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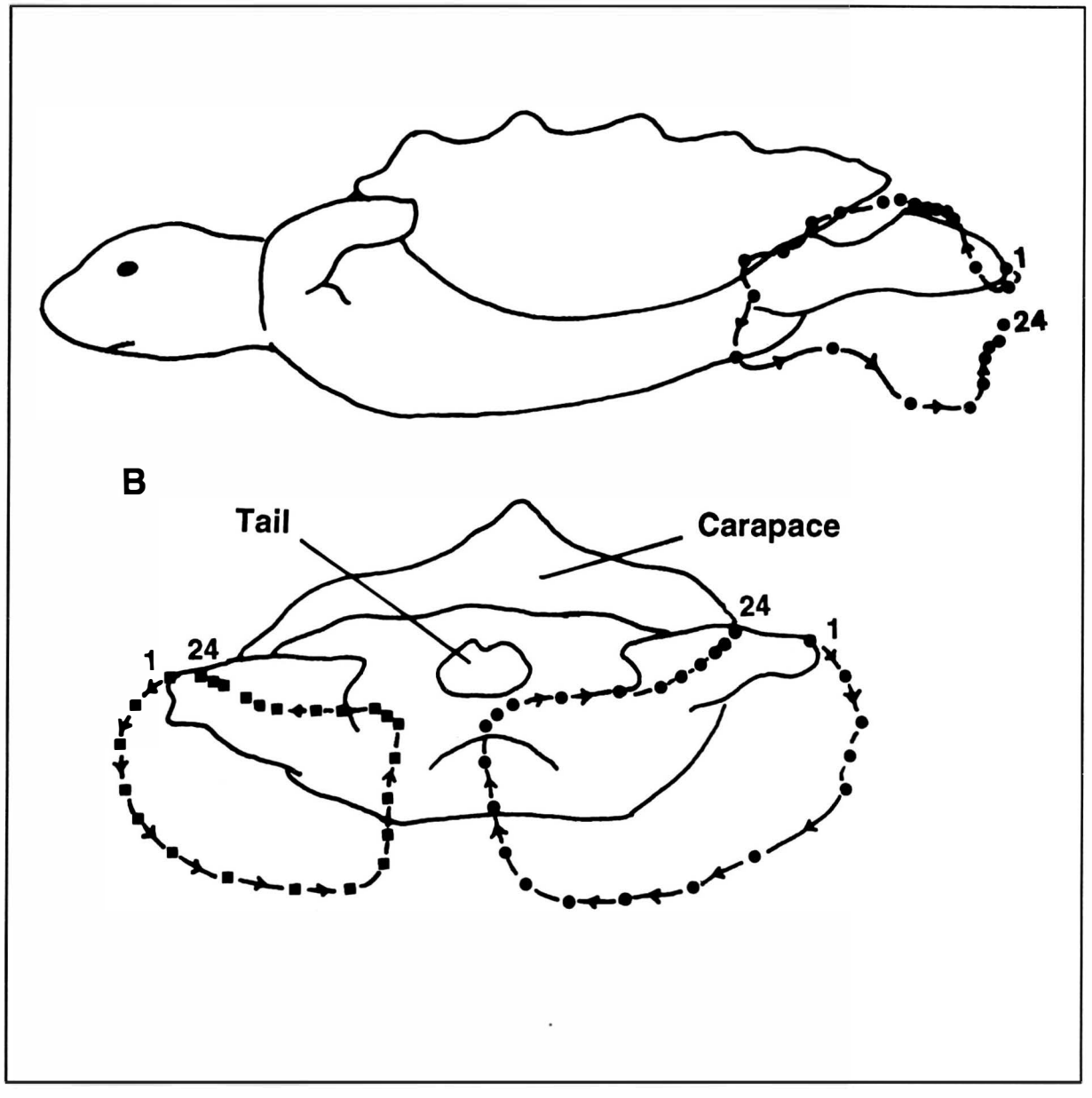

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SHORT NOTES

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OBSERVATIONS ON THE SWIMMING OF THE PACIFIC RIDLEY, *LEPIDOCHELYS OLIVACEA* (ESCHSCHOLTZ, 1829): COMPARISONS WITH OTHER SEA TURTLES

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One of the authors has previously described swimming mechanisms in three species of sea turtles; the green turtle *Chelonia mydas* L. (Davenport, Munks & Oxford, 1984), the loggerhead turtle *Caretta caretta* L. (Davenport & Clough, 1985, 1986), and the leatherback turtle *Dermochelys coriacea* (Vandelli) (Davenport, 1987). Living sea turtles have several common features that separate them from other chelonians (e.g. hypertrophied forelimbs, large pectoral muscles, streamlined shape, poor terrestrial locomotion, large egg clutches). These similarities mask marked ontogenetic and interspecific differences in life style (see Pritchard, 1979; IUCN, 1982 for general reviews). Leatherbacks are specialized oceanic wanderers that eat gelatinous prey, while herbivorous green turtles migrate great distances. The other sea turtles, the hawksbills (*Eretmochelys imbricata* L.), flatbacks (*Chelonia depressa* Garman), loggerheads and ridleys (*Lepidochelys olivacea* [Eschscholtz] and *Ledidochelys kempii* [Garman]) are more coastal and omnivorous.

Hatchling and small juvenile turtles appear to live in the open oceans, drifting with currents, particularly in weedlines, where they may subsist on food very different from the adult diet (e.g. Caldwell, 1968; Smith, 1968; Carr & Meylan, 1980; Stoneburner, Richardson & Williamson, 1982), although it has to be said that virtually all information is for green and loggerhead youngsters; young ridleys, hawksbills and leatherbacks have generally not been observed at sea after swimming offshore in a 'swimming frenzy'.

There are also differences in the diving abilities of young turtles. Hatchling green and loggerhead turtles (particularly the latter) dive with difficulty (Hildebrand & Hatsel, 1927; Milsom, 1975; Davenport *et al.*, 1984), yet neonate leatherbacks dive easily (Davenport, 1987).

Although interest in the locomotion of sea turtles initially centred upon the simultaneous beating of the forelimbs (Carr, 1952; Gray, 1953; Walker, 1971; Blake, 1981; Davenport *et al.*, 1984), later studies have revealed that swimming can be more varied, particularly at low speeds. Davenport & Clough (1986) showed that hatchling loggerheads employ a simultaneous double hindlimb kick for 95% of their swimming; they progressively switch to an alternate-leg forelimb kick as they grow beyond 400 g. Synchronous forelimb beating was seen much more rarely than in green turtles of similar size. In contrast, Davenport (1987) demonstrated that hatchling leatherbacks always swam with a synchronous forelimb beat.

The note reported here stemmed from an opportunity to study and film juvenile Pacific ridley turtles. It is supplemented by some qualitative observations made upon growing *Chelonia mydas*. Pacific ridleys, although widespread in the Pacific, Indian and Atlantic oceans (Pritchard, 1979; IUCN, 1982) are amongst the least studied of all sea turtles. With the Kemps ridley *Lepidochelys kempii* and the loggerhead *Caretta caretta*, they have been said to form a natural group (sometimes described as the subfamily Carettini - see Pritchard, 1979 for discussion). The jaws of the olive ridley are weaker than those of the loggerhead or Kemp's ridley (Pritchard, 1979) and it appears that adults forage for crustaceans in tropical neritic waters of considerable depth; they have been caught in shrimp trawls at 80-110 m, though they are also known to eat surface material such as jellyfish and fish eggs (Fritts, 1981; Mortimer, 1982). Pritchard (1979) reports that young Pacific ridleys have almost never been caught; only hatchlings or subadults have been seen in the wild. This suggests that the young live offshore, probably for several months or years.

The Pacific ridleys investigated (*ca.* 300-600 g body weight) had been held in large open-air tanks (1.5 m deep) for about 8 months at a head start facility at the Muka Head marine biological station of the Universiti Sains Malaysia, Penang, Malaysia. They had been reared from locally laid eggs and were fed on trash fish. Their tanks were continuously supplied with water pumped directly from the sea (35°/$_{oo}$; *ca.* 30°C).

The green turtles investigated were sent as hatchlings from the Lara Reserve, Cyprus, to the School of Ocean Sciences, University College of North Wales, where they were held in tanks of sea water (34°/$_{oo}$; 25°C) for one year, primarily for nutritional studies already reported (Davenport & Scott, 1993*a*, 1993*b*).

Two Pacific ridleys (347 g, 140 mm carapace length; 561 g, 247 mm carapace length) were filmed in a large glass tank (2 x 1 x 0.5 m) with a Panasonic F10 colour videocamera equipped with a high speed (0.001s) shutter. The tank had a 1 cm grid inked onto the rear surface; the turtles were filmed from a distance of 5 m to avoid parallax problems. Film was analysed by freeze-frame and playback through a Panasonic AG 6200 videorecorder and monitor, coupled with drawings made by placing acetate sheets over the monitor screen. Filming of the ridleys in the laboratory was supplemented by visual observations of ridleys and green turtles in their holding tanks.

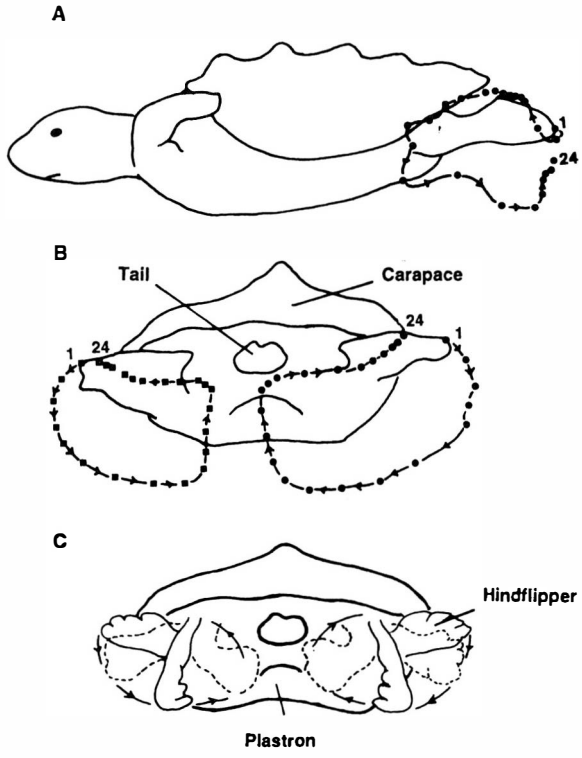

Fig. 1. Forward swimming by synchronized movements of the hindlimbs. Closed circles represent positions of fixed points on hindflippers in successive videofields (0.04 s apart). Numerals represent numbers of first and last fields. A. From side. Note that flipper moves fastest on the backwardly-directed effective stroke. Note also that the foreflippers are motionless. B. View of hindflipper action from behind. Note that effective stroke involves fast medially-directed movement of the hindflipper. C. Appearance of hindflipper at various stages of limbcycle. Note that hindflipper is held in scoop-like fashion at fastest part of effective stroke.

Ridleys were all ($n = 20$) positively buoyant, and had clear difficulty in remaining underwater; when they dived to feed on the bottom of their holding tanks they had to scull with their foreflippers to stay down, and fed with a tail-up attitude. The filmed animals were both very buoyant; if they swam downwards and ceased swimming they quickly bobbed up. The resting posture was very high in the water, with much of the shell protruding above the water line.

Hatchling green turtles had some difficulty in diving at first, but all of the animals studied ($n = 12$) were able to dive and exhibit neutral or negative buoyancy by the time they were 100-150 g.

When undisturbed, the ridleys either floated at the water surface, or swam slowly forwards (< 0.5 body lengths s^{-1}, with a synchronized sculling movement of the hindlimbs only; Fig. 1). The hindlimbs were extended and feathered during the recovery stroke, but curved together like scoops on the effective stroke; the hindlimbs of *Lepidochelys* are considerably larger and more flexible than green turtles of similar size. When swimming in this fashion, the foreflippers were held edge-on to the direction of movement, but were held out laterally and not tucked onto the top of the shell. If the turtle changed direction the hindflipper movements became asynchronous, or, if the animal was turning without forward movement, only one of the hindflippers would be moved. The turtles often swam slowly backwards (< 0.2 body lengths s^{-1}), both in their holding tanks and when filmed, sometimes for considerable distances. To do so they normally swam by approximately synchronized movements of the hindlimbs, though during manœuvres or short bursts of fast backward swimming, alternate-limb action was employed. When swimming slowly backwards with synchronized hindlimb action, the forelimbs were held extended sideways, but when swimming backwards with an alternate-leg action the foreflipper tips were stretched forwards, in front of the snout.

When the ridleys were disturbed by the approach of an observer, they initially responded by swimming with all four limbs in dog-paddle fashion with the limb action synchronized diagonally, the basic cryptodiran pattern (Zug, 1971) also seen in young green and loggerhead turtles (Davenport *et al.*, 1984: Davenport & Clough, 1986; Wyneken, 1988). Only when the turtles were handled did they respond by fast swimming involving synchronized forelimb beating. As with green and loggerhead turtles there was no sign that ridleys beat the forelimb tips in the figure-of-eight fashion claimed for the Family Cheloniidae by Walker (1971). During the upstroke and downstroke of the forelimbs the blade of the foreflipper was held in similar fashion to that of the green turtle (Davenport *et al.*, 1984), so propulsion during vigorous, synchronized foreflipper beating is based partially upon the generation of lift on both up and downstrokes, whereas hindlimb propulsion is purely drag-based (see Blake, 1981; Davenport *et al.*, 1984 for discussion).

All forward swimming in the young green turtles was by synchronized foreflipper beating, or by dog-paddling (as described by Davenport *et al.*, 1984). Only one extra mode of swimming was seen, and then not until the animals had reached a weight of about 500 g. Occasionally, *Chelonia* of this size or larger would swim backwards using an alternate hindlimb action, and with the foreflippers extended so far forwards that they touched in front of the snout, so that the head was completely hidden from the sides.

The swimming and buoyancy of young Pacific ridleys most closely resembles that of loggerheads amongst the living sea turtles so far studied. Like loggerheads they remain positively buoyant and incapable of sustained or deep diving for a long period after hatching. They also propel themselves most of the time by action of the hindlimbs, rather than the foreflippers. However, there are some noticeable differences. Young loggerheads swimming by synchronized hindlimb ac-

Swimming mode	*D. coriacea*	*C. mydas*	*C. caretta*	*L. olivacea*	*L. kempi*	*E. imbricata*
Forwards	+	+	+	+	+	+
Backwards	-	+	+	+	+	+
Foreflipper propulsion	+	+	+	+	+	+
Dogpaddle	-	+	+	+	?	?
Hindflipper forward propulsion						
(a) synch.	-	+	+	+	?	?
(b) alternate	-	-	+	+	?	?
Hindflipper backward propulsion						
(a) synch.	-	-	-	+	?	?
(b) alternate	-	+	+	+	?	?
Dominant part of foreflipper stroke*	up	down	down	down	?	?
Dominant hatchling slow swimming stroke**	foreflipper beat	dog-paddle	hindlimb action (synch.)	hindlimb action (synch.)	hindlimb action (synch.)	?

TABLE 1. Summary of known swimming mechanisms of sea turtles. Key: + = observed/reported; - = not observed/reported: synch. = synchronized; * leatherbacks beat foreflippers downwards and forwards, upwards and backwards; cheloniids beat them downwards and backwards, upwards and forwards: ** observed long after 'swimming frenzy' is over. Sources: this study; Walker (1971); Davenport *et al.*(1984); Davenport & Clough (1986); Davenport (1987); Wyneken (1988); Renous & Bels (1993).

tion fold the forelimbs against the carapace. Davenport & Clough (1986) suggested that such folding would reduce drag and perhaps protect the forelimbs against nibbling by fish. The ridleys did not show such folding. The ridleys also appeared to use synchronized foreflipper propulsion even less than loggerheads, their standard 'escape' response being to use dog-paddling rather than foreflipper beating. Generally they appear to have a low-energy lifestyle, compatible with drifting for long periods at the sea surface.

Wyneken & Salmon (1992) have recently reported on activity levels in hatchling turtles (expressed in terms of the proportion of time spent swimming during and after the swimming frenzy) and report activity levels in the order leatherback > green > loggerhead (though differences between green and loggerheads were minor). There is no doubt that leatherbacks are the most pelagic of living sea turtles, having (relatively) the largest foreflippers throughout life (Renous, Rimblot-Baly, Fretey & Pieau, 1988), and being highly streamlined. Davenport (1987) reported that hatchling leatherbacks could not swim backwards, while Renous & Bels (1993) demonstrated that juvenile leatherbacks (250-6000 g) use synchronized foreflipper action even when swimming slowly, only deviating from full synchrony when turning; they confirm that juveniles, like hatchlings, do not swim backwards or exhibit dog-paddle locomotion.

Green turtles appear to be faster-swimming and to use the foreflippers more than either loggerheads or ridleys; Zangerl (1980) rates cheloniid pelagic specialization in the order hawksbill > green > loggerhead > ridleys. Table 1 summarizes the known swimming modes of the living sea turtles so far studied (data for hawksbills and Kemp's ridleys are limited; no data for flatbacks appear to be available). There appear to be strong inverse correlations between anatomical specialization and flexibility of locomotion; it is also apparent that the 'Carettini' form a natural grouping of swimming styles as well as of general anatomy. Zangerl (1980) regarded ridleys as showing less pelagic specialization (from an anatomical viewpoint) than all other living sea turtles; the results presented here reinforce this conclusion.

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