminated from the end of September through the middle of October. An effort was made to carry out beach surveys on a daily basis. However, in several instances, due to various reasons (e.g., adverse weather conditions, damage to boats), surveys on some beaches were temporarily conducted at intervals of 2–6 days. In these cases, care was taken to check whether female tracks had obliterated by weather conditions or human trampling. If tracks seemed to have been obliterated, the presumed lost emergences (and nests) were estimated by interpolation. Specifically, the mean daily count of the previous 2 and of the next 2 surveys was taken for each intervening day.

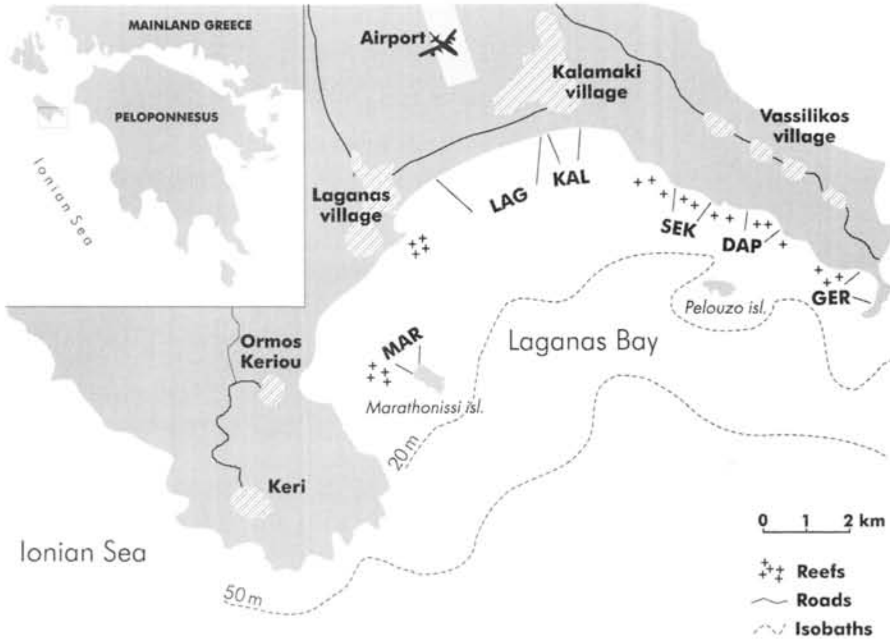

Figure 3. Map of Laganas Bay, Zakynthos Island, Greece, showing the six beaches comprising loggerhead nesting habitat (MAR: Marathonissi, LAG: East Laganas, KAL: Kalamaki, SEK: Sekania, DAP: Daphni, GER: Gerakas).

The seasonality and the duration of the nesting season were assessed by the dates of the first and last emergence, and the first and last nest, of the season. The duration of the nesting season was calculated as the elapsed time (in days) either from first nest to last nest or from first emergence to last emergence. Dates of "first emergence", and "first nest", were considered the dates on which these events were recorded (day 1). Dates of "last emergence", and "last nest", were considered the dates on which these events were recorded but only if these dates were within 12 days from the previously recorded event. Emergences and nests occurring after 12 days from the previous event were considered as "aberrant" cases and were not taken into account. The "hatching period" of the season started from the date of the "first hatch", i.e., the date on which the first hatchling tracks were recorded (day 1).

From 1988 onwards, all hatching nests throughout the nesting habitat were located, marked and counted. The overall fate of nests per season was estimated by comparing the number of hatched nests to the number of laid nests for the particular season. Weather conditions thought to adversely affect incubation (e.g., rain, inundation by high seas), were also noted.

Clutch size, hatching success, and emergence success were calculated from hatched nests that were not relocated or depredated. Hatched nests were excavated at least 8 days after the last hatchling emergence; in 2002 nest excavations were conducted 10–14 days after the first hatchling emergence. Excavation was done by hand and nest contents were sorted and counted as hatched eggs, unhatched eggs, and hatchlings (dead or alive). Hatchlings found live in the nest were considered as not able to exit the nest and therefore non-viable. By counting the grouped categories of nest contents we inferred: (1) clutch size as the sum of hatched and unhatched eggs, (2) hatching success as the percentage of hatched eggs, (3) emergence success as the percentage of eggs which produced hatchlings able to exit the nest (viable hatchlings). Clutch size was derived for each individual nest whereas hatching success and emergence success were calculated as a total for all nests inventoried during a particular season. Clutch sizes of 200 or more eggs were excluded as assumed to be excavation of two nests laid next to each other; not uncommon at the most densely nested beach sections.

Incubation duration, defined as the elapsed period (in days) from egg-laying until the emergence of the first hatchling, was derived from a sample of nests of known egg-laying date. These nests were precisely located, either during observation of egg-laying or by careful digging the day following oviposition. Subsequently, these nests were marked or fenced, and monitored to record the first appearance of hatchlings, i.e., the end of incubation. Mean incubation duration per beach was calculated for all nests sampled from the same beach during the entire study period.

The annual number of viable hatchlings (i.e., hatchlings able to exit nests) was calculated by multiplying the number of hatched nests by the mean clutch size of the season, and the product multiplied by the overall emergence success of the season.

RESULTS

Nesting Activity. — Over the 19-year study period (1984–2002) 95,501 female turtle emergences, of which 24,581 classified as nests, were recorded along the nesting habitat of Laganas Bay (Table 1). The annual number of emergences ranged from 3212 (in 1985) to 8128 (in 1995) with an average of 5026.4 emergences, while the annual number of nests ranged from 857 (in 1985) to 2018 (in 1995)

Table 1. Annual nesting activity over 19 nesting seasons (1984–2002) at Laganas Bay, Zakynthos Island, Greece; E = number of emergences, N = number of nests, NS = nesting success (%), ND = nesting density (nests/km).

	Marathonissi			East Laganas			Kalamaki			Sekania			Daphni			Gerakas			Total			
Year	E	N	NS	E	N	NS	E	N	NS	E	N	NS	E	N	NS	E	N	NS	E	N	NS	ND
1984	284	67	23.6	482	124	25.7	301	92	30.6	1761	595	33.8	627	123	19.6	219	60	27.4	3674	1061	28.9	192.9
1985	318	77	24.2	542	137	25.3	392	104	26.5	1195	333	27.9	587	133	22.7	178	73	41.0	3212	857	26.7	155.8
1986	321	88	27.4	961	190	19.8	349	94	26.9	2506	1046	41.7	1274	294	23.1	497	110	22.1	5908	1822	30.8	331.3
1987	360	105	29.2	778	117	15.0	577	93	16.1	2341	611	26.1	1458	138	9.5	262	46	17.6	5776	1110	19.2	201.8
1988	376	89	23.7	534	127	23.8	560	103	18.4	2838	823	29.0	1020	153	15.0	354	113	31.9	5682	1408	24.8	256.0
1989	459	146	31.8	801	170	21.2	716	185	25.8	2122	859	40.5	1118	212	19.0	327	127	38.8	5543	1699	30.7	308.9
1990	271	80	29.5	346	105	30.3	473	114	24.1	1510	430	28.5	533	124	23.3	237	73	30.8	3370	926	27.5	168.4
1991	432	110	25.5	429	111	25.9	397	76	19.1	1504	535	35.6	687	115	16.7	289	82	28.4	3738	1029	27.5	187.1
1992	242	103	42.6	266	90	33.8	460	128	27.8	1709	724	42.4	711	165	23.2	258	99	38.4	3646	1309	35.9	238.0
1993	553	167	30.2	620	150	24.2	723	148	20.5	3207	731	22.8	984	115	11.7	340	80	23.5	6427	1391	21.6	252.9
1994	399	136	34.1	813	231	28.4	456	72	15.8	3457	846	24.5	864	119	13.8	393	95	24.2	6382	1499	23.5	272.5
1995	691	228	33.0	929	269	29.0	741	156	21.1	3681	972	26.4	1535	267	17.4	551	126	22.9	8128	2018	24.8	366.9
1996	256	103	40.2	601	158	26.3	313	25	8.0	2026	536	26.5	748	111	14.8	203	54	26.6	4147	987	23.8	179.5
1997	366	119	32.5	477	124	26.0	292	71	24.3	1954	528	27.0	629	128	20.3	268	56	20.9	3986	1026	25.7	186.5
1998	376	134	35.6	472	143	30.3	518	65	12.5	2718	714	26.3	778	133	17.1	217	60	27.6	5079	1249	24.6	227.1
1999	261	110	42.1	689	175	25.4	546	110	20.1	3401	795	23.4	1067	161	15.1	239	79	33.1	6203	1430	23.1	260.0
2000	317	144	45.4	483	144	29.8	542	122	22.5	2584	726	28.1	866	141	16.3	268	84	31.3	5060	1361	26.9	247.5
2001	331	130	39.3	446	140	31.4	491	83	16.9	2187	670	30.6	733	119	16.2	229	82	35.8	4417	1224	27.7	222.5
2002	450	124	27.6	544	132	24.3	458	95	20.7	2748	652	23.7	654	90	13.8	269	82	30.5	5123	1175	22.9	213.6
Mean	371.7	118.9	32.0	590.2	149.3	25.3	489.7	101.9	20.8	2392.1	690.8	28.9	888.1	149.5	16.8	294.6	83.2	28.2	5026.4	1293.7	25.7	235.2

with an average of 1293.7 nests (Table 1). No linear trend was detected in the annual number of either emergences ($r^2 = 0.033$, $p = 0.458$) or nests ($r^2 = 0.002$, $p = 0.844$) over the 19-year period (Fig. 4).

The annual nesting success, over the entire habitat, varied over the seasons from 19.2% (in 1987) to 35.9% (in 1992), with an overall mean value of 25.7% (Table 1). The nesting density over the total beach length of 5.5 km ranged from 155.8 to 366.9 nests/km/season with a mean of 235.2 nests/km/season over the 19-year period (Table 1).

The nesting effort varied greatly from beach to beach; the mean annual number of emergences per beach ranged from 294.6 on Gerakas to 2392.1 on Sekania and the mean number of nests from 83.2 on Gerakas to 690.8 on Sekania (Table 1). The percentage contribution of each beach to the total number of nests in the bay is shown in Fig. 5. Sekania was by far the most turtle-frequented beach, receiving 53.4% of all nests over the 19 seasons.

Similarly to nesting effort, nesting success varied per beach both within and among seasons. Low values of nesting success were recorded on Daphni (mean: 16.8%, range: 9.5–23.3) and Kalamaki (mean: 20.8%, range: 8.0–30.6), and relatively high values on Sekania (mean: 28.9%, range: 22.8–42.4) and Marathonissi (mean: 32.0%, range: 23.6–45.4) (Table 1).

Nesting density varied greatly among the individual beaches; lowest nest concentrations were found on East Laganas (mean: 53.7 nests/km, range: 32.4–96.8) and highest concentrations on Sekania (mean: 1062.8 nests/km, range: 512.3–1609.2) and Marathonissi (mean: 321.4 nests/km, range: 181.1–616.2) (Table 2).

The dates of the first and last emergence, and of the first and last nest, as well as the dates of first hatch are shown per season for Sekania, in Table 3. It is thought that Sekania beach, receiving the most nests, is representative of the entire habitat as far as the temporal evolution of nesting and hatching is concerned. Timely and regular beach surveys permitted the precise recording of the above dates during most seasons. However, in five seasons (1986, 1998–2001) the start of the nesting activity was missed because female

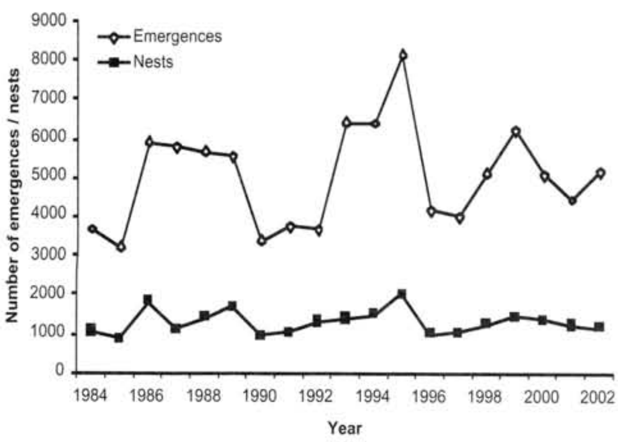

Figure 4. Interannual variation of loggerhead turtle nesting activity (emergences and nests) at Laganas Bay, during the 19-year study period (1984–2002).

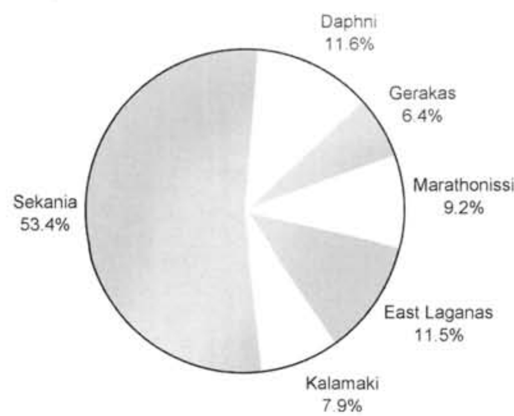

Figure 5. Percentage contribution of individual beaches to total number of nests (n = 24,581) in Laganas Bay, over the 19-year study period (1984–2002).

Table 2. Spatial distribution of the annual nesting density, per beach, in Laganas Bay over the 19-year period 1984-2002.

Nesting beach	Beach length (m)	Annual Nesting Density (nests/km) Mean	Range
Marathonissi	370	321.4	181.1 - 616.2
East Laganas	2780	53.7	32.4 - 96.8
Kalamaki	500	203.8	50.0 - 370.0
Sekania	650	1062.8	512.3 - 1609.2
Daphni	600	249.2	150.0 - 490.0
Gerakas	600	138.7	76.7 - 211.7
Overall	5500	235.2	155.8 - 366.9

tracks were already present on the beach on the first survey. During these five seasons the dates of the first emergence, and nest, were estimated either by the external appearance of the emergence track (if still present) or, retrospectively, by the date of the first hatching of the season, from which the mean incubation duration of the season was subtracted. It is of interest to note that in 9 out of 14 seasons (64.3%) the date of first nest coincided with the first emergence, while in five seasons the first nest occurred 1–3 days after the first emergence. The last emergence coincided with the last nest in 8 seasons (42.1%), while in the remaining 11 seasons, the last emergence occurred 1–12 days after the last nest. There were some "aberrant" cases of late nests: 27 September 1984 (13 days after the previous event) and 11 September 1996 (15 days after the previous event), and a late emergence on 18 September 1989 (14 days after the previous event).

The date of first hatch was precisely recorded in all seasons; it occurred on average 59.2 days (range: 52–64, n = 19 seasons) after the first nest (including the 5 seasons when the date of first nest was estimated) or 58.7 days (range: 52–64, n = 14 seasons) after the first nest (excluding the 5 seasons when the date of first nest was estimated) (Table 3). End of hatching was not possible to record because at the termination of fieldwork a number of nests were still incubating (see dates of last survey in Table 3).

The average nesting season over the 19-year period was 88.8 days (range: 75–100) from first nest to last nest, or 92.3 days (range: 85–102) from first emergence to last emergence (Table 3). If we take into account only the 14 seasons when first emergence and first nest were precisely recorded, the above durations become 86.9 days (range: 75–99) and 90.8 days (range: 85–102), respectively (Table 3).

The evolution of the nesting activity (emergences, nests, nesting success) combined over 11 seasons (1992–2002), is shown in Fig. 6 for the entire nesting habitat. It is interesting to note that nesting success generally decreased with advancement of the season. Combining the total nesting effort for all 19 seasons, we inferred the following monthly distribution of nests: 0.9% in May, 34.6% in June, 50.5% in July, 13.9% in August, and 0.1% in September.

The annual percentage of hatched nests to laid nests ranged from 66.0% (in 1989) to 90.9% (in 1990), with an overall mean of 79.3% over the 15 last seasons (1988–2002) when recording of hatched nests was systematically conducted (Table 4). It must be noted, however, that the recorded numbers of hatched nests are considered an underestimate because: (1) some nests certainly hatched after termination of fieldwork, (2) some hatched nests were undetected due to unfavorable beach characteristics (e.g., coarse sand, which does not show hatchling tracks well), as well as adverse weather conditions (rain, wind, inundation) or human trampling, which can easily erase hatchling tracks, and (3) some nests might have been hatched on days when

Table 3. Start/end dates of nesting activity, dates of first hatch, dates of last survey, elapsed days from first nest to first hatch and duration of nesting season over 19 seasons at Sekania, the most turtle-frequented beach in Laganas Bay; * = estimated dates.

Year	Date of first emergence	first nest	first hatch	last nest	last emergence	last survey	Elapsed days from first nest to first hatch	Duration of nesting season (in days) from first to last nest	first to last emergence
1984	8 Jun	8 Jun	5 Aug	14 Sep	14 Sep	11 Oct	59	99	99
1985	30 May	30 May	31 Jul	24 Aug	26 Aug	5 Oct	63	87	89
1986	20 May *	20 May *	20 Jul	20 Aug	24 Aug	14 Sep	62	93	97
1987	8 Jun	8 Jun	9 Aug	3 Sep	4 Sep	23 Sep	63	88	89
1988	29 May	30 May	28 Jul	21 Aug	21 Aug	17 Sep	60	84	85
1989	2 Jun	2 Jun	4 Aug	4 Sep	4 Sep	29 Sep	64	95	95
1990	2 Jun	3 Jun	28 Jul	30 Aug	30 Aug	16 Oct	56	89	90
1991	15 Jun	15 Jun	12 Aug	28 Aug	9 Sep	17 Oct	59	75	87
1992	13 Jun	13 Jun	12 Aug	29 Aug	5 Sep	9 Oct	61	78	85
1993	1 Jun	4 Jun	1 Aug	4 Sep	10 Sep	12 Oct	59	93	102
1994	30 May	30 May	25 Jul	26 Aug	2 Sep	13 Oct	57	89	96
1995	3 Jun	5 Jun	26 Jul	21 Aug	28 Aug	7 Oct	52	78	87
1996	30 May	30 May	29 Jul	24 Aug	27 Aug	7 Oct	61	87	90
1997	30 May	2 Jun	26 Jul	25 Aug	25 Aug	9 Oct	55	85	88
1998	29 May *	29 May *	27 Jul	18 Aug	25 Aug	6 Oct	60	82	89
1999	23 May *	23 May *	20 Jul	30 Aug	31 Aug	29 Sep	59	100	101
2000	18 May *	18 May *	15 Jul	24 Aug	24 Aug	29 Sep	59	99	99
2001	19 May *	19 May *	20 Jul	23 Aug	23 Aug	17 Oct	63	97	97
2002	23 May	23 May	19 Jul	19 Aug	19 Aug	17 Oct	53	89	89
Mean (n = 19 seasons)							59.2	88.8	92.3
Mean (n = 14 seasons; eliminating estimated dates for 5 seasons)							58.7	86.9	90.8

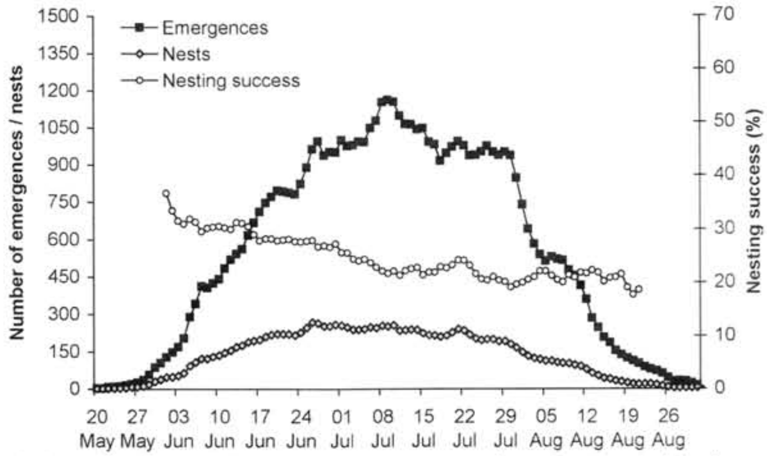

Figure 6. Within-season evolution of nesting activity (emergences, nests, nesting success), combined over 11 seasons (1992–2002) in Laganas Bay, Zakynthos. A 3-day moving average was used to smooth the graph. Nesting success was not plotted at the beginning or end of the nesting season to avoid high fluctuations due to small sample sizes.

monitoring at certain beaches was not done and hatchling tracks subsequently erased. No linear trend was detected in the annual number of hatched nests over the period 1988–2002 ($r^2 = 0.0003$, $p = 0.92$).

Considering the causes of nest failure, we can take advantage of a sample of 522 nests, which were fenced *in situ* in the period 1990–2002. All these nests were monitored from egg-laying until their post-hatch excavation or, if not hatched, until their excavation. From these nests, 42 (8.0%) did not hatch at all. Excavation of unhatched clutches revealed that most of them were affected by (1) invasion of nearby vegetation roots, (2) rise of the underground water table, or (3) insect larvae.

Reproductive Output. — The mean clutch size per season, ranging from 110.0 eggs (in 2000) to 130.4 eggs (in 1992), exhibited significant differences among seasons (one-way ANOVA, df = 18, F = 13.40, $p < 0.01$) (Table 5). However, no linear trend was detected over the seasons ($r^2 = 0.013$, $p = 0.642$).

Mean annual hatching success ranged from 61.7% (in 1989) to 80.2% (in 1985) whereas emergence success ranged from 58.9% (in 1992) to 78.5% (in 1985) (Table 5). Overall mean values gave 71.5% for hatching success and 66.6% for emergence success, indicating an overall within-nest hatchling mortality of 4.9% (of the total number of eggs), ranging from 0.8% (in 1989) to 8.4% (in 1998). As witnessed during nest excavations, the main apparent reasons for in-nest hatchling mortality were vegetation roots, especially of tamarisk trees (*Tamarix* sp.) at East Laganas, flooding of nests by rising of the water table (at Gerakas), and deposition of clay, eroded by rainfall from nearby slopes (particularly at Sekania) which after hardening did not allow hatchlings to exit the nest. No linear trend over the years was detected either for hatching success ($r^2 = 0.0888$, $p = 0.215$) or for emergence success ($r^2 = 0.0127$, $p = 0.646$).

The overall mean incubation duration, weighted as per overall distribution of nesting to individual beaches, was calculated to 55.2 days (range: 42–89, $n = 666$ clutches). However, there were substantial differences among the beaches; short durations at Kalamaki (51.3 days), Daphni (52.0 days) and Sekania (52.7 days), and longer durations at

Table 4. Number of laid and hatched nests per season, percentage of hatched nests (until termination of field work) and major weather events affecting incubation in Laganas Bay.

Year	Laid nests	Hatched nests	Percent hatched	Major weather events during incubation
1988	1408	1120	79.5	Rainstorms and major inundations (14-17/9)
1989	1699	1121	66.0	Repeated rainstorms and major inundations from 3/9 onwards
1990	926	842	90.9	Minor inundations (13/9, 8/10); rains (17-23/9)
1991	1029	856	83.2	Rains (19/9, 24/9); minor inundation (9/10)
1992	1309	985	75.2	Rainstorms and major inundations (25-26/9, 2-7/10); practically no hatch after 2/10
1993	1391	1125	80.9	Rains (5-6/9, 29/9, 5/10); major inundation (3-4/10)
1994	1499	1292	86.2	Rain (20/9)
1995	2018	1415	70.1	Rains and inundations from 15/8 onwards; little hatch after a major inundation (29/9)
1996	987	772	78.2	Rainstorms from 13/9 onwards; major inundations (13-14/9, 27/9); no hatch after 27/9
1997	1026	760	74.1	Repeated rainstorms from 20/8 onwards; major inundations (18-19/9, 24-26/9)
1998	1249	1114	89.2	Rains from 13/9 onwards; minor inundation (3/10)
1999	1430	1250	87.4	Rainstorms from 29/8 onwards; minor inundations (12-14/9, 17-19/9)
2000	1361	1124	82.6	Rain (6/9); minor inundations (9/9, 27-28/9)
2001	1224	1068	87.3	Rains from 23/8 onwards
2002	1175	810	68.9	Rainstorms and inundations from 27/7 onwards; major inundation (11-12/8)
Overall mean			79.3	

Table 5. Clutch size, hatching success, emergence success, and in-nest hatchling mortality per season in Laganas Bay. Data were extracted from hatched nests that were not relocated or depredated. Sample size (n) was the same per season for all calculated parameters. Mean clutch sizes with the same letter were not significantly different (p > 0.05) based on a Student-Newman-Keuls test for post hoc comparisons among means.

Year	Clutch Size				Hatching success (%)	Emergence success (%)	Hatchling mortality in nest (%)
	Mean		Range	*n* (clutches)			
1984	115.4	abcd	46-193	102	68.0	64.5	3.5
1985	111.9	abc	48-162	94	80.2	78.5	1.7
1986	111.4	ab	15-194	49	74.5	69.4	5.1
1987	115.8	abcd	32-190	157	66.8	64.9	1.9
1988	123.4	d	11-179	161	68.1	64.6	3.5
1989	121.2	cd	19-191	208	61.7	60.9	0.8
1990	112.6	abc	14-198	122	72.2	66.3	5.9
1991	113.7	abc	12-188	149	71.1	66.7	4.4
1992	130.4	e	44-199	177	63.7	58.9	4.8
1993	129.7	e	26-197	349	68.7	63.9	4.8
1994	116.9	abcd	14-187	531	67.9	60.0	7.9
1995	119.6	bcd	17-198	598	69.8	66.6	3.2
1996	117.2	abcd	18-186	350	75.2	70.1	5.1
1997	115.3	abcd	24-195	543	72.7	68.5	4.2
1998	116.8	abcd	34-195	383	69.3	60.9	8.4
1999	119.5	abcd	38-186	196	75.9	70.5	5.4
2000	110.0	a	7-197	638	76.9	70.1	6.8
2001	110.5	ab	12-198	661	73.9	69.2	4.7
2002	112.7	abc	41-199	504	74.6	71.9	2.7
Overall	116.5		7-199	5972	71.5	66.6	4.9

Gerakas (56.2 days), East Laganas (60.8 days), and Marathonissi (69.8 days) (Fig. 7).

The annual number of viable hatchlings, over the entire habitat, ranged from 60,025 (in 1997) to 112,710 (in 1995) with a weighted annual mean of 81,128 hatchlings in the 15-year period 1988–2002 (Table 6). It should be noted that these figures are considered as conservative because the recorded hatched nests were underestimated. Further, it must be stressed that these numbers represent emerged hatchlings and do not include losses afterwards. Possible predators of hatchlings, after their exit from nests, were, mainly at night, martens (*Martes foina*) and rats (*Rattus* spp.) and, during the day, various species of seagulls and crows (Margaritoulis, 1985). Also, a number of hatchlings were disorientated by artificial lights at night and lost on land. Although no specific study was done to quantify this type of loss, circumstantial evidence suggests that it was not extensive.

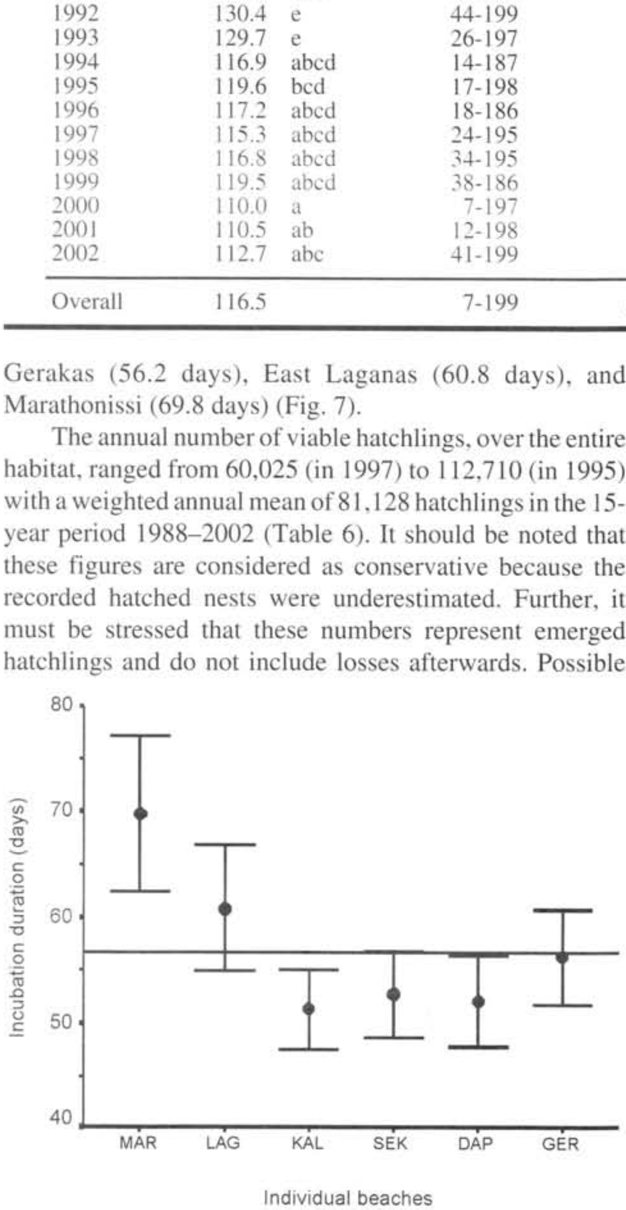

Figure 7. Mean incubation durations (± 1 SD) per beach in Laganas Bay. MAR: Marathonissi (69.8 days, range: 56–89, $n = 100$), LAG: East Laganas (60.8 days, range: 46–78, $n = 194$), KAL: Kalamaki (51.3 days, range: 42–60, $n = 28$), SEK: Sekania (52.7 days, range: 44–75, $n = 216$), DAP: Daphni (52.0 days, range: 47–59, $n = 10$), GER: Gerakas (56.2 days, range: 48–69, $n = 118$). The horizontal line represents the pivotal incubation duration (56.6 days) at nearby Kyparissia Bay (Mrosovsky et al., 2002).

It is interesting to note that annual fluctuations in the number of emerged hatchlings do not necessarily follow those of laid eggs, e.g., in 1989, a particularly "good" season with 1699 nests (205,919 laid eggs), produced only 82,742 hatchlings (Fig. 8). No trend was detected over the years either in the number of eggs laid ($r^2 = 0.0503$, $p = 0.422$) or

Table 6. Calculated number of viable hatchlings emerged annually during the period 1988–2002 at Laganas Bay, Zakynthos Island, Greece.

Year	Number of hatched nests	Mean clutch size	Emergence success (%)	Emerged hatchlings
1988	1120	123.4	64.6	89,282
1989	1121	121.2	60.9	82,742
1990	842	112.6	66.3	62,858
1991	856	113.7	66.7	64,917
1992	985	130.4	58.9	75,654
1993	1125	129.7	63.9	93,238
1994	1292	116.9	60.0	90,621
1995	1415	119.6	66.6	112,710
1996	772	117.2	70.1	63,425
1997	760	115.3	68.5	60,025
1998	1114	116.8	60.9	79,240
1999	1250	119.5	70.5	105,309
2000	1124	110.0	70.1	86,672
2001	1068	110.5	69.2	81,666
2002	810	112.7	71.9	65,635

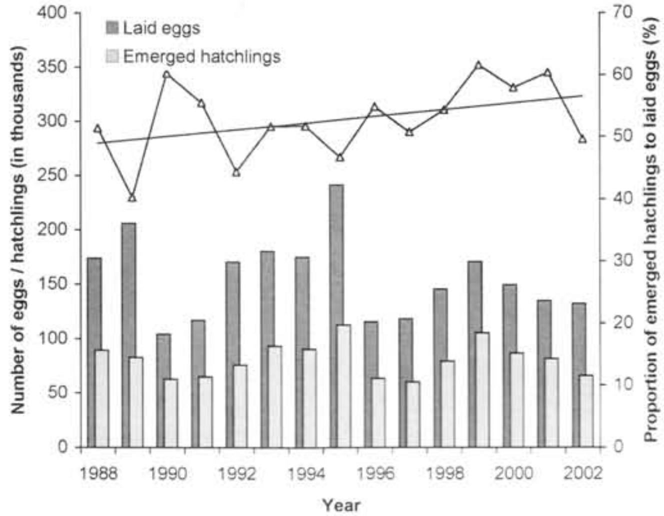

Figure 8. Annual variation of the reproductive output (eggs laid and emerged hatchlings) of the loggerhead population nesting at Laganas Bay for the period 1988–2002. Graph on top shows the proportion of emerged hatchlings to eggs laid; the straight line is the apparent trend (not significant).

in the number of emerged hatchlings ($r^2 = 0.0007$, $p = 0.927$). However, the proportion of emerged hatchlings to eggs laid demonstrated an upward trend over the seasons, although this was not significant ($r^2 = 0.1597$, $p = 0.14$) (Fig. 8).

DISCUSSION

Nesting Activity. — The main loggerhead nesting concentrations in the Mediterranean are found in Greece, Turkey, and Cyprus (Margaritoulis et al., 2003, and references therein). Substantial nesting has also been reported in Libya (Laurent et al., 1997) but the nesting effort there has not been quantified in the course of a monitoring project. Few nests also occur in Egypt, Israel, Italy, Syria, Tunisia (Margaritoulis et al., 2003, and references therein), Lebanon (Newbury et al., 2002), and occasional nests in Spain (Llorente et al., 1993; Tomás et al., 2002).

The documented loggerhead nesting effort in the Mediterranean reaches an average of 5031 nests/season; of these, 60.6% (3050.6 nests/season) are in Greece, 27.2% (1365.9 nests/season) in Turkey, 11.4% (571.6 nests/season) in Cyprus, and the remaining in Israel and Tunisia (Margaritoulis et al., 2003). It must be noted that the above figures do not include nests outside the monitored areas or in countries where regular monitoring has not yet been initiated (e.g., Libya). The average annual number of nests in Laganas Bay (1293.7 nests in the context of the present 19-year study) represents 42.4% of the total nesting effort in Greece and 25.7% of the total nesting effort in the Mediterranean. Thus, Laganas Bay hosts, over 5.5 km of beach length, the largest nesting aggregation of loggerheads in the Mediterranean.

This is followed, in a regional perspective, by the 44-km Kyparissia Bay, western Peloponnesus, Greece, with an estimated 17-year average of 620 nests/season (Margaritoulis and Rees, 2001), and then by the 10.8-km Rethymno beach on the island of Crete, with an average of 387.3 nests/season (Margaritoulis et al., 2003). Greece hosts the three largest nesting assemblages of the loggerhead turtle in the Mediterranean, and these three assemblages hold about 45.7% of the total monitored nesting effort in the Mediterranean.

Interannual fluctuations of nesting effort are rather common in loggerhead populations around the globe; e.g., South Africa (Hughes, 1974), Florida (Davis and Whiting, 1977), South Carolina (Talbert et al., 1980), Brazil (Marcovaldi and Laurent, 1996), Japan (Sato et al., 1997). Also, in the Mediterranean there are examples of interannual fluctuations in nest numbers; in Turkey (Fethiye beach) and in Cyprus, annual fluctuations over 3 seasons reached, respectively, 117% (Türkozan, 2000) and 112% (Broderick and Godley, 1996). In Kyparissia Bay, in the 17-year period 1984–2000, the annual number of nests exhibited a maximum fluctuation of 224% (erroneously stated as 324% in Margaritoulis and Rees, 2001). High interannual fluctuations in the number of nests are probably a result of specific reproductive characteristics of sea turtles; most individuals do not nest every season but exhibit irregular remigration patterns and a portion of nesting females nests several times within the same season (Dodd, 1988, and references therein).

The absence of an apparent trend in the annual nesting effort, after 19 years of systematic monitoring work in Laganas Bay, should not be interpreted as indicating a "stable nesting population" because a possible trend may be obscured by the high interannual fluctuations (see also Limpus, 1995). It seems that more years of monitoring the nesting activity are necessary to allow a reliable evaluation of trends in Laganas Bay.

Although sea turtles may abort nesting attempts for inexplicable reasons (Dodd, 1988), nesting success provides a measure of the difficulties encountered by turtles during the nesting procedure. Factors decreasing nesting success may have environmental and/or human origins. In Laganas Bay, annual fluctuations in nesting success (see Table 1) are mainly attributed to the dryness of the sand; when sand lacks appropriate moisture, turtles have difficulty in excavating egg-chambers. The gradual decrease of nesting success as the season progresses (and the sand becomes drier because of decreased precipitation; see Fig. 2), noted in both Laganas Bay (see Fig. 6) and Kyparissia Bay (Margaritoulis and Rees, 2001) over a number of nesting seasons, supports this explanation. Similarly, Limpus et al. (2001) noted that for green turtles in Australia the primary reason for poor nesting success is dry sand. Other causes of failed nesting attempts, observed in Laganas Bay, include buried objects (e.g. stones, rubbish) or vegetation roots precluding the digging of an egg-chamber, disturbance when turtles crawled into each other (especially at the densely nested Sekania beach) or into items of beach furniture as well as disturbance by people. It must be noted, however, that human perturbations at night, restricted to certain sections of the nesting habitat (see Appendix), are generally similar over the seasons and do not seem to cause major interseasonal disruptions of nesting success. Therefore, the dryness of beach sand is considered the primary factor to account for the annual changes in the overall nesting success.

In Kyparissia Bay, over an 11-year period (1990–2000), nesting success was 38.6% (annual range: 28.6–57.6) (Margaritoulis and Rees, 2001) which is 13.3% higher than the nesting success in Laganas Bay (25.3% for the same 11-year period); the difference is attributed primarily to the better environmental conditions (wide beach, ample sand) at Kyparissia Bay and secondly to the lesser human disturbances there (Margaritoulis and Rees, 2001).

Laganas Bay does not only feature the greatest number of loggerhead nests in the Mediterranean but, with an overall nesting density of 235.2 nests/km/season, is by far the most densely nested area in the region (Table 7). Trying to explain this high nesting concentration of loggerheads, rather atypical for the region, one could attribute this to habitat restriction. However, in the bay there is also a 2-km beach sector (the West Laganas beach) which has been almost fully developed and, since the start of this project, not used by turtles. If we consider this additional sector as part of the nesting habitat, the overall nesting density drops to about 172 nests/km/season, which is again considered as very high in a regional context (Table 7).

Another factor that would probably account for the high nesting density in Laganas Bay is the lack of any serious nest predation. It is known that in other nesting areas in the Mediterranean, nest predation, particularly by large mammals (e.g., foxes), affects a substantial percentage of clutches. The loggerhead population nesting in Zakynthos seems to have avoided this natural regulating mechanism.

Uneven spatial distribution of loggerhead activity, within a nesting habitat, has been observed throughout the species' range, e.g., South Africa (Hughes, 1974), USA (Worth and Smith, 1976; Talbert et al., 1980; Shoop et al., 1985), Brazil (Marcovaldi and Laurent, 1996), Turkey (Türkozan and Baran, 1996; Yerli and Dolezel, 1998).

In Laganas Bay, there is tremendous variation in nesting density among the individual beaches of the nesting habitat (Table 2). Although nest site selection is a complicated process (Wood and Bjorndal, 2000), differences in beach preference by nesting turtles can be correlated to human disturbances (Fangman and Rittmaster, 1994; Katselidis and Dimopoulos, 2000). Indeed, the beaches of Sekania and Marathonissi, showing the highest nesting densities, are not developed and have the least human presence at night (see Appendix). The beaches of East Laganas, Kalamaki, and Daphni, featuring moderate to low nesting densities, are characterized by a variety of human disturbances at night, including human presence and artificial lights.

Differences in nesting success among individual beaches (Table 1) can be explained by various factors. The relatively high overall nesting success documented on Marathonissi (32.0%), Sekania (28.9%), and Gerakas (28.2%) are attributed to the good sand conditions and the lack of human disturbances at night. On the contrary, the low nesting success on Kalamaki (20.8%) is most probably caused by the high degree of human presence, while the lowest recorded nesting success on Daphni (16.8%) is a combined effect of human disturbance and a troublesome nesting terrain, comprised of a large percentage of pebbles and stones. Another cause of lowered nesting success on Kalamaki was the accumulation on the beach, during certain seasons, of a thick mattress of dried leaves of *Posidonia oceanica* which rendered excavation of egg-chambers impossible. Although these sea grass mounts were usually collected by the munici-

Table 7. Annual nesting densities at Laganas Bay and other loggerhead rookeries in the Mediterranean.

Nesting Beach	Season(s)	Nesting density (nests/km)	Source
Laganas Bay, Greece	1984-2002	155.8–366.9	Present study
Kyparissia Bay, Greece	1994-2000	34.8–82.0	Margaritoulis and Rees, 2001
Rethymno, Greece	1990-1997	29.3–47.8	Margaritoulis, 2000
Alagadi, Cyprus	1993-1998	19.0–47.5	Godley et al., 2001
Dalyan, Turkey	1997	28.7	Ilgaz and Baran, 2001
Kizilot, Turkey	1996-1997	24.0–27.7	Türkozan, 2000
El-Mansouri, Lebanon	2001	26.4	Newbury et al., 2002
Koroni, Greece	1995-2002	13.0–24.4	Margaritoulis and Rees, in press
Fethiye, Turkey	1993-1997	11.0–23.9	Türkozan and Baran, 1996; Baran and Türkozan, 1996; Türkozan, 2000
Anamur, Turkey	1996	15.6	Yerli and Dolezel, 1998
Belek, Turkey	1997	9.9	Sak and Baran, 2001
Patara, Turkey	1997	7.4	Taskin and Baran, 2001

pality before the start of nesting, during certain seasons this was not done in time. For example, in 1996 large amounts of sea grass were left on Kalamaki beach during a large part of the nesting season and this resulted in the unusually low nesting success of 8% (Table 1).

The Mediterranean Sea hosts, globally, the northernmost nesting areas of the loggerhead turtle; therefore nesting activity is highly seasonal as turtles exploit the relatively narrow window of favorable environmental conditions. However, at the margin of the nesting range, small differences in various environmental factors may cause recognizable changes in the seasonality of nesting and specifically in the start/end dates of the nesting season (e.g., sea temperature, suggested by Hughes (1974) to advance or retard the nesting season). Indeed, Margaritoulis and Rees (2001) noted that loggerheads in Kyparissia Bay start and terminate their nesting later than loggerheads in Turkey and Cyprus. Loggerheads in Turkey and Cyprus complete more than 60% of their annual nesting in the months of May and June, while in Kyparissia Bay the number of nests during these months accounts for less that 40% of the annual nesting effort (Margaritoulis and Rees, 2001). In Laganas Bay the number of nests made in May and June, over the 19-year study period, accounted for 35.5% of the total nests.

An apparent consequence of this regional difference in nesting seasonality is that loggerheads in Laganas Bay, nesting generally later in the season, have to face more anthropogenic disturbances than those in Turkey and Cyprus, because of the dramatic increase of human presence in Laganas Bay from June to July (see Arianoutsou, 1988).

Loggerheads in Laganas Bay do not face the stress of nest predation by mammals, as is the case in several other Mediterranean areas. In Turkey, nest predation by mammals is a major problem on most loggerhead beaches, e.g., in Dalyan 65-70% of nests were depredated by foxes (Erk'akan, 1993), in Anamur at least 26.7% of nests were depredated by foxes and dogs (Yerli and Dolezel, 1998), in Göksu Delta 40.2% of nests were depredated (van Piggelen and Strijbosch, 1993), in Patara 35% of nests were totally (and 11% partially) depredated by foxes (Erdogan et al., 2001). In northern Cyprus, 36% of nests were depredated (Broderick and Godley, 1996). In mainland Greece nest predation is also a major problem, e.g., in Kyparissia Bay 48.4% of nests were disturbed by predators (mainly foxes) (Margaritoulis, 1988a).

Lack of mammalian predation in Laganas Bay is mainly due to the absence of the red fox *Vulpes vulpes*, a notable turtle nest predator. A relatively small number of nests (estimated at 5-10 per season), partly depredated by dogs and, more rarely, by martens and rats, do not have a sizeable impact on the overall fate of nests. In addition, some nests are lost to the specific causes already mentioned above (invasion by roots, rise of the water table, insect larvae).

Anthropogenic destruction of clutches is also considered very low in Laganas Bay. This is because the increased beach use by people (especially during the last years) has been partially "regulated" through intensive public awareness projects, on-site safeguarding and wardening, by encouraging beach users to avoid nesting zones and to stay close to the water, whereas nests made close to the sea are generally fenced or relocated to safer areas (Dimopoulos, 1995; Dimopoulos et al., 1999).

A serious cause of nest destruction in Laganas Bay is adverse weather conditions and, specifically, severe inundation episodes. Indeed, fluctuations in the annual percentage of hatched nests can be accounted for, to some extent, by weather conditions during the main period of incubation. The relatively low percentage of hatched nests in seasons 1989 (66.0%), 1992 (75.2%), 1995 (70.1%), 1996 (78.2%), 1997 (74.1%), and 2002 (68.9%) can be partly explained by the heavy rainfall and the strong southern winds that caused severe inundations in periods with relatively many nests under incubation (Table 4). Strong southern and southeastern winds, causing major inundation episodes on the southeastern oriented beaches of Laganas Bay, usually predominate in November and December (Andreakos, 1978), i.e., after hatching of the great majority of nests and, thus, have negligible impact. Occasionally, however, southerlies may start blowing earlier in the season, when many nests are still incubating, and this usually has a measurable impact on the overall fate of nests. This phenomenon was particularly prevalent in 1989 and 2002 when seawater covered almost completely the nesting beaches in the bay and apparently reduced substantially the percentage of hatched nests (Table 4). Nevertheless, the rather normal proportion of hatched nests during 1998, 1999, and 2001, periods with repeated rainfall during incubation (see Table 4), is an indication that the effect of inundation on eggs is not so simple and that it depends also on other parameters (e.g., duration of the inundation), which were not investigated in this study.

Reproductive Output. — The overall clutch size recorded in Laganas Bay over the 19-year period (mean: 116.5, SD = 27.9, range: 7–199 eggs, n = 5972 clutches) is similar to that documented in Kyparissia Bay by Margaritoulis (1988a) (mean: 117.7, SD = 22.7, n = 52 clutches) and by Tiwari and Bjorndal (2000) (mean: 116.4, SD = 26.4, n = 20 clutches) as well as at other nesting areas in Greece (Margaritoulis et al., 2003; Margaritoulis and Rees, in press). Clutch size in Laganas Bay was substantially larger than those documented in Cyprus (Broderick and Godley, 1996) and Turkey (Erk'akan, 1993; Baran and Türkozan, 1996; Türkozan and Baran 1996; Yerli and Dolezel, 1998).

Although loggerheads nesting in the Mediterranean originate from the western Atlantic stock, they have diverged genetically from it (Bowen et al., 1993; Laurent et al., 1998). It seems that genetic divergence is more prominent in nesting colonies in Turkey (Laurent et al., 1993). Further, loggerheads nesting in Greece are substantially larger from those nesting in Cyprus and Turkey (Margaritoulis et al., 2003, and references therein). Tiwari and Bjorndal (2000), investigating loggerhead clutch sizes in three geographically separate nesting areas (Brazil, Florida, Greece), found that Greek turtles produce the largest clutches relative to body size. Therefore, the noted variation in reproductive output between loggerhead nesting colonies in Greece and in Cyprus/Turkey is probably a result of a body size difference.

Hatching success and emergence success differed strongly from season to season (Table 5) but no particular trend was detected. Seasonal and spatial variations of hatching success are mainly attributed to changes within the nest environment in three main areas influencing egg development: gas exchange, humidity, and temperature (Miller, 1997, and references therein).

Incubation duration can provide information on the sex ratio of hatchlings. Loggerheads exhibit temperature-dependent sex determination. During a critical period in the incubation period, nest temperatures higher than the pivotal temperature (the constant temperature that provides 50% of each sex) produce more female hatchlings and lower nest temperatures provide more male hatchlings (Yntema and Mrosovsky, 1982). Because incubation duration is highly negatively correlated to incubation temperature, it can be used as an index of hatchling sex ratio (Marcovaldi et al., 1997). Further, Mrosovsky et al. (1999) stipulated that estimation of hatchling sex ratio from incubation durations works for groups of nests, not for individual clutches, and should be best based on multi-seasonal data.

The sex ratio of loggerhead hatchlings, around the world, seems to be overwhelmingly female-biased. More than 93% female hatchlings seem to emerge on Florida beaches (Mrosovsky and Provancha, 1989) and 82.5% in Brazil (Marcovaldi et al., 1997). In the Mediterranean, Kaska et al. (1998) found a mean sex ratio of 81.6% females in a small sample ($n = 8$) of loggerhead nests at four sites in Cyprus and Turkey, and Godley et al. (2001) estimated that on Alagadi beach, Cyprus, 89–99% of hatchlings were females. It is not known, however, if highly female-biased sex ratios in loggerhead turtles are a typical situation deviating from the Fisherian theory of 1:1 (see Mrosovsky and Provancha, 1989, for further discussion).

For loggerheads nesting in Greece (Kyparissia Bay), the pivotal temperature has been determined at 29.3°C and the pivotal incubation duration at 56.6 days (Mrosovsky et al., 2002). Since Laganas Bay is situated about 85 km from Kyparissia Bay we can assume that it has a similar, if not the same, pivotal incubation duration. Examining Fig. 7, we can hypothesize that Kalamaki, Sekania, and Daphni (totalling 72.9% of all nests in Laganas Bay), having shorter incubation periods, produced predominantly female hatchlings, and that two beaches, Marathonissi and East Laganas (totalling 20.7% of all nests), having longer incubation periods, produced predominantly males, and one beach (Gerakas) was very close to the pivotal value (50% of each sex). However, this classification should be qualified as tentative because other variables (e.g. clutch size, metabolic heating, sand compaction), described in detail by Mrosovsky et al. (1999), might influence the relationship between incubation duration and sex ratio.

It is very clear, however, that Marathonissi beach represents a very particular case, featuring an unusually long overall incubation duration of 69.8 days with a range extending to 89 days. This male-biased beach, contributing 9.2% of the total nests in Laganas Bay (Fig. 5), has a northward orientation and its sand looks different from the sands on the other beaches both in quality and color. However, specific research is needed to validate the reasons for such long incubation durations. This resembles the situation in Brazil where, despite most nesting areas being largely female-biased, there seem to be some predominantly male-producing areas (Baptistotte et al., 1999).

Conservation Considerations

Degradation of sea turtle nesting habitats interferes with vital processes of reproduction and has adverse effects on reproductive output. In the Mediterranean, numerous factors make beaches increasingly unavailable or less suitable for turtle nesting. Therefore, protection of nesting beaches is a priority and plays an increasingly important role in the survival of marine turtle populations.

Badly planned and intensively constructed facilities catering to the increasing tourist trade, starting in the 1980s, constitute the biggest problem in the Bay of Laganas. Legislation imposed since 1983 has restricted development and has been met with strong local opposition. However, several actions mainly by environmental organizations have kept the general situation under some control; e.g., the summertime presence of an international team of volunteers coupled with an intensive public awareness program (Dimopoulos, 1995), the acquisition of land behind Sekania to prevent development on the most densely nested beach (Charalambides and Katsoupas, 1994), and continuous lobbying at various levels. Recently, the establishment of a National Marine Park and, more importantly, the creation of a Management Agency comprising government, local authorities and communities, and environmental organizations (Dimopoulos, 2001) are expected to play a decisive role in the establishment of a more balanced situation incorporating local views and interests. Nevertheless, if this prospect is to work effectively, it will need a long-time effort and persistence on the part of the government, local authorities, and involved environmental organizations.

While concentration of efforts in conserving the nesting beaches is fully justified, threats at other life history stages of the loggerhead turtle should not be ignored. Demographic models have shown that protection of eggs and hatchlings alone cannot compensate for heavy, mostly human-inflicted, losses of juveniles and adults (Crouse et al., 1987; Laurent et al., 1992). In the Mediterranean, these losses occur mostly through incidental catch in fisheries (summarized in Gerosa and Casale, 1999).

Long-range tag returns have shown that loggerheads nesting in Laganas Bay disperse to widely scattered feeding grounds in the Mediterranean, most of which are outside the boundaries of Greece (Margaritoulis, 1988b; Lazar et al., 2004). The migratory nature of the species renders sea turtle conservation an inter-governmental regional issue and, correctly, international conventions and organizations are actively involved in attempting to provide wide-ranging solutions (Margaritoulis et al., 2003).

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APPENDIX

Some general regulations imposed at the nesting beaches of Laganas Bay are as follows. Public access is not allowed on Sekania, day or night, while on the other beaches is allowed only during daylight. Limited use of beach furniture is permitted on East Laganas, Kalamaki, and Gerakas. No vehicles are allowed on any beaches. No mechanized boating is allowed in a maritime zone containing the beaches of Sekania, Daphni, and Gerakas, while in the rest of the bay a reduced speed limit (6 knots) is required.

Marathonissi (370 m). — This is a coarse-sand beach, curved around the northern end of the uninhabited islet of Marathonissi. The beach is backed by low dunes that in places extend landwards as far as 50 m and then by a hilly mass covered with dense Mediterranean vegetation. An old chapel, belonging to the local Church of Lithakia, is the only building on the islet. Tourists visit the beach during the day, mainly on organized boat trips. Lights from the residential areas of the bay are visible from the beach at night.

East Laganas (2780 m). — This beach is characterized by fine sand, mixed in places with small pebbles, and an extensive dune field. The western part of the beach has several tamarisk trees. There are several hotels and houses, especially at the two ends of the beach. The beach is visited during the day by people originating mainly from the area's tourist facilities. Beach furniture is deployed along the most popular parts of the beach, at times exceeding the permitted quota. Vehicles may be seen occasionally driving along the beach, despite regulations. Lights and noise from the nearby villages and the airport affect a large part of the beach. Night flights have been greatly reduced or stopped in recent years.

Kalamaki (500 m). — This is a rather narrow fine-sand beach, separated from East Laganas by a rocky outcrop. Behind the beach there are low clay cliffs. The area has easy access through a paved road, and is visited by many people during the day, and occasionally at night despite existing regulations. A hotel above the western part of the beach, in operation since 1982, affects a large beach section by its lights and noise. During certain seasons, large mounds of sea grass *Posidonia* were deposited on the beach, rendering most of the beach unsuitable for nesting. Beach furniture usually exceeds the permitted quota.

Sekania (650 m). — This is a rather remote beach, divided into two sectors by a low rocky headland. Both sectors are backed by steep clay hills covered with maquis vegetation. The eastern sector is characterized by ample sand extending about 30 m landwards. The western sector is narrower and has a rather difficult approach from the sea due to submerged rocks. The hillsides behind the beach are totally undeveloped. Until 1994, the beach was accessible through a rough road, which had to be repaired by the owners each year. Despite the existence of the road, human presence on the beach was generally minimal. During strong rainfalls, fine material from exposed soil, due to road repairs and occasional brush fires, was deposited on the beach, altering, in places, the quality of the sand. In 1994, WWF Greece purchased most of the private land behind the beach to prevent development. As a result the road was left unattended and destroyed. After the establishment of the National Marine Park the area has been declared a "Site of Absolute Protection" and human access is strictly controlled.

Daphni (600 m). — This beach has a large proportion of pebbles and stones but there are also parts of fine soft sand. The beach is moderately unstable, as some of the sands are eroded and re-deposited alternatively. The approach from the sea is problematic because there are series of submerged rocks leaving few openings. The beach is backed by steep hills covered with maquis vegetation. The area is privately owned and since 1984 there has been a progressive increase in human presence as well as in the number of buildings, most of them built illegally and used as holiday homes or rented to visitors. Occasional brush fires in conjunction with the construction of new roads and buildings has caused considerable erosion that has degraded the quality of the sand in certain parts of the beach. At night there is moderate disturbance from house lights as well as from headlights from cars driving down the roads. Beach furniture was deployed illegally during certain seasons. Boats frequently land on the beach despite regulations.

Gerakas (600 m). — This is a 15–30 m wide beach, with mostly fine and soft sand. The beach is backed by clay cliffs (15–20 m high) which shield the lights of low buildings further inland. There is only one access to the beach, through a trail, coming down the cliffs. The seabed is sandy, rendering a smooth approach from the sea. Gerakas attracts hundreds of day visitors during the summer. Beach furniture, usually exceeding the permitted quota, is generally deployed close to the water's edge (i.e., away from the nesting zone) and is collected at sunset.