


**Recent Advances in  
Sea Turtle Biology and  
Conservation, 1995**



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To: Authors of new sections in the revised edition of  
*Biology and Conservation of Sea Turtles*

From: Karen Bjorndal

Date: 10 November 1995

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I have received many positive comments on the revised edition. I hope you are also pleased with the outcome. Thank you for your contribution.

**Biology and Conservation of**

# **Sea Turtles**

**Revised Edition**



**Edited by Karen A. Bjorndal**

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## **Nesting Biology of Sea Turtles**

The literature on the reproductive biology of marine turtles is immense (e.g., Hirth 1971; Pritchard 1971; Anon. 1980; Bjorndal 1982; Witzell 1983; Miller 1985; Dodd 1988; Groombridge and Luxmoore 1989; Márquez M. 1990; National Research Council 1990). Much of the recent literature is contained in the Proceedings of the Annual Symposia on Sea Turtle Biology and Conservation (NOAA Technical Memoranda).

Marine turtles share a generalized life cycle that includes iteroparous reproduction (Hirth 1980; National Research Council 1990) with the possible exception of the Kemp's ridley, stereotyped nest-building behavior (Hendrickson, this volume), laying of relatively large numbers of eggs several times during the reproductive period (Hirth 1980; Van Buskirk and Crowder 1994), and relatively strong attachment to particular locations for nesting (e.g., Bjorndal et al. 1985; Limpus et al. 1992), but inter- and intra-specific variation exists (Van Buskirk and Crowder 1994).

Determining the details of the nesting biology of sea turtles requires the identification of individual turtles, usually through tagging. The position of application on the flipper, habitat (i.e., nesting area/foraging area), type of tag (monel, inconel, titanium), and the species of turtle tagged affect the rate of tag loss (Limpus 1992). With proper assessment of tag loss, the probability of recapturing tagged turtles increases (Limpus et al. 1994).

### **Nesting Biology**

The nesting biology of marine turtles is deceptively simple. Mating occurs during a relatively short female receptive period in the vicinity of the nesting beach (Owens 1980; National Research Council 1990); the individual's mating season is completed before egg laying commences.

The nesting process is similar among all species of sea turtles. Several behavioral sequences have been

described but the real differences are small (Hendrickson, this volume). The reproductive and ovipositional cycles are regulated by changes in specific serum gonadotropins and gonadal steroids (Guillette et al. 1991; Wibbels et al. 1992).

### Reproductive Output

All sea turtles lay several clutches during a nesting season (Hirth 1980; Van Buskirk and Crowder 1994). Determining the number of times a turtle nests during a season is important, particularly if such data are averaged and used in calculations to estimate the number of female turtles in the population (Pritchard 1990). However, the number of clutches laid is often derived from incomplete coverage of the nesting season or nesting area, or loss of the individual from the nesting group (Bjorndal et al. 1985).

The number of eggs laid per clutch varies among the species (Hirth 1980; Van Buskirk and Crowder 1994). Smaller species typically lay more, smaller eggs than larger species, with two exceptions: flatback turtles typically lay about 50 large eggs and leatherback turtles lay only about 100 large eggs.

The embryological development of Cheloniidae and Dermochelyidae sea turtles (based on green, hawksbill, loggerhead, flatback and leatherback turtles) is similar in detail up to stage 22, after which generic and species specific characters become increasingly evident (Miller 1985).

Clutches of sea turtle eggs typically have a high hatching success (80% or more) unless external factors (e.g., predation, environmental change, microbial infection) intervene (National Research Council 1990). To assess the reproductive output of a nesting population, the emergence success should be calculated using a large number of nests including nests that do not produce hatchlings.

### Periodicity

The mean remigration interval reported for sea turtles is 2, 3, 4, or 5 years, with a range of from 1 to 9 or more years (Dodd 1988; Limpus et al. 1994; Van Buskirk and Crowder 1994) depending on the species. The actual remigration interval for the population may be longer; the discrepancy may result from tag loss, incomplete survey coverage, too short of a study period, or some as yet undocumented aspect of their biology.

### Philopatry

Genetic studies and tagging studies provide evidence that sea turtles exhibit a high degree of philopatry in

subsequent nesting seasons (Limpus et al. 1984, 1994; Bjorndal et al. 1985; Bowen et al. 1992; Norman et al. 1994). However, not all turtles return to the nesting site in subsequent seasons (Limpus et al. 1994); some utilize other nesting sites in the general area (Dodd 1988). The determination of philopatry depends on identification of the individual and the coverage of the nesting season and nesting beach.

### Site Fixity

Within a season, a turtle will tend to reneest in relatively close proximity (0–5 km) during subsequent nesting attempts, although a small percentage may utilize more distant nesting sites in the general area (Limpus et al. 1984; Bjorndal et al. 1985; Dodd 1988; Eckert et al. 1989). The ecological consequences of this behavior require elucidation.

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## Hatchling Orientation

As hatchlings, sea turtles begin a life of astonishing migratory feats. When the first edition of this volume was published, movements of sea turtles at many life-history stages were well documented, but an understanding of orientation cues and guidance mechanisms was just beginning. At that time, Archie Carr described the lack of tenable theories to explain migratory abilities as "an embarrassment to science" (this volume). In the years since this prompting, substantial progress has been made toward redemption.

### Sea-finding Orientation

The orientation of hatchling sea turtles from nest to sea is a robust behavior that lends itself well to experimentation. Capitalizing on the strong propensity of hatchlings to move in the brightest direction, N. Mrosovsky and colleagues conducted numerous studies to develop a model describing how orienting hatchlings use light cues (Mrosovsky and Kingsmill 1985). Their experiments with partially blindfolded hatchlings showed that their turning toward brightness is initiated by light angle and intensity differences that are "measured" at the retina. In this measurement, a hatchling's eyes seem to function as if each were a complex array of light detectors. With this orientation mechanism, hatchlings average brightness input over a wide horizontal range ( $\sim 180^\circ$ ) and a narrow vertical range ( $\sim 10^\circ$ ) (Witherington 1992).

The perception of brightness is dependent upon light wavelength and intensity. Experiments have shown that independent of intensity, short-wavelength light (near-ultraviolet, blue, green) is more attractive to hatchlings than long-wavelength light (yellow, red) (Witherington and Bjorndal 1991a). Unlike other species, loggerhead (*Caretta caretta*) hatchlings have a unique tendency to orient away from monochromatic yellow light (Witherington and Bjorndal 1991b).

In addition to brightness, horizon silhouette and/or shapes associated with the horizon also influence hatchling orientation (Salmon et al. 1992; Witherington 1992). Hatchlings orient away from vertical stripes and elevated silhouettes, generally irrespective of brightest direction. In highly directed light fields, however, with brightness in one direction far exceeding that of competing directions, hatchlings move toward brightness. Beach conditions under which hatchlings orient seaward without the seaward direction being brightest are common. Under these conditions, hatchlings deprived of form vision by waxed paper cannot orient seaward (Witherington 1992).

Artificial sources near nesting beaches produce highly directed light fields that misdirect hatchlings (Verheijen 1985). Mortality from this behavioral disruption remains a substantial conservation problem. Although darkening beaches is the only complete solution, replacing problem light sources with low-pressure-sodium-vapor sources, which emit monochromatic yellow light, reduces effects on orienting hatchlings (Witherington and Bjorndal 1991b).

#### Orientation at Sea

After they enter the sea, hatchlings depend on cues other than light to lead them away from land (Salmon and Wyneken 1994). At least two sets of cues, wave direction and the geomagnetic field, direct swimming orientation. Swimming hatchlings orient into oncoming waves, which establishes seaward movement in the near-shore zone (Wyneken et al. 1990). Geomagnetic cues seem to be responsible for guiding a seaward course as hatchlings travel offshore (Lohmann and Lohmann 1994).

Laboratory studies show that hatchlings are guided by an inclination compass, like that of birds, rather than a polar compass (Light et al. 1993). An inclination compass functions by distinguishing the angle of the Earth's magnetic field lines, which vary with latitude, and can provide information both on poleward direction and degree of latitude.

Hatchlings acquire a magnetic directional preference during their initial swimming (Lohmann and Lohmann 1994). Once this preference is established in the laboratory, hatchlings will adjust their bearing predictably when the magnetic field around them is altered to imitate inclination angles at different latitudes (Lohmann and Lohmann, in press). Sea turtles are the first animals to show an ability to determine latitude magnetically. The magnetic sense in hatchlings has the potential to indicate both direction and position and may be the key to a guidance system used by sea turtles at all life-history stages.

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**Biology of the Early Pelagic Stage—  
The "Lost Year"**

The life history of sea turtle hatchlings from the time they leave the nesting beach, enter the sea, and become part of the pelagic community until they return to coastal, benthic foraging habitats as juveniles, has been known as the "mystery of the lost year" (Carr, this volume). Research efforts to unravel the mystery of this early pelagic stage have focused on the North Atlantic and North Pacific loggerhead populations (*Caretta caretta*). Despite considerable effort, researchers have not found areas where pelagic-stage turtles can be consistently found for any other population or species. The flatback turtle (*Natator depressus*) may not have a true pelagic stage (Walker and Parmenter 1990).

The orientation behavior and sensory cues used by hatchlings first to find the sea and then to maintain direction once in the sea are reviewed by Witherington (this volume). Wyneken and Salmon (1992) have analyzed the swimming frenzy that occurs once the hatchlings have entered the sea. Variation in the Earth's magnetic field may provide the cues for the post-hatchlings to orient while in the pelagic current systems (Lohmann and Lohmann 1994, in press).

Archie Carr (1986, 1987a,b) hypothesized that the lost year turtles were associated with driftlines, convergences, and rips in the North Atlantic Gyre system. Carr (1986) suggested that loggerhead hatchlings from the southeastern USA rookeries become incorporated into the Gulf Stream Current and from there, those post-hatchlings that are in the eastern portion of the Gulf Stream become incorporated into the "Azorean" Current that carries them past the Azores, Madeira, Canary Islands and back again to the western Atlantic. The size frequency distribution of loggerheads in the eastern Atlantic complements the "missing" size classes in the western Atlantic (Carr 1986; Bolten et al. 1993) and was the first line of evidence that the turtles in the two regions belong to the same population. Mitochondrial DNA sequence patterns are being analyzed to confirm this relationship. In addition, the movement patterns that

Carr (1986) hypothesized within the North Atlantic Gyre system have been documented (Eckert and Martins 1989; Bolten and Martins 1990; Bolten et al. 1992a,b; Bjorndal et al. 1994). Satellite telemetry is being used to document specific movement patterns within the North Atlantic Gyre (Bolten et al., unpublished data). Movement of Atlantic turtles into the Mediterranean has been documented by tag returns (Manzella et al. 1988; Bolten et al. 1992a) and confirmed by genetic analyses (Laurent et al. 1993). Transoceanic movements for loggerheads in the North Pacific have been documented using genetic analyses (Bowen et al., in press).

Duration of the pelagic stage has important demographic implications. Preliminary results comparing growth rates estimated from recaptures and those estimated from length-frequency analysis suggest the "lost year" for the Atlantic loggerheads is more likely a "lost decade" (Bolten et al., in press). Zug et al. (in press) using skeletochronology, report a similar time period for the North Pacific loggerheads.

Jellyfish (e.g., *Pelagia noctiluca*) are the major natural diet component of pelagic loggerheads in the North Atlantic; in the North Pacific, the principal food sources are the neustonic coelenterate *Velevella* and the gastropod *Janthina* sp. Young post-hatchlings feed on a variety of invertebrates (including insects) that are associated with the *Sargassum* ecosystem (Richardson and McGillivray 1991; Witherington 1994).

Ingestion of and entanglement in marine debris (e.g., plastics, tar, and discarded fishing gear) have an impact on survivorship of pelagic populations (Balazs 1985; Carr 1987a,b; Witherington 1994). Incidental take in commercial fisheries (e.g., driftnets and long-line fisheries) poses another major threat to pelagic turtles (Aguilar et al. 1992 and 1993 as summarized in Balazs and Pooley 1994; Wetherall et al. 1993; Balazs and Pooley 1994; Bolten et al. 1994).

Genetic markers may provide the necessary tools to link pelagic populations with specific rookeries. From this linkage, and through collaborative efforts with oceanographers, factors affecting distribution and movement patterns may be elucidated in the future.

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## **Telemetry and the Behavior of Sea Turtles**

The modern era of microelectronics has provided unique insight into the movements of sea turtles. In this rapidly evolving field, many studies are aired only in symposia proceedings, and techniques are often obsolete at the time of publication. Prospective investigators should contact their active colleagues. White and Garrott (1990) is an indispensable reference.

Early attempts to electronically monitor movement used VHF radio transmitters which emit a signal at a preprogrammed rate (Murphy 1979; Chan et al. 1991; Liew and Chan 1993). Individual transmitters are identified by frequency or pulse rate and located using a receiver and directional antennae; transmitters can be modified for data transmission. Active investigators include myself (Hubbs-Sea World Research Institute; leatherbacks), Javier Alvarado (University of Michoacán, Mexico; East Pacific green turtles), and Steve Morreale (Cornell University) and André Landry (Texas A&M University) (Kemp's ridleys).

Instead of a radio signal, sonic transponders emit a moderate to high frequency sonic pulse detectable using a directional hydrophone (Ogden et al. 1983; Standora et al. 1984; Yano and Tanaka 1991). Transponders can also be modified to transmit non-local data (e.g., temperature, depth). Caveats include short range and battery life; background noise can confuse interpretation. Active investigators include Ed Standora (State University College of Buffalo; loggerheads), Liew Hock Chark and Chan Eng Heng (Universiti Pertanian Malaysia; green turtles), and Joanne Braun and Sheryan Epperly (National Marine Fisheries Service, Beaufort; technique development).

Platform transmitter terminals (PTT) transmit data to an orbiting satellite. Life expectancy is highly variable depending on battery configuration. Loggerhead and leatherback studies have been published by Hays et al. (1991) and Keinath and Musick (1993), respectively. Active investigators include myself (leatherbacks), Steve Morreale (leatherbacks, Kemp's ridleys), Pamela Plotkin (Texas A&M University; olive ridleys), George Balazs (National Marine Fisheries

Service, Honolulu; green turtles), and Richard Byles (U.S. Fish and Wildlife Service, Albuquerque; several species).

Microprocessor data-loggers sample and record sensor data (e.g., velocity turbines, pressure transducers, electrical signals, ambient light, or thermocouples) (Eckert et al. 1989; Sakamoto et al. 1993). Multiple variables can be measured without compromising behavior, and resolution (accuracy) exceeds that provided by direct observation techniques. The disadvantage is that instruments must be recovered for data retrieval. Active investigators include myself (leatherbacks), Yasuhiko Naito (Japanese National Institute of Polar Research; loggerheads), and Robert Van Dam (Scripps Institution of Oceanography; hawksbills).

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## **Molecular Genetic Studies of Marine Turtles**

Molecular genetic analyses of marine turtles have provided much information over the last five years, and this body of conservation-oriented research will expand substantially over the next decade. Most of the research accomplished to date has utilized mitochondrial DNA (mtDNA). The idiosyncrasies of this maternally inherited genome may limit utility for some aspects of population genetics and molecular evolution, but these same features provide powerful applications in cases where maternal behaviors (such as natal homing) define population structure (Awise, in press). Nuclear DNA analyses are likely to yield many revelations in the decade to come, as indicated by Karl et al. (1992) and FitzSimmons et al. (1995). For a more comprehensive review of the papers summarized here, the reader is referred to Bowen and Awise (in press).

### **Natal Homing**

Based on the nest site fidelity of adult females, Carr (1967) and others suggested that marine turtles nest on their natal beach. Hendrickson (1958) proposed an alternative scenario in which neophyte nesters subsequently use this site for nesting effort. These alternate scenarios have been tested for three species with mtDNA analyses. Evidence from green turtles (Meylan et al. 1990; Bowen et al. 1992; Allard et al. 1994; Norman et al. 1994; Encalada et al., in review), loggerhead turtles (Bowen et al. 1993a), and hawksbill turtles (Broderick et al. 1994; Bass et al., in review) are concordant in supporting the natal homing hypothesis for these species. An important corollary of these findings is that nesting populations are distinct demographic units. Depletion of nesting aggregates will not be compensated by recruitment from other populations.

## Phylogeography and Molecular Evolution

The mtDNA data indicate that green turtle rookeries within an ocean basin are demographically independent over ecological timescales but closely related in an evolutionary sense (Bowen et al. 1989; Encalada et al., in review). Subsequent analyses have extended this qualitative conclusion to loggerhead turtles (Bowen et al. 1993a) and hawksbill turtles (Bass et al., in review). Over intervals of thousands of years, changes in climate and coastal geography probably drive an ongoing process of rookery extinction and colonization. Furthermore, occasional lapses in natal homing must occur to allow the colonization of new nesting habitat. These processes may limit the development of deep evolutionary separations within each ocean basin. Despite this mixing, patterns of regional colonization may be inferred from mtDNA sequences (Encalada et al., in review).

In regard to the global phylogeography of cheloniid species, evidence from ridleys (Bowen et al. 1991), green turtles (Bowen et al. 1992) and loggerheads (Bowen et al., in press a) indicate that continental barriers have been of overriding importance. Deeper evolutionary history of marine turtles has also been analyzed with mtDNA sequence data. Findings of relevance to marine turtle biology include confirmation of a distant relationship between *Natator depressus* and other cheloniid species, the affiliation of *Eretmochelys* with the tribe Carettini rather than Cheloniini, the genetic distinctiveness of *Lepidochelys kempi* from *L. olivacea*, and the paraphyly of *Chelonia mydas* with respect to the putative *C. agassizi* (Bowen et al. 1991, 1993b). Nuclear DNA and mtDNA analyses do not support the taxonomic distinction of *C. agassizi* (Bowen et al. 1992; Karl et al. 1992). Sequence divergences at intergeneric and interfamilial levels, when assessed against fossil-based separation times, indicate that marine turtle mtDNA evolves more slowly than under the "conventional" vertebrate molecular clock (Avisé et al. 1992).

## Mixed Stock Analysis of Feeding Populations

One outcome of the mtDNA analyses reviewed here is the discovery that many nesting populations of green, loggerhead, and hawksbill turtles contain unique haplotypes (Norman et al. 1994; Lahanas et al. 1994). These "endemic" nucleotide sequences, and corresponding haplotype frequency shifts between nesting populations, may be used to estimate the contribution of reproductive aggregates to feeding grounds or migratory corridors (Avisé and Bowen 1994; Bowen et al., in press b).

In an analysis of mtDNA polymorphisms in juve-

nile green turtles, Lahanas et al. (in review) demonstrate that nesting colonies contribute to a Caribbean feeding habitat in cohorts which are roughly proportional to the size of source (breeding) populations and suggest that this feeding population represents a random mix of individuals from regional nesting populations. In contrast, Sears et al. (in press) conclude that loggerheads in a South Carolina feeding aggregate are not a random mix of individuals from regional nesting populations, but appear to be drawn at higher than expected frequency from the Georgia/South Carolina nesting population relative to the larger Florida nesting population. Broderick et al. (1994) demonstrate that two hawksbill foraging areas in northern Australian waters are genetically distinct from proximal nesting beaches, consistent with the hypothesis that hawksbill nesting cohorts overlap extensively in feeding areas (see also Bowen et al., in press c).

Molecular genetic markers have also been used to document unusually long migrations in juvenile loggerhead turtles. Laurent et al. (1993) demonstrated that mtDNA genotypes endemic to West Atlantic nesting colonies occur in Mediterranean feeding populations. Bowen et al. (in press b) demonstrate that haplotypes endemic to Japanese and Australian nesting populations occur in juvenile turtles off Baja California, indicating a developmental migration of over 10,000 km.

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## Applied and Behavioral Endocrinology

Behavioral endocrinology studies, initiated at Cayman Turtle Farm, first on *Chelonia mydas* (Owens and Morris 1985) and more recently on *Lepidochelys kempi* (Rostal 1991), have now been expanded to wild populations using several different species (Wibbels et al. 1990; Rostal 1991).

The preliminary gonadotropin work of Licht (1984) has been significantly modified with the realization that what was originally thought to be an assay for follicle stimulating hormone (FSH) was in actuality an assay for neurophysin, which is a carrier molecule for arginine vasotocin (AVT) (Licht et al. 1984). The AVT and neurophysin are secreted at the same time and in a very dynamic way during oviposition (Figler et al. 1989), as are prostaglandins (Guillette et al. 1991). Using a new FSH assay in *Caretta caretta* and *C. mydas*, Wibbels et al. (1992) found FSH and LH secreted simultaneously at ovulation. Thyroid hormone levels have also been correlated to nesting, growth, migration and hibernation (Moon 1992).

In wild turtles progesterone levels peak with ovulation (Wibbels et al. 1992), and the ovulatory process may be impacted by stress as correlated to corticosterone (B) (Valverde et al. 1994). There are several additional stress/B studies in progress at various labs. Estrogen (E) is significantly elevated during the follicular development period prior to migration, while testosterone (T) peaks dramatically and E drops as migration begins (Wibbels et al. 1990). The ratio of E to T in the allantoic fluid of hatchlings (Crain et al. 1994) has shown promise as a hatchling sexing technique.

The T-based sex determination (TSD) technique for immatures has been validated and used in several studies (Wibbels et al. 1991). The method has proven useful where the effects of TSD could be important to their conservation (Bolten et al. 1992). We have recently been able to estimate the number of nests that a female has deposited by the changes in her T levels. The technique has proven useful when researchers

could not actually monitor each female for each of her nests (Rostal 1991). In addition, the circulating steroids in an adult can now be used to predict their reproductive status (Wibbels et al. 1990, 1992).

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## **Metabolism, Physiology, and Thermoregulation**

Considerable progress has been made in the last 15 years in elucidating the physiological mechanisms of sea turtles. This has been accomplished by laboratory studies and by the application of sophisticated physiological techniques to field conditions. Radio, sonic, and satellite telemetry have demonstrated that sea turtles range widely in the oceans and dive to great depths: as much as 233 m in loggerheads and 1000 m in leatherbacks (Eckert et al. 1986, 1989; Sakamoto et al. 1990). Sea turtles have complexly subdivided multicameral lungs with small terminal air sacs through which a high flux of oxygen can occur (Jackson 1985; Lutcavage et al. 1987). Cartilaginous support, and perhaps the smooth muscles distributed throughout the lungs, allows gas exchange at rates up to  $12 \text{ L sec}^{-1}$ . This is equivalent to one vital capacity per second and approximates the flow velocity of adult humans during a maximal forced expiration. This support apparently allows nearly complete lung collapse which prevents gas trapping when turtles dive to great depths (Jackson 1985). Loggerhead and green turtles use their lungs as the principal  $\text{O}_2$  store to support aerobic diving to moderate depths because their blood and tissue  $\text{O}_2$  stores are similar to those of their terrestrial relatives (Wood et al. 1984; Lutcavage et al. 1987, 1989, 1991).

Leatherback turtles are unique because of their ability to dive to great depths, their long distance migrations into cold temperate waters, their diving physiology, and their metabolic adaptations (Paladino et al. 1990). Deep dives by leatherbacks appear to be supported by an increased  $\text{O}_2$  carrying capacity of blood and tissue because the lungs undoubtedly collapse owing to increased hydrostatic pressure. Hematocrits and hemoglobin and myoglobin concentrations are among the highest recorded in reptiles, and approach levels found in diving mammals. However, blood  $\text{O}_2$  affinity, Hill coefficient, and Bohr effect are similar to other turtles (Lutcavage et al. 1990). Resting metabolic rates of leatherbacks are three times those predicted from allometric relation-

ships for green turtles and other reptiles scaled to leatherback size ( $0.387 \text{ W kg}^{-1}$ ,  $1.15 \text{ ml O}_2 \text{ kg}^{-1} \text{ min}^{-1}$ ), but half the values predicted for mammals of this size (Paladino et al. 1990). Lutcavage et al. (1992) reported a resting metabolic rate of  $1.1 \text{ ml kg}^{-1} \text{ min}^{-1}$  and calculated a range of dive times of 5 to 70 min that could be supported aerobically. The lower value for metabolic rate reported by Lutcavage et al. (1990) appeared to be due to a reduced tidal volume caused by an increased resistance to air flow inherent in their gas collection system. They used a small Hans Rudolph valve (no. 2600) and relatively small (34 L) Douglas bag as compared to the giant (7200) Hans Rudolph valve and 200 L Douglas bag used by Paladino et al. (1990). The smaller apparatus is sufficient for most sea turtles but it is inadequate for the leatherback.

The thermal biology of sea turtles depends upon the heat transfer properties of their environment as well as the physical and physiological characteristics of the turtles (Spotila and Standora 1985). Large sea turtles use a unique combination of thermoregulatory adaptations to control body temperature. Green turtles display regional endothermy. Warm pectoral muscles probably increase this turtle's swimming ability and may facilitate long-distance migrations (Standora et al. 1982). A resting leatherback has internal temperatures higher than carapace and ambient temperatures indicating that heat is generated internally and not absorbed from the environment (Standora et al. 1984). Mathematical modelling indicates that leatherbacks can use large body size, peripheral tissues as insulation, and circulatory changes to maintain warm temperatures in cold water and to avoid overheating in warm water (gigantothermy) (Paladino et al. 1990). Future research is needed to elucidate the cellular basis for these adaptations and to determine the effect of body size on physiological thermoregulation.

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## Diseases of Marine Turtles

This synopsis of marine turtle diseases is presented to raise awareness about their potential role as direct causes of morbidity and mortality in marine turtles.

### Viral

#### *Gray-patch disease.*

**ETIOLOGY:** Herpesvirus (Rebell et al. 1975).

**PATHOLOGY:** Focal papules or spreading plaques of epidermal necrosis.

**SIGNIFICANCE:** High morbidity and mortality in post-hatchling mariculture-reared green turtles. Stress may be a factor in outbreaks (Kleese 1984). While latent infection may be ubiquitous, disease in wild turtles has not been documented (Haines 1978).

#### *Lung-eye-trachea disease (LETD).*

**ETIOLOGY:** Herpesvirus (Jacobson et al. 1986).

**PATHOLOGY:** Conjunctivitis, pharyngitis, tracheitis, and bronchopneumonia.

**SIGNIFICANCE:** Only reported in mariculture-reared green turtles.

### Bacterial

#### *Various bacterial infections.*

**ETIOLOGY:** Variety of Gram positive and Gram negative bacteria (reviewed by Lauckner 1985; Glazebrook and Campbell 1990a,b; Aguirre et al. 1994). *Vibrio alginolyticus*, *Aeromonas hydrophila*, and *Flavobacterium* sp. are associated with ulcerative stomatitis-obstructive rhinitis-pneumonia complex (Glazebrook et al. 1993).

**PATHOLOGY:** Abscesses and granulomas, septicemia, toxemia.

**SIGNIFICANCE:** Many are opportunistic pathogens requiring predisposing factors. Several species (e.g., *Mycobacterium*, *Vibrio*, *Salmonella* sp.) may be pathogenic to humans.

### *Chlamydiosis.*

**ETIOLOGY:** *Chlamydia* sp. (Homer et al. 1994).

**PATHOLOGY:** Myocarditis.

**SIGNIFICANCE:** Mortality in mariculture-reared green turtles. Significance to wild populations is unclear.

### **Fungal**

**ETIOLOGY:** Various species including *Sporotrichium*, *Cladosporium*, *Paecilomyces* spp., and *Penicillium* (Jacobson et al. 1979; Lauckner 1985; Glazebrook et al. 1993).

**PATHOLOGY:** Fungal dermatitis and fungal bronchopneumonia.

**SIGNIFICANCE:** All reports are from captive green turtles and loggerheads. Most fungi require predisposing factors to cause disease.

### **Protozoal**

#### *Amebiasis.*

**ETIOLOGY:** *Entamoeba invadens* (Lauckner 1985).

**PATHOLOGY:** Enteritis and hepatitis.

**SIGNIFICANCE:** Mortality reported in captive marine turtles only.

#### *Coccidiosis.*

**ETIOLOGY:** *Caryospora cheloniae* (Leibovitz et al. 1978).

**PATHOLOGY:** Intestinal mucosal epithelial necrosis and encephalitis.

**SIGNIFICANCE:** Mass mortality in captive hatchling and juvenile green turtles and in free-ranging green turtles from Australia (Gordon et al. 1993).

### **Endoparasites**

#### *Trematodiasis.*

**ETIOLOGY:** Diverse fauna of digenean trematodes in gastrointestinal and cardiovascular systems (Lauckner 1985).

**PATHOLOGY:** Usually inapparent infections. Gastrointestinal species may cause enteritis and cardiovascular trematodes may cause systemic vascular and perivascular inflammation. One species associated with gallbladder papillomatous hyperplasia in green turtles (Lauckner 1985).

**SIGNIFICANCE:** Gastrointestinal trematodiasis contributes to debilitation in severe cases. Cardiovascular trematodiasis may cause sporadic mortality.

#### *Cestodiasis.*

**ETIOLOGY:** Cestodes (tapeworms).

**PATHOLOGY:** Adult pseudophyllidean tapeworms reported in the gastrointestinal tract are probably non-pathogenic. Tetrarhynchid cestode cysts on serosa of gastrointestinal tract and in other viscera.

**SIGNIFICANCE:** Rare. Reported only in loggerheads which may be an aberrant host (Lauckner 1985).

#### *Nematodiasis.*

**ETIOLOGY:** Variety of gastrointestinal nematode species have been described (Lauckner 1985). *Sulcas-caris sulcata* (Ascaridoidae) commonly affects *C. mydas* and *C. caretta*.

**PATHOLOGY:** Enteritis, gastrointestinal obstruction.

**SIGNIFICANCE:** Heavy infections may cause debilitation and death.

### **Ectoparasites**

#### *Leeches (Hirudinea).*

**ETIOLOGY:** *Ozobranchus* species.

**PATHOLOGY:** Erosive skin lesions at attachment sites. Heavy infestations associated with severe anemia.

**SIGNIFICANCE:** May infest all marine turtle species although not reported from *Dermochelys*. Mortality in captive green turtles and loggerheads attributed to heavy infestation (Schwartz 1974). Potential vectors of bloodborne disease although none reported.

## Crustacea (barnacles).

**ETIOLOGY:** Encrusting and burrowing barnacle species (Lauckner 1985).

**PATHOLOGY:** Shell lesions, oropharyngeal obstruction, visceral and joint lesions in burrowing species.

**SIGNIFICANCE:** Most are innocuous epibionts. Severely debilitated turtles may have increased epibiont loads. Heavy loads may increase the costs of locomotion. Burrowing species (e.g., *Tubicinella* sp.) may penetrate the body cavity and kill their host.

## Neoplastic

### Green turtle fibropapillomatosis (GTFP).

**ETIOLOGY:** Probably viral (Herbst et al., in press). Role of herpesvirus demonstrated in tumors is unproven.

**PATHOLOGY:** Cutaneous fibropapillomas and visceral fibromas.

**SIGNIFICANCE:** Cosmopolitan; high prevalence among wild juvenile and adult green turtles in some areas. Reported in captive green turtles. Similar condition reported in loggerheads, flatbacks, and olive ridleys (Herbst 1994).

## Conclusion

The causes of individual strandings and mass mortalities among free-ranging marine turtles are poorly documented, especially when not self-evident (entanglement, trauma). Although some non-infectious disease problems are well documented in free-ranging populations, we have a better understanding of infectious diseases in captive turtles. A fuller appreciation of the significance of disease in the ecology of free-ranging sea turtles will require prompt, carefully conducted necropsies of stranded turtles and the development and application of diagnostic reagents specific for marine turtle diseases (Herbst and Klein, in press).

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## Temperature and Sex Ratio

In the 1979 meeting (Mrosovsky and Yntema, this volume), we raised three priorities for those managing sea turtles: 1) learning about the effects of fluctuating temperatures, including those in styrofoam boxes; 2) studying within-species variation in pivotal temperatures; 3) locating thermosensitive periods within incubation. To these I now add another: discovering what sex ratios are in nature. This could provide a benchmark against which to assess changes resulting from global warming or from conservation practices (this is not the same as saying that one should always aim to maintain natural ratios). Apart from demonstrations that incubation in styrofoam boxes does indeed introduce masculinizing biases (e.g., Dutton et al. 1985), data on the priorities raised in 1979 remain sketchy. By default, practice or theory is sometimes based on pivots from only one or two clutches, not a safe way to estimate population means. Knowledge of variance in pivots is important for assessing how turtles might fare during global warming.

Nevertheless, much has been learned about thermal influences on sexual differentiation in reptiles. The proceedings of a recent symposium (Lance 1994) provide access to this literature. Unfortunately a gap still exists between the variable temperatures in nature and the constant temperatures in most laboratory work. This makes it difficult to predict sex ratio accurately from nest temperatures. One relevant finding, with freshwater turtles, is that excursions above the pivotal are more influential than similar-sized excursions below the pivotal (Bull 1985). For definitions of terminology, see Mrosovsky and Pieau (1991).

Another problem in estimating sex ratios from nest temperature is lack of detailed information on thermosensitive periods, except for a study on leatherbacks (Desvages et al. 1993). The reason for wanting to estimate sex ratios is to avoid having to sacrifice hatchlings and the associated histology. The glycerine method (van der Heiden et al. 1985) for sexing has not been adequately validated for sea turtles, and two

failures to do this have been reported (Jackson et al. 1987; Mrosovsky and Benabib 1990). No endorsement of the glycerine method for sea turtles by histology has been published as far as I am aware. Choosing an appropriate method of sexing is basic for any study. Regrettably, fixing the gonad and subsequent histology is still probably the most feasible reliable method to use in remote areas. It is hoped that this may soon change.

Since 1979, the idea that temperature directs sexual differentiation has moved from fringe to orthodox, so much so that temperatures are now being recorded on beaches in many parts of the world. In some cases inattention to methodology reduces the value of the data. Even a few tenths of a degree can make a difference to sex ratio. It is not possible to be too obsessive about calibration; for this a good quality Hg thermometer is advised. Paying one or two thousand dollars for dataloggers does not guarantee that circuitry will remain in unblemished perfection in the wet salty sand of a tropical beach. For those using thermocouples, the how-to-do-it manual by Spotila et al. (1983) is invaluable.

Clearer formulation of aims might improve some studies. It is often appropriate to measure temperatures within the egg mass. However, if the aim is to compare thermal profiles in one situation to those in another (northern vs. southern rookery, renourished vs. natural beach, hatchery site vs. nesting area), then burying some temperature probes in the sand rather than in nests themselves should be considered—unless one can arrange for turtles to nest on the same date in the different areas, depositing standard numbers of eggs at standard depths, with nests disposed in representative transects.

Finally, on methods, nest temperatures change over the course of a day. There are various solutions to this problem (Godfrey and Mrosovsky 1994). In case it is not feasible to take readings at appropriate times, I place some probes 60 cm below the surface; at this depth temperature variation is reduced.

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## **Growth and Age of Sea Turtles**

During the 1979 conference, the very slow growth rates of sea turtles under natural conditions were revealed (Balazs, this volume, and references cited therein). Previously, sea turtle growth rates had been assumed to be moderately rapid with most cheloniids attaining sexual maturity in five to six years. The new estimates of as many as 40–60 years to attain sexual maturity revolutionized our view of the life history of sea turtles and of the time frame required for conservation actions. Considerable effort has been invested in the studies of growth and age in wild sea turtles because both parameters are critical for demographic studies and development of appropriate management programs. These studies have taken four basic approaches.

First, growth models (e.g., von Bertalanffy, logistic, Gompertz) have been applied to mark-recapture data (Frazer and Ehrhart 1985; Frazer and Ladner 1986; Bjorndal and Bolten 1988; Boulon and Frazer 1990). The von Bertalanffy model usually has the best fit for turtle data (Frazer et al. 1990). Most studies have used the models to extrapolate beyond the studied size range to estimate age at sexual maturity. Such extrapolation requires caution, although tests on a data set of known-aged freshwater turtles (Frazer et al. 1990) revealed that the removal of smaller individuals from the data caused little change in the asymptote of the growth curve and thus in the maturity estimate. Removal of large individuals caused significant changes in the asymptote, which would affect estimates of maturity. Maturity estimates depend upon the body size selected to represent maturity; mean size of nesting females is considered the best index (Frazer and Ehrhart 1985).

Second, some studies have calculated growth rates based on mark-recapture data and presented mean growth rates for 5- or 10-cm size classes of turtles (Bjorndal and Bolten 1988; Collazo et al. 1992; Limpus 1992; Boulon 1994). Years to grow through each size class are calculated and summed to estimate the number of years necessary to grow through the size

interval of the study population. This approach offers conservative growth estimates, particularly if there is no extrapolation beyond the size range of the study population.

Third, skeletochronology—based on periosteal layers in the humerus—provides estimates of age and growth rates without the time investment required for mark-recapture studies (Frazier 1985; Zug et al. 1986; Zug 1991). The technique is handicapped by the natural process of remodeling that progressively eliminates the inner (younger) growth layers as the turtle grows (Zug 1990). Protocols are available for estimating the number of lost layers and ages, but researchers must be aware of the assumptions and bias of each protocol (Parham and Zug, unpublished manuscript). Periosteal layers represent annual growth layers in juvenile loggerheads in temperate waters (Klinger and Musick 1992).

Fourth, length-frequency analysis, in which estimates of von Bertalanffy growth parameters are generated from length distributions of sample populations, does not require long time investments to study growth and age. This technique successfully estimated growth rates for a population of immature green turtles of known growth rates based on a mark-recapture study (Bjorndal and Bolten 1995; Bjorndal et al. 1995).

Many questions remain unanswered. Research effort has been uneven among species of sea turtles—the pelagic leatherback and olive ridley are, not surprisingly, the poorest known. From the studies cited above and others, we know that there is substantial variation among species, and among populations and geographic regions for any species. However, at least for immature green turtles, growth rates apparently do not vary between sexes in a population (Bolten et al. 1992). Growth rates and age estimates based on captive-raised specimens have proved unreliable (Bjorndal 1985) and should be avoided.

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## **Population Models and Structure**

The size and growth of any population depend on the annual number of births and deaths, and on the timing of maturation, reproduction, and death in each individual's life. Population modelling consists of using known or estimated birth, growth, and death rates to make projections about the future. The accuracy and usefulness of a model depend upon its design and the quality of input variables. To provide meaningful output for management decisions the model must reasonably mimic the life history of the population and the input values must be realistic. By varying each rate in a model and comparing its effects on population growth, the relative impact of natural or human-induced changes can be evaluated. This can help to prioritize management strategies and future research needs.

Since the first publication of this volume, estimates of classic demographic parameters (i.e., age-specific fecundity, survivorship, and age at maturity) have become available for two populations of loggerheads—one in the southeastern United States and one in Queensland, Australia. The data used by Richardson (1982) and by Richardson and Richardson (this volume) for an early model of loggerhead population dynamics have been reanalyzed (Frazer 1983a,b, 1984, 1986) and combined with additional data on growth (Frazer 1983a; Frazer and Schwartz 1984; Frazer and Ehrhart 1985) and survival (Frazer 1983a, 1987) to provide estimates suitable for an age-specific life table. Using these parameter estimates, Crouse et al. (1987) constructed a stage-based matrix model for this population and concluded that changes in survivorship of larger juveniles and adults would likely have a much greater effect on future population growth than changes in the egg/hatchling stage. In other words, effort put into nest protection might be wasted if large juvenile and adult survival is not also increased, by reducing mortality due to drowning in shrimp trawl nets.

The data gathered by Limpus (1985) for Australian loggerheads also have been recast to provide inputs

for a stage-based matrix model (Heppell, Limpus, Crouse, Frazer, and Crowder, unpublished manuscript). Although there are important differences between the two populations, including a longer estimated maturation time for the Australian loggerheads (Frazer et al. 1994), the Heppell et al. model affirms many of the findings of the Crouse et al. (1987) model.

Interesting insights from the loggerhead models relate to the size (age) structure of populations. Delayed maturity requires that a very large number of eggs, hatchlings, juveniles and subadults be maintained in the population in order to sustain a relatively small but important number of reproductively active adults. For example, in the U.S. loggerhead model (Crouse et al. 1987), more than 498,000 female eggs and immatures would be necessary to maintain a stable adult female population of only 1277. Thus, a large number of observed immature individuals (for example 300,000) does not necessarily mean that a population is robust; nor does releasing large numbers of juveniles into the wild ensure that a population will grow. Likewise, because of the relatively small number of adults compared to other age classes, focusing protection only on adults may be less effective than increasing survivorship in the much larger juvenile (or subadult) population. Finally, the effects of management may take decades to materialize, particularly if monitoring focuses only on one stage, such as adults on the nesting beach. Additional modelling by Crowder et al. (1994) has shown that it may take up to 70 years or more before the deployment of turtle excluder devices (TEDs) on shrimp trawls results in any substantial observable increase in the numbers of nesting turtles. If juvenile and adult survival have been low, an increase in adult survival may result in more nesting for a decade or two, as current adults survive to return to nest more often. However, this increase may be followed by a transient decrease in nesting animals (Crowder et al. 1994), as the relatively fewer offspring produced by the smaller adult population decades earlier begin to mature.

Early computer programmers developed a concept known as GIGO (garbage in, garbage out) to help them remember that even the best models could not provide reliable output if input values were unrealistic or flawed. Providing good input values for sea turtle models is no small task. Reliable estimates of fecundity require almost constant beach patrols every night of the nesting season to determine clutch frequency (Frazer and Richardson 1985), which then must be adjusted for the re-nesting or remigration interval (Frazer 1984). Adult female survivorship estimates must take into account the confounding effects of both tag loss and remigration interval (Frazer

1983b). Because there are no reliable means of aging sea turtles, time to maturity must be estimated using capture/recapture data and growth trajectories (Frazer and Ehrhart 1985) or data of questionable value from captive studies (Frazer and Schwartz 1984).

Owing to the complex life cycle of sea turtles, with different life stages inhabiting distant habitats, data gathered in the wild may cover only a portion of the size class distribution and lead to erroneous conclusions. For example, small loggerheads (<50 cm) do not typically appear in Florida (USA) waters and were not included in the growth analysis by Frazer and Ehrhart (1985). The small loggerheads inhabiting the eastern Atlantic near the Azores probably come from western Atlantic rookeries. These turtles grow much slower than predicted by Frazer and Ehrhart's (1985) Florida model (A. Bolten, pers. comm.). Thus, Frazer and Ehrhart probably underestimated average age at maturity for the Florida adult females. Fortunately, the results of such errors can be assessed by conducting a sensitivity analysis to determine the effect of changing the values on model input, and the loggerhead models are fairly robust in terms of the effects of errors in estimating age at maturity (Crouse et al. 1987).

The problems of relative inaccessibility or unknown whereabouts of certain life stages will continue to plague those who seek dependable input values for sea turtle models. Fortunately, some insight can be gained from long-term studies of freshwater turtles. Small and large, young and old, these turtles inhabit the same pond in close proximity. Thus, they can be followed and recaptured much more easily to determine survival and growth rates. Furthermore, age at maturity often can be determined exactly, as reliable growth (age) annuli may be discernable on specimens that are first caught when relatively young. Unlike sea turtles, the shells of these turtles can be permanently marked with notches or by drilling holes, and individuals recaptured even decades later can then be reliably aged once again.

Population models of late-maturing freshwater species such as Blanding's turtles, *Emydoidea blandingii* (maturing at 14 to 17 years old: Congdon et al. 1993), and snapping turtles, *Chelydra serpentina* (maturing at 11 to 16 years old: Congdon et al. 1994), indicate that high survival rates are necessary at each life stage to ensure that enough individuals survive and reproduce to maintain a population. These models lead to the inescapable conclusions that: (a) successful management and conservation programs for turtles must protect all life stages, and (b) sustainable commercial harvests of long-lived, late-maturing turtle species may well be an impossibility (Congdon et al. 1993, 1994). Given the similar-

ities in their life histories, the results for freshwater turtles add support to the implications provided by the sea turtle models (Crouse et al. 1987; Crowder et al. 1994).

For now, the best models we have indicate that successful conservation efforts for sea turtles will be those that do not neglect any life stage, and that commercial harvests of sea turtles probably are not sustainable. In the future, those who model sea turtle populations must remember the concept of GIGO and recognize that providing reliable input values for survivorship, fecundity, and age at maturity is not a simple task. Given the robustness of the current models, we suspect that the recent findings for sea turtles (Crouse et al. 1987; Crowder et al. 1994; Heppell et al., unpublished manuscript) and freshwater turtles (Congdon et al. 1993, 1994) will be further substantiated as even better estimates of demographic parameters emerge over the next decade.

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## **Global Overview of the Status of Marine Turtles: A 1995 Viewpoint**

### ***Caretta caretta*, loggerhead turtle**

Many of the problems described by Ross (this volume) for this species remain. Major status changes include the 50–80% decline in nesting females at eastern Australian rookeries since the mid 1970s (Limpus and Reimer 1994) and the listing of the loggerhead as an endangered species under the Australian Endangered Species Protection Act 1992. Nesting populations of Georgia and South Carolina, USA, have undergone substantial declines while Florida rookeries appear to have changed little (National Research Council 1990). This latter conclusion may reflect the limited long-term census data. In contrast, the South African loggerhead population has more than doubled since the early 1960s when strong protective measures were introduced (Hughes 1989). Populations currently not identified as in decline may well be under threat from a diversity of impacts.

### ***Chelonia mydas*, green turtle**

Most population declines identified in 1979 by King (this volume) are continuing, along with many additional ones. In Indonesia, green turtle populations subjected to long-term intense egg harvests (Berau Turtle Islands, Pangumbahan) have suffered order-of-magnitude declines in egg production since the 1940s (Limpus 1994); the Aru Island green turtle population has been decimated by harvest of nesting females, largely to supply turtles to Bali (J. P. Schulz, pers. comm.). In Japan, the decimation of the Ogasawara green turtle stock through overharvest of the nesting turtles during the late 1800s and early 1900s has been summarized (Horikoshi et al. 1994). The French Polynesian nesting population appears to have declined by approximately 90% (P. Siu, pers. comm.).

The largest slaughter of green turtles globally occurs within the Australasian region, including Indonesia, Papua New Guinea, Australia, Solomon Islands, Vanuatu, New Caledonia, and Fiji where, in



order of magnitude, 100,000 green turtles, mostly big females, are harvested each year. This harvest threatens the stability of the large nesting populations in Australia and contributes to the decline of other regional stocks. Near-total egg harvest still characterises the green turtle nesting populations of Indonesia, Thailand, and Terengganu in Malaysia. The decline in the Sarawak Turtle Islands population remains the best documented case study of the long-term impact of intense harvest of green turtle eggs (Fig. 1). Strong conservation management operating for decades on depleted populations has resulted in some recoveries: Sabah (Fig. 1; Basintal and Lakim 1994), Hawaii (Wetherall and Balazs, in press), and Florida (Owen et al. 1994).

#### ***Eretmochelys imbricata*, hawksbill turtle**

Contrary to the 1979 summary (King, this volume), hawksbill turtles do/did nest in large aggregations (dispersed nesting today is probably the result of overharvest of previously large colonies, e.g. Caribbean Panama, U.S. Virgin Islands). Recent studies have highlighted the ongoing overharvest of this turtle (Bjorndal et al. 1993; Miranda and Frazier 1994). The last remaining large rookeries appear to be in Australia where thousands of hawksbills breed annually, but these have no long-term census data.

Although the Japanese Government banned the importation of turtle products in 1994, a substantial harvest for domestic consumption of meat and scale continues in Cuba, Indonesia, Solomon Islands, Fiji and elsewhere. A large proportion of eggs appear to be harvested in Malaysia (Terengganu), Thailand, Indonesia, and possibly Philippines.

Hawksbill turtles are apparently increasing in only one region (Trono 1994). After 25 years of strong protection, hawksbill nesting at the Sabah Turtle Islands, Malaysia, has increased more than tenfold since 1969 (Fig. 2).

#### ***Natator depressus*, flatback turtle**

The marine turtle endemic to the Australian continental shelf currently has an annual nesting population of the order of five to ten thousand females but most populations have never been monitored. Therefore, long-term population trends cannot be detected. Significant negative impacts include large egg losses through pig and varanid predation and potentially large losses in trawl and gillnet fisheries around Australia, Indonesia, and Papua New Guinea.

#### ***Lepidochelys kempii*, Kemp's ridley turtle**

Decades of intense conservation management effort appear to be succeeding. Clutch production at Rancho Nuevo, Mexico, has increased steadily in recent years (Fig. 3). Whether this is the result of increased hatchling production at the rookeries or increased survivorship of adults and near adults resulting from the use of turtle excluder devices (TEDs) in shrimp trawls remains to be seen.

#### ***Lepidochelys olivacea*, olive ridley turtle**

This species remains the most abundant of the world's marine turtles (Ross, this volume). Long-term population trends for the species at its arribada beaches are not well documented. In Mexico, although only the Escobilla arribada functions as a major population, the future for the depleted stocks is promising given the current protection regime. The Orissa, India, arribada has in recent times been under threat of incidental mortality in gillnet fisheries, trawling, coastal and port developments and substantial egg harvests.

There are no demonstrated recovering populations for this species. Declines have been demonstrated for some small populations. Terengganu (Malaysia) stock has declined from possibly thousands annually to approximately 20 per year in the early 1990s, and the stock in the Andaman Sea of Thailand has been decimated to only tens of females nesting annually as a result of long-term excessive egg harvest. The Surinam arribada has declined to a few hundred females annually in part due to trawling bycatch. This species is probably suffering from the assumption that, because it occurs in large numbers at some localities, it does not warrant special conservation effort. This species may not be as secure as it superficially appears.

#### ***Dermochelys coriacea*, leatherback turtle**

Since 1979, census data on most rookeries have improved and the global population estimate increased, especially because of reassessment of the Pacific Mexican population and the discovery of the large population in Irian Jaya, Indonesia (Pritchard 1982). For most populations, long-term census data from which to assess population stability are insufficient (Ross, this volume). In Malaysia, the dramatic decline to fewer than 20 nesting females in 1993 at the famous Terengganu rookery illustrates the consequences of harvesting most eggs for more than a generation (Fig. 4). Incidental mortality in fishing nets probably accelerated this decline (Chan et al. 1988). A similar decimation of the nesting population of the Andaman Sea area of western Thailand apparently occurred

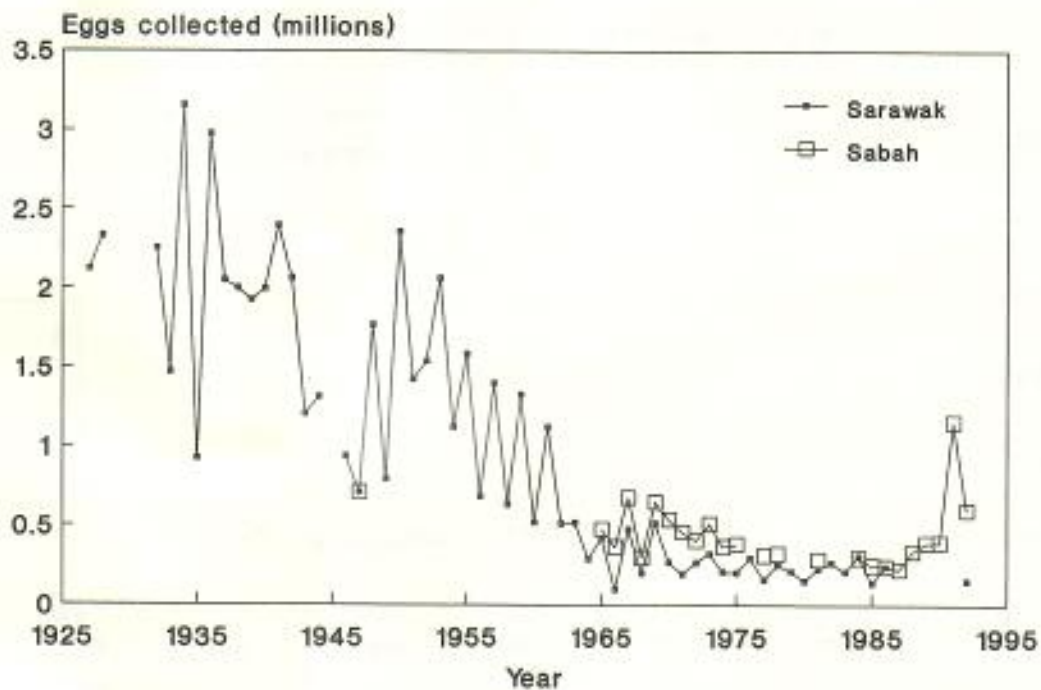


Figure 1. Annual egg production by the green turtle populations of Sarawak and Sabah in Malaysia. Data supplied by the Sarawak Museum and the Sabah National Parks staff.

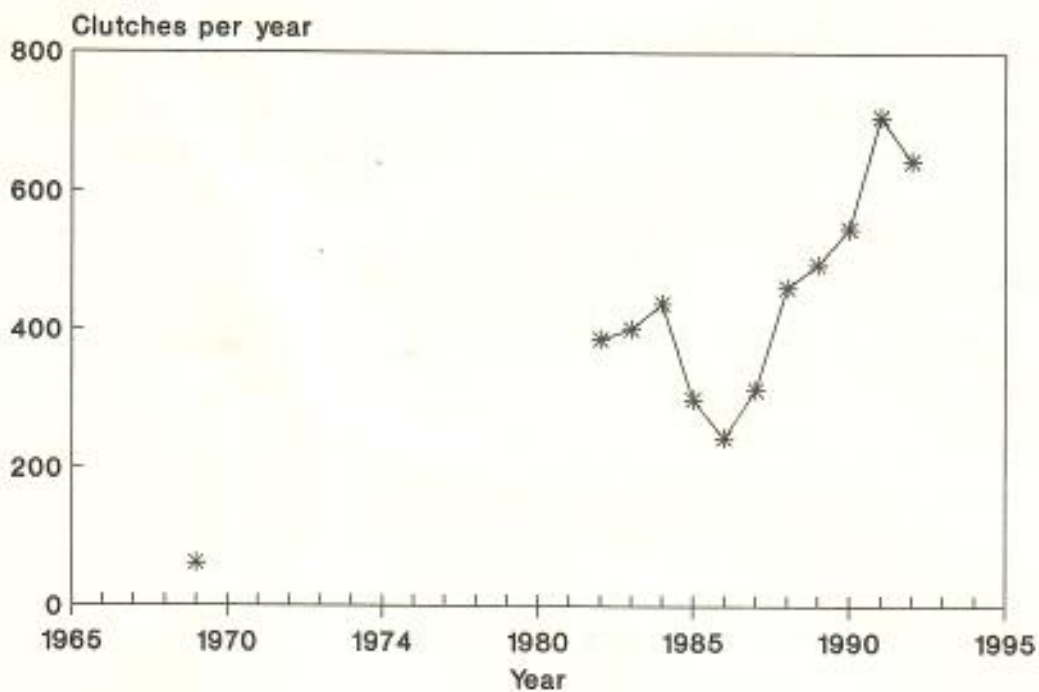


Figure 2. Hawksbill turtle nesting population (using egg production as an index) in the Sabah Turtle Islands National Park since the park was declared. Data supplied by the Sabah National Parks staff.

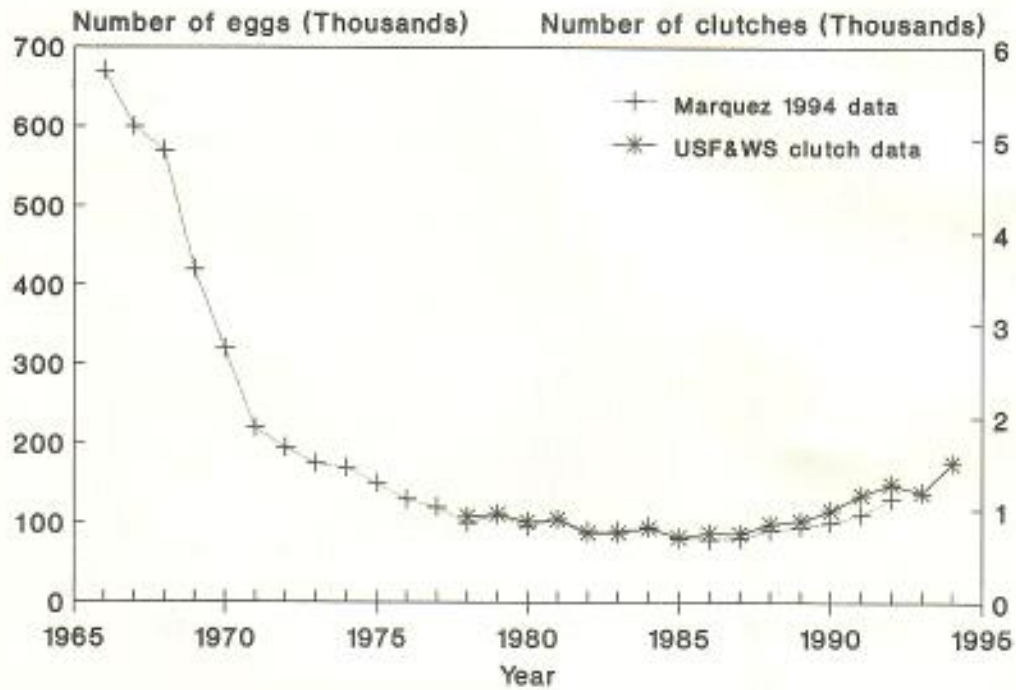


Figure 3. Rancho Nuevo Kemp's ridley turtle nesting population using egg production as an index.

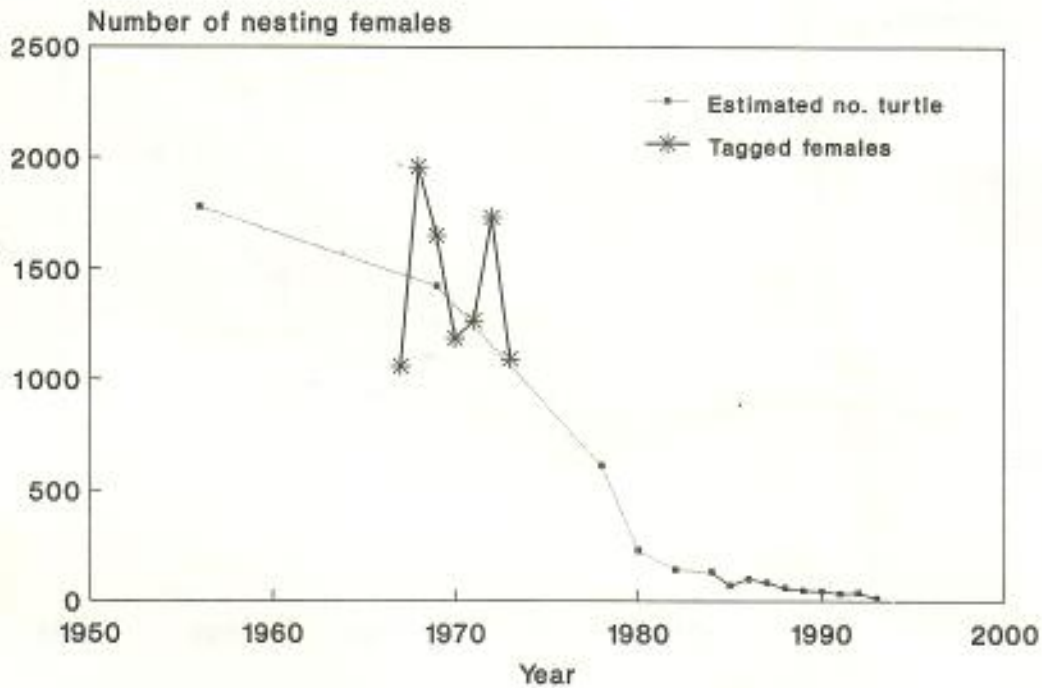


Figure 4. Leatherback nesting population in Terengganu, Malaysia, estimated from egg production data and from tagging data of nesting leatherbacks in Terengganu in the late 1960s and early 1970s. Data supplied by Malaysian Fisheries Department.

through near-total, long-term egg harvest. Similar levels of egg loss through harvest and pig predation characterize the nesting beaches of Irian Jaya, Indonesia, and northern Papua New Guinea, the last major leatherback nesting populations of the Australasian region.

In South Africa, thirty years of strong protection have been paralleled by an increase in annual nesting population from 20 to 90 leatherbacks (Hughes 1989).

Since the 1979 Washington World Conference, the losses have been extensive and the gains small in terms of numbers of turtles. Globally, marine turtles are still on the decline. No species is secure. The devastation caused by long-term near-total egg harvests is clear. However, major progress in understanding marine turtle biology and management should make it easier for turtle managers to make better headway in the next 15 years. Marine turtle population declines can be reversed, but decades of dedicated conservation effort are necessary to achieve just small progress. Marine turtles cannot cope with increased mortality substantially above natural levels. They can survive only if we provide effective long-term conservation management.

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## **Anthropogenic Threats to Sea Turtles**

Persistent overexploitation, especially of breeding adults, for meat, shell, oil and/or skin is largely responsible for depleted populations of sea turtles (Groombridge and Luxmoore 1989; Eckert 1993). Once-vast populations are on the verge of ruin (e.g., Indonesia: Greenpeace 1989). In some cases, egg collection alone has been implicated in population demise (e.g., Malaysia: Chan 1991). International trade has played a prominent role in the depletion of sea turtles, especially hawksbills (Milliken and Tokunaga 1987). Japanese sea turtle imports since 1970 represent a minimum of 2,250,000 turtles (Canin 1991). Japan recently banned the import of hawksbill shell (Donnelly 1991) and removed the last of its CITES reservations on sea turtles in July 1994.

Incidental capture in shrimp trawls has been implicated in population declines in the USA and Mexico (National Research Council 1990), Suriname (Reichart and Fretey 1993), and Australia (Limpus and Reimer 1994). Turtle excluder devices (TEDs) release trapped turtles, generally without compromising shrimp catch (Crouse et al. 1992), and are mandatory in U.S. waters. Longlines hook and kill an estimated tens of thousands of turtles every year (Nishemura and Nakahigashi 1990; Balazs and Pooley 1994) and driftnets kill many thousands more (Wetherall et al. 1993). Losses due to purse seines and tangle nets (e.g., Frazier and Brito 1990) have not been estimated.

Nesting beaches are degraded or lost to expanding urban development and a thriving global tourist industry. The literature is replete with specifics, including rising human activity, high-density coastal construction, beachfront lighting, erosion control structures, sand mining, port development, and indiscriminate waste disposal (Groombridge 1990; Eckert and Honebrink 1992; Meylan et al., in press; Witherington and Martin, in press). At sea, oil spills (Lutcavage et al., in press), persistent marine debris (Balazs 1985; Witzell and Teas 1994), pollution (Hutchinson and Simmonds 1992), and damage to

coral reefs and seagrass (e.g., anchoring, dredging) threaten dispersal and migratory routes, nursery habitats, and foraging grounds (e.g., Allen 1992).

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**Headstarting as a  
Management Tool**

Headstarting is the practice of growing hatchlings in captivity to a size that (theoretically) will protect them from the (presumably) high rates of natural predation that would have otherwise occurred in their early months. The rationale is that these turtles will continue to enjoy high rates of survival even after they are released to the wild. Headstarting has long been a subject of controversy among sea turtle biologists (note conflicting views expressed by Dodd, Ehrenfeld, Klima and McVey, and Reichart in this volume). Nevertheless, in virtually every country where sea turtles occur, people have repeatedly undertaken to headstart turtles. Donnelly (1994) reviews many of these cases and presents detailed evaluations of why three of the most prominent, well-funded and long-lived headstarting programs in the world—for green turtles in Florida (1959–1989), Kemp's ridleys in the United States (1978–1993), and hawksbills in Palau (1982–1991)—have all been terminated.

Critics argue that headstarting is not a proven management technique and may actually be harmful to turtles. They cite biological concerns that nutritional deficiencies and behavioral modifications associated with captivity (including insufficient exercise, lacking or inappropriate sensory stimuli, the unavailability of natural food, etc.) may interfere with the ability of headstarted turtles to survive in the open sea and with those imprinting mechanisms necessary to guide their breeding migrations (Mrosovsky 1983; Mortimer 1988; National Research Council 1990; Woody 1990, 1991; Taubes 1992; Donnelly 1994; Eckert et al. 1994). Disease is another problem, with some 27 sets of disease symptoms (many serious) common in captive turtles (Leong et al. 1989). In crowded conditions turtles bite each other causing injuries commonly invaded by secondary infections that can lead to loss of body parts (Mortimer 1988). Concern exists that captive-reared turtles might introduce or spread diseases among wild populations after their release (Woody 1981; Jacobson 1993; Donnelly 1994).

The most heavily subsidized headstarting programs, especially those at the Galveston Lab of NMFS and the Cayman Turtle Farm (both with multimillion dollar budgets), have produced useful information on sea turtle husbandry, behavior and physiology (Caillouet and Landry 1989; Caillouet 1993). Proponents claim that the emotional appeal commanded by headstarting enhances public concern for turtles (Allen 1990, 1992). Others argue that a few captive turtles would serve the same purpose and that the feel good appeal of headstarting siphons money from other programs which, though lacking popular appeal, are known to be effective (Mortimer 1988; Woody 1990, 1991; Donnelly 1994).

Ultimately, the success of headstarting as a management tool will be proven only by demonstrating that the proportion of nesting headstarted females has increased relative to the proportion of non-headstarted nesting females in the population (Mrosovsky 1983; Mortimer 1988; National Research Council 1990; Eckert et al. 1994). A critical point is that the headstarted turtles must nest at the appropriate beach in order to contribute effectively to the gene pool of the population (Bowen et al. 1994). Headstarting has always been considered experimental, but until recently, it has been an experiment lacking design and controls. In an effort to remedy this, based on recommendations by Wibbels et al. (1989) and Eckert et al. (1994), termination of the Kemp's ridley headstart program will be accompanied by intensive marking of wild hatchlings (as a control) and monitoring of those headstarted Kemp's turtles that have already been released (Byles 1993; Williams 1993; Donnelly 1994).

Modelling studies based on the analysis of reproductive value (Crouse et al. 1987) indicate that headstarting is unlikely to ever meet its goal of increased recruitment into the adult population without a simultaneous reduction in juvenile mortality in the wild (National Research Council 1990). Heppell and Crowder (1994) evaluated stage-based and age-based population models for Kemp's ridley and concluded that headstarting could not be a viable tool for species recovery because the addition of headstarted turtles is not sufficient to compensate for the annual loss of fecund adults. These models indicate that attempting to compensate for natural hatchling mortality without addressing the real causes of the decline of the species—i.e., overharvest, mortality in fishing gear, and habitat destruction—is not the best use of the limited resources available for conservation programs.

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# **Biology and Conservation of Sea Turtles**

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**Edited by  
Karen A. Bjorndal**  
University of Florida

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Front cover: Adult female green turtle, *Chelonia mydas*, at French  
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