Aquatic Ecology **37:** 183–190, 2003.

Swimming behaviour and dispersal patterns of headstarted loggerhead turtles *Caretta caretta*

I. Nagelkerken[1,2,*], L.P.J.J. Pors[2] and P. Hoetjes[3,4]
*[1]Department of Animal Ecology and Ecophysiology, University of Nijmegen, Toernooiveld 1, Nijmegen, 6525 ED, The Netherlands; [2]Carmabi Foundation, Piscaderabaai z/n, P.O. Box 2090, Curaçao, Netherlands Antilles; [3]Curaçao Seaquarium, Bapor Kibra z/n, Curaçao, Netherlands Antilles; [4]Current address: Department of Public Health and Environmental Hygiene, Environmental Section, Schouwburgweg 24 – 4th floor, Curaçao, Netherlands Antilles; *Author for correspondence (e-mail: i.nagelkerken@sci.kun.nl; fax: + 31-24-3652134)*

Received 3 September 2001; accepted in revised form 22 November 2002

Key words: Captive-rearing, Dive performance, Hatchling behaviour, Offshore migration, Swimming speed

Abstract

Swimming behaviour and dispersal patterns were studied in headstarted loggerhead turtles *Caretta caretta* which were released at three different sites on the Caribbean island of Curaçao (Netherlands Antilles) and at one site on the neighbouring island of Klein Curaçao, after 1–2.5 yrs of captivity. Turtles were tagged and followed up to a distance of 6125 m offshore, using a boat with a Global Positioning Unit. The released turtles reverted to typical hatchling behaviour and showed an offshore migration almost perpendicular to the coastline. No significant differences were found in directional swimming among the four sites. The turtles swam almost continuously about 30 cm under the water surface; their mean overall swimming speed was higher than in adult wild loggerheads suggesting a ’frenzy’-like swimming stage. The turtles exhibited diving behaviour, and the dive frequency and duration was comparable to that of similar-sized (wild) turtles. The present study demonstrates that upon release the headstarted loggerheads behave naturally and show dispersal patterns similar to wild hatchling turtles. The fact that the released turtles were still able to show offshore directional swimming suggests that the headstarting did not affect their short-term orientation abilities.

Introduction

Sea turtles spend almost their entire life in marine or estuarine habitats and four ontogenetic stages of habitat utilisation can be distinguished: 1) early juvenile nursery habitat (usually pelagic and oceanic), 2) later juvenile developmental habitat (usually demersal and neritic), 3) adult foraging habitat, and 4) adult internesting and/or breeding habitat (Musick and Limpus 1997). Juvenile turtles mostly hatch at night and once in the water show a ‘frenzy’ period in which they swim almost continuously during one day in an offshore direction; this probably serves as a fast escape from the shallow coastal waters which harbour many predators (Wyneken and Salmon 1992). Under natural conditions hatchlings sequentially use three cues to maintain their offshore migration (see review by Lohmann and Lohmann (1996a): 1) when emerging from their nests the hatchlings find the ocean by crawling towards the lower, brighter seaward horizon and away from the dark, elevated silhouettes of the vegetation and dunes, 2) upon entering the ocean the hatchlings orient seawards by swimming into the waves, and 3) after entering deeper water the hatchlings use the Earth’s magnetic field as a cue for compass orientation (Lohmann and Lohmann 1996b). When reaching deep offshore waters, most turtles migrate passively by drifting pelagically in oceanic gyres for a few years after which they recruit to demersal coastal habitats. During their pelagic stage the turtles are often associated with floating mats of *Sargassum* weed where they feed on a variety of pelagic organisms (Carr 1986). When approaching maturity the turtles migrate to adult foraging habitats, and upon maturity and at the start of the nesting season they migrate toward their nesting beaches located in the region of their natal beaches (Musick and Limpus 1997).

Sea turtles have declined in numbers during the last few decades as a result of human activities, to a point where they are considered threatened or endangered on a world-wide basis. Human influences nowadays impact every stage of their life cycle, and include destruction and alteration of nesting beaches and foraging habitats, pollution of the ocean and coastal zone, and intense fishing activities (Lutcavage et al. 1997). The sharp decline in the population size of sea turtles had led to various headstart programs, in which hatchlings are held in captivity during the initial part of their life stage. The underlying assumption of these programs is that by helping the hatchlings through this vulnerable period when they are most subject to predation, their survivorship will increase and they will contribute more to the breeding population (Mrosovsky 1983). However, the result of a large headstart program in the Kemp's ridley sea turtle *Lepidochelys kempi* showed that after 1.5 decade none of the 18,000 headstarted turtles had been recorded anywhere emerging to nest (Taubes 1992).

Release of headstarted turtles suffers from several potential problems: 1) the turtles may become dependant on food which is not readily available after they are released, 2) they may continue to associate the presence of humans with food, 3) they may undertake an offshore migration at a size at which they would normally be settling in coastal benthic habitats which provide for sufficient nutritional resources, 4) they may not properly develop their migratory guidance system which is thought to be influenced by imprinting during their crawl to the sea, 5) upon release turtles may be in a sub-optimal condition due to diseases or nutritional imbalances, 6) the captive rearing may impact the physiological development of the turtles (muscle development, diving response, immunology), and 7) as a result of absence of predators during the rearing period they may become unwary and fail to avoid sharks and humans (Pritchard 1980; Mrosovsky 1983; Woody 1991; Bowen et al. 1994).

Several studies have provided indirect evidence that released headstarted turtles show a different behaviour than wild turtles. Recaptures of headstarted turtles suggested abnormal migratory behaviour, and turtles sometimes occurred in areas from which they had never been recorded (Bolten et al. 1990; Manzella et al. 1991; Taubes 1992). Released captive-reared turtles have been observed to crawl back onto land a few days after their release, yearlings released in *Sargassum* fields washed ashore within two weeks, while turtles have been captured while approaching humans (Ehrenfeld 1974; Taubes 1992).

Very little detailed or quantitative information is present, however, on the effect of headstarting on the swimming behaviour and dispersal patterns of loggerhead turtles released back into the wild. Many studies on orientation cues of hatchling loggerhead turtles have been done in laboratory experiments (Lohmann 1991; Light et al. 1993; Lohmann et al. 1995). Field studies have often been focussed on longer-term monitoring of dispersal patterns of adult wild turtles using satellite telemetry (Stoneburner 1982; Hays et al. 1991; Renaud and Carpenter 1994), while direct observations in the field on swimming behaviour and dispersal patterns of loggerheads have mainly focussed on wild hatchling turtles (Frick 1967; Salmon and Wyneken 1987; Witherington 1991).

During August 1993, a nest of emerging hatchling loggerhead turtles was collected by beach visitors in Curaçao (Netherlands Antilles) and brought to the local sea aquarium. After a headstart of 1–2.5 yrs, several of the surviving turtles were released back into the wild. Given the concerns on the possible negative effects of headstarting on turtle behaviour we studied the short-term swimming behaviour and dispersal patterns of released captive-reared loggerheads to determine the characteristics of their offshore migration.

Materials and methods

The loggerhead sea turtles studied in the present study hatched on a beach at the exposed north-east coast of Curaçao in August 1993, and were collected by beach visitors who were concerned about their chances of survival. The hatchlings were collected in a box and brought to the Curaçao Seaquarium where they were kept in the public aquaria. In 1994 and in 1995–1996, the Curaçao Seaquarium decided to release some of the surviving loggerheads which provided us with the opportunity to study the swimming behaviour and dispersal patterns of 23 turtles.

Before release into the wild, each turtle was marked with a visual tag and a small radio transmitter. The visual tag consisted of a small partly inflated (air) balloon attached to the turtle with a fine 6 m long monofilament line and a rubber band (20 × 1 × 0.1 cm). The rubber band was passed through a small hole drilled through a posterior marginal scute and was tied in a single knot, just a bit larger in size than the hole through the scute. Since the hole in the scute increases after some time, turtles which could not be recaptured to remove the tag before the end of the experiment were presumed to lose their tag automatically (Witham et al. 1973). Only three turtles were lost with their tags still attached. This method also could prevent turtles from drowning if the monofilament line became entangled on the reef, as the force exerted by the continued swimming of an entangled turtle would stretch the rubber band making the knot thinner, allowing it to slip through the hole in the scute (pers. observ.). Since most turtles swam directly offshore to the deep ocean this was not a major concern in this study, however one turtle became entangled on the coral reef, but lost its tag almost immediately.

Tagging with a radio transmitter was necessary to relocate the turtles after surfacing from dives deeper than 6 m (i.e., the length of the monofilament line of the visual tag). The small transmitter was placed inside a 50 ml plastic bottle, with the 10 cm long antenna sticking out through a small hole sealed with waterproof silicone. The remaining air space within the bottle was filled up with paper to reduce the buoyancy. The plastic bottle was attached to the balloon. Total weight of the tags was about 100 g which corresponded to on average 1.8% (range = 0.4–6.5%) of the turtles' total body weight. The balloon had a total air volume of approximately 1 l and did not appear to significantly affect the swimming behaviour of the turtles. The partly inflated balloon drifted on the water surface and did not cause any significant drag, while the plastic bottle was much longer than wide so as to reduce the drag. The positive buoyancy of the tags may have affected the dive length or depth, however. Whether the tags had any effect on the urge to dive is unknown, but as shown in the results the turtles made frequent dives at which depths of > 35 m could be exceeded. After surfacing from a dive, the tagged turtles were relocated using a hand-held antenna attached to a LA 12-DS Receiver (AVM Instruments Company, Ltd., California, USA).

Upon release, the turtles were placed on the beach (at Seaquarium on the rocky shore) about 4–7 m away from the waterline, so they were forced to crawl to the sea by themselves. Once in the water, turtles were followed by a boat at a distance of approximately 40 m behind the turtle. Initially, the turtles were followed at different angles to test for the effect of the presence of the boat on their behaviour. The turtles did not appear to be attracted nor scared off by the boat. The behaviour of all released turtles was noted during their dispersal and their position determined every five minutes using a Global Positioning System (Philips GPS MK6 navigator, ± 100 m). This procedure was done for one turtle at a time and at the end of the experiment the tags were recollected and the turtles set free.

A total of 23 turtles were released between 1994 and 1996 (Table 1, Figure 1). Ten headstarted loggerheads were released at the sheltered pocket beach of Blauwbaai (Figure 2a) between 14 September and 6 December 1994, and three turtles were released from the more exposed rocky shore of Seaquarium (Figure 2b) on 2 October 1994, all at an age and time of captivity between 1 and 1.5 yrs and a size of 27.0–35.5 cm SCL. About one year later, two turtles were released from Blauwbaai (Figure 2a) on 13 December 1995, four turtles from the sheltered pocket beach of St. Michielbaai (Figure 2c) between 4 and 9 January 1996, and four turtles from the sheltered beach of Klein Curaçao (Figure 2d), a small island located 11 km eastwards off the coast of Curaçao, on 10 February 1996. All turtles released in the second year showed an age and time of captivity of about 2.5 yrs and a size between 43.0 and 57.0 cm SCL.

During each release, the direction of the waves was measured with a hand-held compass. Additionally, the general direction (i.e., either north-westwardly or south-eastwardly) of the surface ocean currents was determined by tracking the direction of drift of a piece of slightly negatively buoyant rope (about 30 m long) which was tied to the boat at one side and thrown into the water, sinking to about 2–5 m depth.

Results

Swimming behaviour

During their release the loggerheads made fast powerstroke-style swimming movements while still held in the air and immediately started crawling towards the sea when put down onto the beach. Observations from the boat through the clear ocean water showed that once in the water, the turtles submerged directly and swam rapidly away from shore just above the

Table 1. Details on the sizes, releases and swimming behaviour of each loggerhead turtle. Turtle #: A refers to 1–1.5 years of captivity, B refers to 2.5 years of captivity. SCL = Straight Carapace Length. Site of release: 1 = Blauwbaai, 2 = Seaquarium, 3 = St. Michielbaai, 4 = Klein Curaçao. nd = no data. Ocean current direction indicates the direction from which currents originate.

Turtle #	SCL (cm)	Weight (kg)	Site of release	Time tracked (min.)	Distance tracked (m)	Ocean current direction/speed	Mean swimming direction (°)	Overall swimming speed ($m.s^{-1}$)	No. of dives (hr^{-1})	No. of resting stops (hr^{-1})
A1	29.0	3.8	1	75	1925	SE: normal	215	0.43	nd	nd
A2	27.0	1.6	1	nd	7675	SE: normal	204	nd	nd	nd
A3	32.5	4.5	1	125	3688	SE: normal	234	0.49	0.5	0.5
A4	31.5	4.4	1	82	2213	SE: normal	217	0.45	1.5	0.7
A6	29.0	3.7	1	157	3575	SE: normal	198	0.38	0.8	0.4
A7	35.5	6.3	1	243	5850	SE: strong	291	0.40	0.2	0.2
A8	31.0	4.5	1	149	5375	SE: normal	231	0.60	0.0	0.0
A9	27.0	3.2	1	155	6850	SE: normal	273	0.74	1.2	0.0
A10	35.0	6.5	1	149	4188	SE: normal	236	0.47	2.0	0.8
A11	34.0	6.1	1	120	5300	SE: normal	223	0.74	1.0	0.0
A12	30.0	3.6	2	nd	2475	SE: normal	220	nd	nd	nd
A13	28.0	3.3	2	nd	1925	SE: normal	235	nd	nd	nd
A14	28.5	3.6	2	nd	3025	SE: normal	212	nd	nd	nd
B1	47.0	15.0	1	45	1538	SE: normal	193	0.57	2.7	0.0
B2	43.0	12.0	1	69	2113	SE: normal	207	0.51	3.5	0.0
B3	50.0	18.0	3	63	1263	SE: normal	250	0.33	3.8	1.0
B4	50.0	18.0	3	57	2188	SE: strong	197	0.64	2.1	0.0
B5	53.0	19.0	3	70	1925	NW: strong	273	0.46	2.6	0.0
B6	57.0	24.0	3	61	2138	NW: strong	267	0.58	3.9	1.0
B7	54.0	20.0	4	72	2725	SE: normal	241	0.63	2.5	0.0
B8	52.0	19.0	4	75	3863	SE: normal	249	0.86	0.0	0.0
B9	49.0	16.0	4	60	3025	SE: normal	263	0.84	1.0	0.0
B10	52.0	19.0	4	68	3060	SE: normal	257	0.75	1.8	0.0

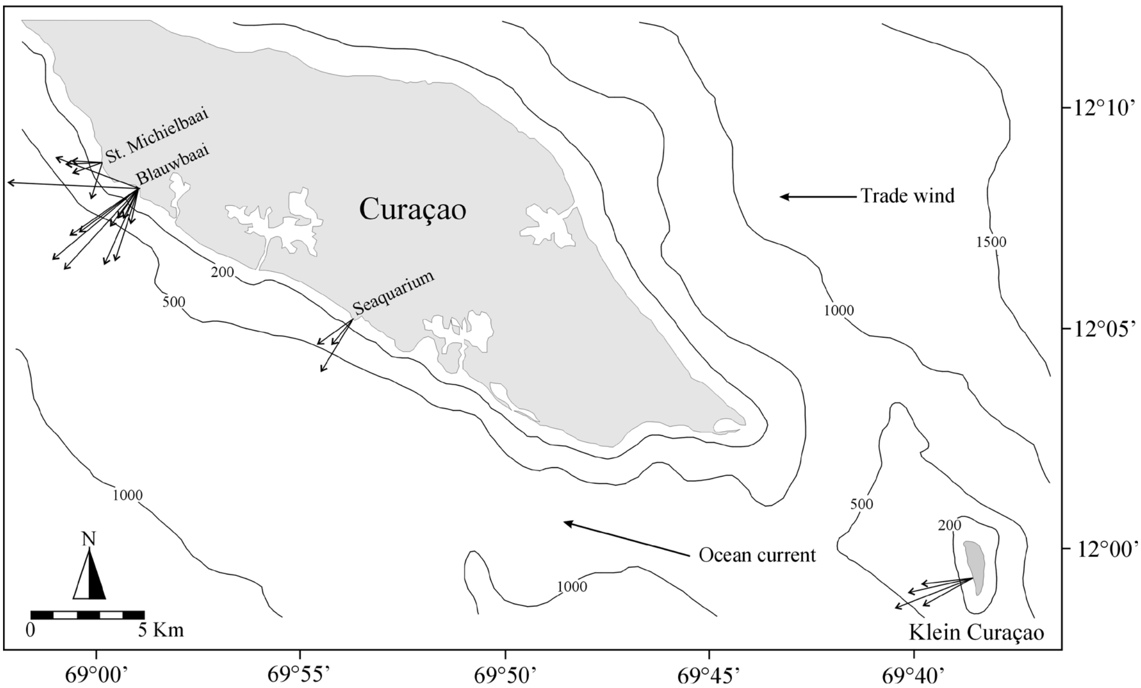

Figure 1. Release sites at Curaçao and Klein Curaçao, and overview of the dispersal patterns of headstarted loggerheads. The fitted lines show the mean direction of dispersal for each turtle, as calculated from the original data on basis of least squares. Isobath lines around the islands show water depth in meters.

bottom of the submarine reef terrace which slowly slopes off in a seaward direction (about 7–9 m depth over a horizontal distance of 50–200 m). Almost all turtles surfaced to take a first breath when reaching the end of the reef terrace (the 'drop off' zone), where the reef sharply plunges into the deep. Having thus reached the deep coastal waters, the turtles continued swimming offshore at a slower pace (strokes at least half as fast as over the reef terrace), always at about 30 cm under the water surface. About every 2–3 minutes the turtles briefly stopped to take a quick breath. The mean (± SD) overall swimming speed (i.e., total distance covered by each turtle divided by total time elapsed) was 0.57 ± 0.16 $m.s^{-1}$ (range: 0.33–0.86 $m.s^{-1}$, n = 19, Table 1). At times the turtles stopped swimming and made a dive (Table 1, mean: 1.7 ± 1.3 dives hr^{-1}, range: 0 dives-3.9 dives hr^{-1}, n = 18). Dives were undertaken after taking a quick breath, and were characterised by the turtles swimming almost straight down and staying submerged for 0.5–10 minutes (pooled mean for all dives: 4.6 ± 2.8 min., n = 18). Dive depths could not be recorded but exceeded depths at which the submerged tags could still be seen from the surface (approx. > 15 m). During two dives made by two different turtles near the steep fore-reef, which were observed with snorkelling gear, dive depth exceeded about 35 m. After having covered a distance of 1–3 km from shore, several of the turtles stopped swimming and rested at the surface on one or more occasions (Table 1, mean: 0.3 ± 0.4 rests hr^{-1}, range: 0 rests–1.0 rests hr^{-1}, n = 18) for 0.5–6 minutes (pooled mean for all rests: 2.5 ± 2.1 min., n = 18).

Offshore dispersal pattern

A significant proportion of all turtles (87 ± 14%; binomial approximation, Walpole and Myers (1978)) released across different years and different locations, swam offshore in a direction almost perpendicular to the coastline (Figures 1, 2). The mean orientation of the turtles (mean = 234°) did not differ significantly ($F_{3,19}$ = 1.69, Watson-Williams test; Zar (1996)) between sites. There was no significant difference ($p > 0.05$, Mann Whitney *U*-test) observed in the mean swimming speed and rest frequency between the two age-classes (Table 1). Only the dive frequency was significantly higher in the 2.5 yr group (p = 0.013). Since size is more likely to affect swimming performance than time of captivity, linear regressions were

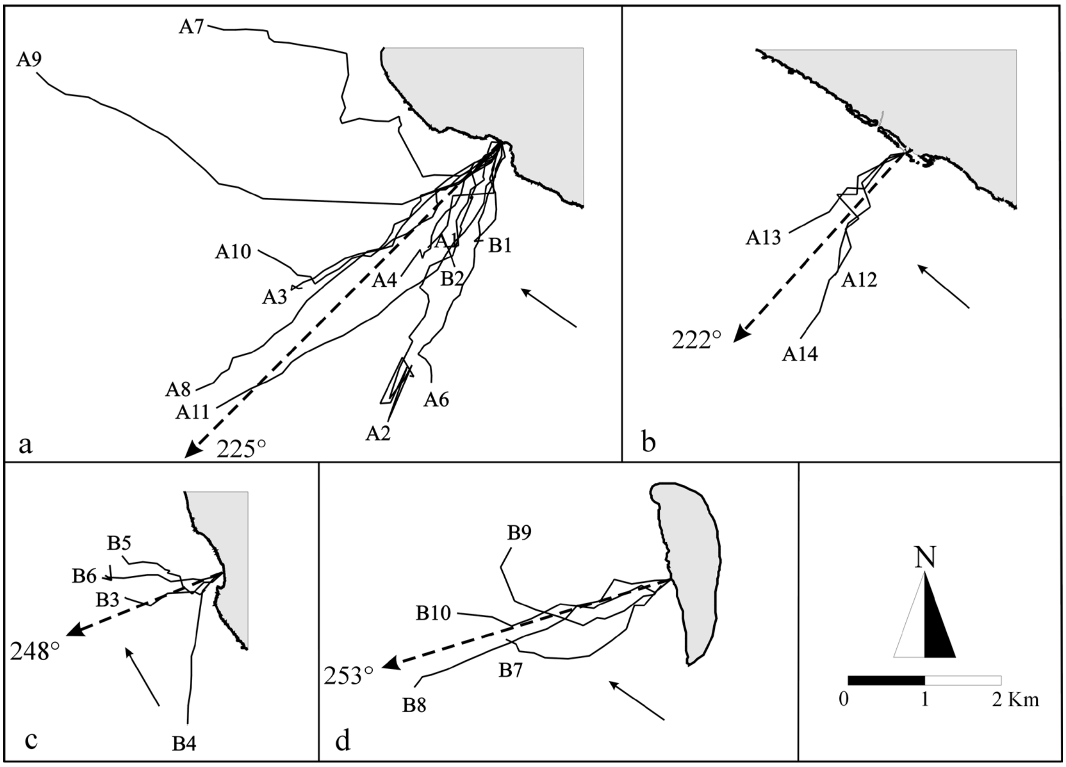

Figure 2. Dispersal patterns of headstarted loggerheads at (a) Blauwbaai (site of release: 12°7′58,9″ N 68°58′40,8″ W), (b) Seaquarium (12°5′18,3″ N 68°53′28,3″ W), (c) St. Michielbaai (12°8′44,6″ N 68°59′32,5″ W), and (d) Klein Curaçao (11°59′4,9″ N 68°38′14,5″ W). Stippled arrows indicate the mean heading of all turtles of each site. Turtles A1–A14 were 1–1.5 yrs of age, turtles B1–B10 were 2.5 yrs of age. Small arrows show the direction of the ocean waves. Waves coming in straight towards the coast were experienced by turtles A3 and B2. Turtles are numbered following Table 1.

also performed on the size data. The swimming speed and rest frequency did not increase linearly with length or weight of the turtles ($r^2 < 0.07$, linear regression), although dive frequency did show a small positive correlation with length ($r^2 = 0.33$) and weight ($r^2 = 0.35$).

Effect of deviating current direction

Three of the 23 turtles deviated from the typical dispersal pattern, probably caused by unusual strong currents. At Blauwbaai, turtle A7 experienced a very strong current (from the south-east) and did not get far out at sea, but showed a drift several kilometres down-current instead (Figure 2a). Turtle B4 at St. Michielbaai also experienced an unusual strong current from the south-east and swam almost straight into the waves and current instead of in offshore direction, resulting in an up-current deviation (Figure 2c). Turtle A9 at Blauwbaai did not experience an unusual direction or strength of the ocean current, but swam straight ahead resulting into a significant down-current drift (Figure 2a). All remaining turtles, on the other hand, regularly altered their offshore swimming direction (i.e., south-westerly) by swimming several minutes straight into the direction of the waves or ocean current (i.e., south-easterly), which resulted in an offshore dispersal almost perpendicular to the coastline.

Discussion

The present study shows that the headstarted loggerhead turtles were still able to revert to typical hatchling behaviour after a time of captivity ranging between 1–2.5 yrs. Similar to hatchlings, the headstarted loggerheads showed an initial prolonged dive following release. It cannot be ruled out, however, that this was an evasive reaction following release. After the prolonged dive the turtles continued swimming just below the water surface, surfacing regularly to take a short breath (Salmon and Wyneken 1987). Just like hatchlings, the turtles swam straight offshore over deep water in a direction which was almost perpendicular to the coastline (Carr 1986; Salmon and Wyneken 1987; Salmon and Lohmann 1989; Witherington 1991), and did not remain disoriented in nearshore waters as is the case for adult loggerheads. Likewise, Keinath (1993) found that headstarted loggerheads released after two years of captivity still showed hatchling swimming behaviour and migrated offshore. A turtle released after three years, however, became demersal and showed the same behaviour as wild demersal juveniles. In the present study, various turtles had a size at which they are normally observed in shallow coastal waters, but an age at which they still have an oceanic existence (Carr 1986; Musick and Limpus 1997). Since all turtles in the present study showed a hatchling offshore dispersal, it is suggested that age is a more important trigger for the offshore migration than size.

The mean swimming speed of headstarted loggerheads of 0.57 $m.s^{-1}$ was higher than that of adult loggerheads in the Gulf of Mexico (0.11–0.39 $m.s^{-1}$, Renaud and Carpenter (1994)) and that of hatchling loggerheads during their frenzy swimming period (0.36 $m.s^{-1}$, Salmon and Wyneken (1987); 0.23–0.36 $m.s^{-1}$, Witherington (1991)). The high swimming speed of the headstarted turtles suggests a frenzy-like swimming stage, or some kind of escape reaction away from the coast. The frenzy stage normally serves as a fast escape from shallow coastal waters harbouring many predators (Wyneken and Salmon 1992). The presence of such a stage/reaction would explain the higher swimming speed compared to wild adult turtles, whereas the larger size of the headstarted loggerheads and hence faster swimming capabilities may explain the higher swimming speed compared to hatchlings in the frenzy stage.

The dive frequency (1.7 dives hr^{-1}) was within the range noted for adult loggerheads (0.08 and 0.87 hr^{-1}, Sakamoto et al. (1993); 3.8–14.9 hr^{-1}, Renaud and Carpenter (1994)), whereas the mean dive duration (4.6 min) was comparable to similar-sized loggerheads studied in outdoor tanks (1.2–4.9 min, Lutz and Bentley (1985)). The similarity in dive performance between the headstarted turtles and large loggerheads as opposed to hatchlings is probably more related to size and physiological abilities than to differences in behaviour. It cannot be ruled out, however, that the positive buoyancy of the tags had an effect on the dive behaviour such as suppressing the desire to dive and a reduction of the dive duration.

The majority of the turtles headed in a direction almost straight offshore, up to a distance of at least 6125 m from shore. Studies have shown that turtles can acquire a magnetic heading which leads them offshore, by crawling a short distance on land, by using visual cues, and by swimming into the waves (Lohmann et al. 1997). The fact that the released turtles were still able to show offshore directional swimming suggests that the headstarting had not affected their short-term orientation abilities needed for their immediate offshore migration. Only three turtles showed a deviation in dispersal pattern, two of them suffering from unusually strong ocean currents. One other turtle (A2) showed some erratic swimming behaviour at the end of the trial but no explanation could be found for this.

Several studies have suggested that headstarted turtles may not show normal behaviour upon release and feared that turtles would not survive. Most concerns are based on circumstantial data, however, since very few detailed studies are present on the behaviour of headstarted turtles after release. Several release and recapture studies on headstarted green and Kemp's ridley turtles have shown long-term and long-distance survival (Witham 1980; Fontaine et al. 1989; Wood and Wood 1993). The present study supports these findings by showing that upon release headstarted loggerheads show natural behaviour and dispersal patterns similar to wild hatchling turtles, including the offshore migration. However, the long-term effects of headstarting on dispersal of the headstarted loggerheads were not determined in the present study, and it remains unknown whether the headstarting in this study had any long-lasting effects on their survival.

Acknowledgements

This work was made possible by the annual subsidy of the Island Government of Curaçao and the Central Government of the Netherlands Antilles to the CARMABI Foundation, and by the Curaçao Seaquarium. We wish to thank M. Wiltjer, S. Scheffers, R. Gomez, M. Hoetmer and A. Schrier for logistic support in the field. We are indebted to the Citizens Rescue Organisation (CITRO) which provided boats and manpower for the releases at Klein Curaçao. We also thank Dr

K. Lohmann for his comments on an earlier version of the manuscript and the remainder of the staff and personnel of CARMABI for their cooperation with this project. This is CWE contribution # 282.

References

Bolten A.B., Martins H.R., Natali M.L., Thome J.C. and Marcovaldi M.A. 1990. Loggerhead released in Brazil recaptured in Azores. Mar. Turtle Newsl. 48: 24–25.

Bowen B.W., Conant T.A. and Hopkins-Murphy S.R. 1994. Where are they now? The Kemp's ridley headstart project. Conserv. Biol. 8: 853–856.

Carr A. 1986. Rips, FADS, and little loggerheads. BioScience 36: 92–100.

Ehrenfeld D. 1974. Conserving the edible sea turtle: can mariculture help? Am. Sci. 62: 23–31.

Fontaine C.T., Manzella S.A., Williams T.D., Harris R.M. and Browning W.I. 1989. Distribution, growth and survival of head started, tagged, and released Kemp's ridley (*Lepidochelys kempi*) from year classes of 1978–1983. In: Proc. 1st Int Symp Kemp's ridley sea turtle biol conserv management., pp. 124–144.

Frick J. 1967. Orientation and behaviour of hatchling green turtles (*Chelonia mydas*) in the sea. Anim. Behav. 24: 849–857.

Hays G.C., Webb P.I., Hayes J.P., Priede I.G. and French J. 1991. Satellite tracking of a loggerhead turtle (*Caretta caretta*) in the Mediterranean. J. Mar. Biol. Ass. UK 71: 743–746.

Keinath J.A. 1993. Movements and behavior of wild and head-started sea turtles. PhD Dissertation, College of William and Mary, USA.

Light P., Salmon M. and Lohmann K.J. 1993. Geomagnetic orientation of loggerhead sea turtles: evidence for an inclination compass. J. Exp. Biol. 182: 1–10.

Lohmann K.J. 1991. Magnetic orientation by hatchling loggerhead sea turtles (*Caretta caretta*). J. Exp. Biol. 155: 37–49.

Lohmann K.J. and Lohmann C.M.F. 1996a. Orientation and open-sea navigation in sea turtles. J. Exp. Biol. 199: 73–81.

Lohmann K.J. and Lohmann C.M.F. 1996b. Detection of magnetic field intensity by sea turtles. Nature 380: 59–61.

Lohmann K.J., Swartz A.W. and Lohmann C.M.F. 1995. Perception of ocean wave direction by sea turtles. J. Exp. Biol. 198: 1079–1085.

Lohmann K.J., Witherington B.E., Lohmann C.M.F. and Salmon M. 1997. Orientation, navigation, and natal beach homing in sea turtles. In: Lutz P.J. and Musick J.A. (eds), The Biology of Sea Turtles. CRC Press, Boca Raton, pp. 107–135.

Lutcavage M.E., Plotkin P., Witherington B. and Lutz P.L. 1997. Human impacts on sea turtle survival. In: Lutz P.J. and Musick J.A. (eds), The Biology of Sea Turtles. CRC Press, Boca Raton, pp. 387–409.

Lutz P.L. and Bentley T.B. 1985. Respiratory physiology of diving in the sea turtle. Copeia 1985: 671–679.

Manzella S.A., Bjorndal K. and Lagueux C. 1991. Head-started Kemp's ridley recaptured in Caribbean. Mar. Turtle Newsl. 54: 13–14.

Mrosovsky N. 1983. Conserving Sea Turtles. British Herpetological Society, London.

Musick J.A. and Limpus C.J. 1997. Habitat utilization and migration in juvenile sea turtles. In: Lutz P.J. and Musick J.A. (eds), The Biology of Sea Turtles. CRC Press, Boca Raton, pp. 137–163.

Pritchard P.C.H. 1980. The conservation of sea turtles: practices and problems. Amer. Zool. 20: 609–617.

Renaud M.L. and Carpenter J.A. 1994. Movements and submergence patterns of loggerhead turtles (*Caretta caretta*) in the Gulf of Mexico determined through satellite telemetry. Bull. Mar. Sci. 55: 1–15.

Sakamoto W., Sato K., Tanaka H. and Naito Y. 1993. Diving patterns and swimming environment of two loggerhead turtles during internesting. Nippon Suisan Gakkaishi 59: 1129–1137.

Salmon M. and Lohmann K.J. 1989. Orientation cues used by hatchling loggerhead sea turtle (*Caretta caretta* L.) during their offshore migration. Ethology 83: 215–228.

Salmon M. and Wyneken J. 1987. Orientation and swimming behavior of hatchling loggerhead turtles *Caretta caretta* L. during their offshore migration. J. Exp. Mar. Biol. Ecol. 109: 137–153.

Stoneburner D.L. 1982. Satellite telemetry of loggerhead sea turtle movement in the Georgia Bight. Copeia 1982: 400–408.

Taubes G. 1992. A dubious battle to save Kemp's ridley sea turtles. Science 256: 614–616.

Walpole R.E. and Myers R.H. 1978. Probability and Statistics for Engineers and Scientists. 2nd edn. Macmillan Publ. Co., New York.

Witham R. 1980. The "lost year" question in young sea turtles. Amer. Zool. 20: 525–530.

Witham R., Gallagher R.M. and Hollinger M.L. 1973. Tracking green turtles with fluorescent dye. Prog. Fish Cult. 35: 239–240.

Witherington B.E. 1991. Orientation of hatchling loggerhead turtles at sea off artificially lighted and dark beaches. J. Exp. Mar. Biol. Ecol. 149: 1–11.

Wood F. and Wood J. 1993. Release and recapture of captive-reared green sea turtles *Chelonia mydas*, in the waters surrounding the Cayman Islands. Herpetol. J. 3: 84–89.

Woody J.B. 1991. Is 'headstarting' a reasonable conservation measure? "On the surface, yes; in reality, no". Mar. Turtle Newsl. 54: 7–8.

Wyneken J. and Salmon M. 1992. Frenzy and postfrenzy swimming activity in loggerhead, leatherback, and green sea turtles. Copeia 1992: 478–484.

Zar J.H. 1996. Biostatistical Analysis. 3rd edn. Prentice-Hall, New Jersey.