

## INVITED REVIEW

# Population genetics and phylogeography of sea turtles

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## Abstract

The seven species of sea turtles occupy a diversity of niches, and have a history tracing back over 100 million years, yet all share basic life-history features, including exceptional navigation skills and periodic migrations from feeding to breeding habitats. Here, we review the biogeographic, behavioural, and ecological factors that shape the distribution of genetic diversity in sea turtles. Natal homing, wherein turtles return to their region of origin for mating and nesting, has been demonstrated with mtDNA sequences. These maternally inherited markers show strong population structure among nesting colonies while nuclear loci reveal a contrasting pattern of male-mediated gene flow, a phenomenon termed 'complex population structure'. Mixed-stock analyses indicate that multiple nesting colonies can contribute to feeding aggregates, such that exploitation of turtles in these habitats can reduce breeding populations across the region. The mtDNA data also demonstrate migrations across entire ocean basins, some of the longest movements of marine vertebrates. Multiple paternity occurs at reported rates of 0–100%, and can vary by as much as 9–100% within species. Hybridization in almost every combination among members of the Cheloniidae has been documented but the frequency and ultimate ramifications of hybridization are not clear. The global phylogeography of sea turtles reveals a gradient based on habitat preference and thermal regime. The cold-tolerant leatherback turtle (*Dermochelys coriacea*) shows no evolutionary partitions between Indo-Pacific and Atlantic populations, while the tropical green (*Chelonia mydas*), hawksbill (*Eretmochelys imbricata*), and ridleys (*Lepidochelys olivacea* vs. *L. kempfi*) have ancient separations between oceans. Ridleys and loggerhead (*Caretta caretta*) also show more recent colonization between ocean basins, probably mediated by warm-water gyres that occasionally traverse the frigid upwelling zone in southern Africa. These rare events may be sufficient to prevent allopatric speciation under contemporary geographic and climatic conditions. Genetic studies have advanced our understanding of marine turtle biology and evolution, but significant gaps persist and provide challenges for the next generation of sea turtle geneticists.

*Keywords:* complex population structure, endangered species, homing, marine turtles, multiple paternity, sex-biased dispersal

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## Introduction

The seven species of sea turtle encompass a diversity of ecological niches, from the oceanic leatherback (*Dermochelys coriacea*) and olive ridley (*Lepidochelys olivacea*) to the sponge-eating hawksbills (*Eretmochelys imbricata*) to the herbivorous green turtle (*Chelonia mydas*). The loggerhead (*Caretta caretta*) and Kemp's ridley (*Lepidochelys kempfi*) are coastal

carnivores with a more cosmopolitan diet. All sea turtles have a juvenile oceanic phase, except the flatback (*Natator depressus*) which is restricted to Australia, New Guinea, and adjacent oceans.

Sea turtles are classified in two taxonomic families, the Cheloniidae with six species, and the Dermochelyiidae with a single highly derived species, the leatherback turtle. A generalized life history of sea turtles includes two stages between hatching and sexual maturity, corresponding to juvenile and subadult. The hatchlings emerge from the nest, scurry to the water, and initiate a swimming frenzy

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into offshore currents. The juveniles spend a few years in an oceanic habitat, before switching to a bottom-feeding subadult stage where they remain for about a decade before maturity. The primary exceptions to this life-history model are the flatback (as noted above) and the leatherback. In the latter case, the biology of the animal before sexual maturity is unknown, a lapse lent urgency by strong conservation concerns.

Sea turtle research is focused on the nesting beaches, where females and hatchlings are readily observed, tagged, and sampled. The body of scientific knowledge from these efforts is extensive (Bowen & Witzell 1996; Lutz & Musick 1996; Bolten & Witherington 2003; Lutz *et al.* 2003), but the terrestrial nesting and hatching intervals involves only adult females and a tiny fraction of the life cycle. Studies of the animals in the water have been slower in coming, and much more resource intensive. Coverage of nesting populations is far more advanced than the surveys of corresponding feeding aggregates or most other aspects of sea turtle biology. Genetic studies were instigated to help fill this gap in our knowledge and to provide a new perspective on the biology and evolution of these unique animals (Awise 2007).

The first population genetic assessments were nesting beach surveys of loggerhead and green turtle with protein electrophoresis (Smith *et al.* 1977). These demonstrated low genetic diversity, a theme that would recur in subsequent studies of mitochondrial DNA (mtDNA) and nuclear DNA (nDNA), possibly because of low metabolic rate and long generation time (Awise *et al.* 1992; Karl *et al.* 1992; Martin & Palumbi 1993). This low level of variation prompted most researchers to rely on the mtDNA control region for population assessments, although more recently, assessments of hypervariable microsatellite loci have gained momentum.

In this review, we synthesize the available genetic data on population genetics, mating behaviour, and phylogeography of sea turtles. We touch on aspects of phylogeny and hybridization, but these topics are addressed elsewhere with greater coverage (Karl *et al.* 1995; Dutton *et al.* 1996; Karl & Bowen 1999; Lara-Ruiz *et al.* 2006). Here, we address natal homing and the complex population structure of sea turtles, the mixed-stock analyses of feeding populations, the discordance between nDNA and mtDNA data sets, genetic aspects of breeding behaviour, the influence of habitat preference on global phylogeography, and corresponding evolutionary and conservation implications.

### Population structure: a test of natal homing

One of the first observations to emerge from tagging studies in the 1950s and 1960s was that adult female green turtles return habitually to the same nesting beach, in reproductive cycles of about 2 to 4 years. This prompted Archie Carr to postulate that female turtles migrate to their natal nesting

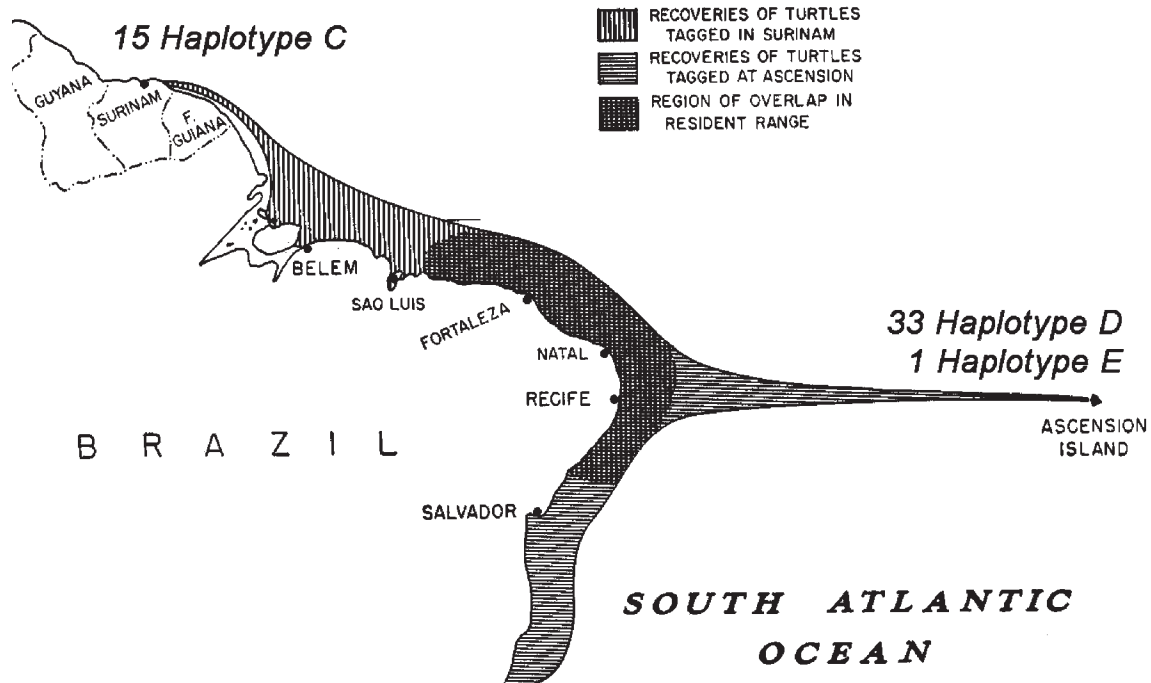
beach to reproduce (natal homing; Carr 1967). Hendrickson (1958) proposed an alternative explanation for female nest-site fidelity, wherein first-time nesting females follow experienced breeders from the feeding habitat to a nesting beach, and use this site for all subsequent nesting (see Owens *et al.* 1982). This social facilitation can explain the site fidelity of nesting turtles without invoking the extreme behaviour of hatchlings remembering a beach location and finding it decades later for reproduction.

Natal homing and social facilitation hypotheses proved difficult to test directly, as no tag applied to a 5-cm hatchling has been successfully recovered decades later from a 100- to 200-cm adult. Natal site philopatry, however, generates a testable prediction about the genetic partitioning of nesting populations. If females return faithfully to their rookery of origin, then each nesting population should possess a unique genetic signature in terms of female-transmitted mtDNA. In contrast, social facilitation would allow high rates of female-mediated gene flow between nesting populations that overlap on feeding grounds. Hence, the most robust tests of natal homing involve populations that overlap on feeding habitats, so that females have a 'choice' between natal homing and social facilitation. Here, we summarize mtDNA-based tests of nesting population structure and homing for six of the seven species. The seventh species (Kemp's ridley) nests only in the western Gulf of Mexico so that no assessment of population differentiation is warranted.

### Green turtle (*Chelonia mydas*)

The first test of natal homing involved two of the nesting colonies that originally prompted Archie Carr's hypothesis of natal homing. Tagging studies demonstrated that Brazilian feeding pastures are shared by turtles from nesting colonies in Surinam (South America) and Ascension Island (mid-Atlantic ridge) (Carr 1975; Pritchard 1976). Analyses of mtDNA sequences demonstrated that individuals from the Surinam rookery possess a haplotype at 100% frequency that is not observed at Ascension Island (Fig. 1). Despite extensive overlap on feeding habitats, there are fixed genetic differences (e.g. no sharing of haplotypes) between Surinam and Ascension samples (Bowen *et al.* 1992). These genetic data demonstrate a barrier to female dispersal between nesting populations, meeting the genetic expectations of the natal homing hypothesis. The mtDNA data set also indicates that the Ascension nesting colony was the product of a recent colonization event, probably from a Brazilian nesting colony in the last hundred thousand years.

The support for natal homing in South Atlantic green turtles could not be considered conclusive, however, without validation elsewhere in the global range of *Chelonia mydas*. Capricorn/Bunker Islands represents the primary nesting area in the southern Great Barrier Reef, and Raine



**Fig. 1** South Atlantic nesting colonies for the green turtle, and corresponding haplotype distributions (Carr 1975; Bowen *et al.* 1992). These turtles overlap extensively on feeding habitat, yet retain diagnostic differences in mtDNA haplotype composition, providing strong support for a natal homing hypothesis. Figure modified from Carr (1975) with permission of the American Society of Ichthyologists and Herpetologists.

Island is the largest nesting colony in the northern Great Barrier Reef. Tagging data demonstrate that these populations overlap along the margins of Australia and the Coral Sea (Limpus *et al.* 1992). Despite this overlap, Raine Island and Capricorn/Bunker are characterized by a nearly fixed difference in the distribution of mtDNA haplotypes (Norman *et al.* 1994; Dethmers *et al.* 2006), indicating natal homing in West Pacific green turtles, and confirming the generality of this reproductive behaviour in *Chelonia mydas*.

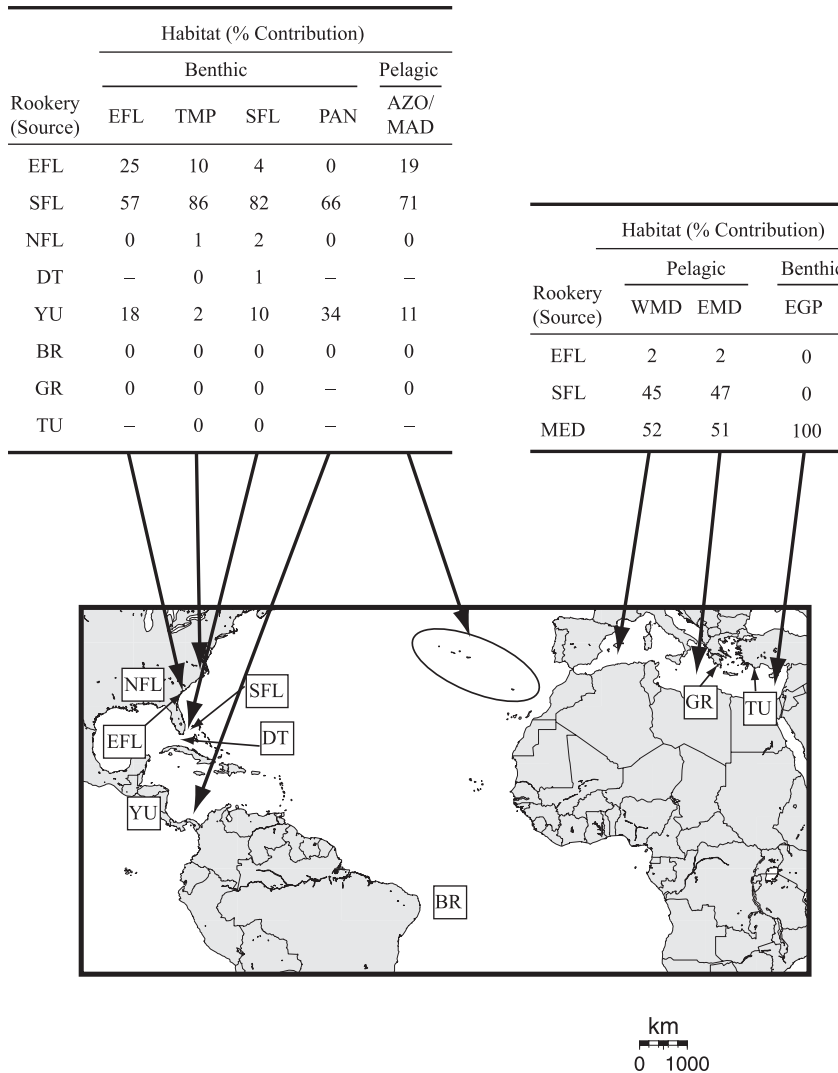
Recently, researchers have been turning their attention to more fine-scale analyses of natal homing. Although it is clear that female turtles returned to nest at their natal beaches, the geographic specificity of homing is uncertain. In initial mtDNA studies, nesting beaches were stretches of 10s or 100s of kilometres of coastline. The outstanding issue is whether females returned precisely to their natal site or if a nesting beach is more loosely defined on a regional scale. For example, Bjørndal *et al.* (2006) observed mtDNA population structure among Brazilian offshore islands separated by 1800 km, but not between islands separated by 150 km. Bourjea *et al.* (2007) found genetic differentiation among sites > 500 km apart but not < 150 km in the south-western Indian Ocean. Microsatellite surveys along proximal or continuous nesting beaches have begun to resolve this issue. Lee *et al.* (2007) used assignment tests to assess natal homing on a scale of a few kilometres at Ascension Island,

UK. They observed a modest but significant signal for two of three beaches. A similar study by Peare & Parker (1996) reported population structure among nesting locations on a scale of 10 km at Tortuguero Beach, Costa Rica but not at Melbourne Beach, Florida, USA. Clearly the issue of precision in natal homing needs more research.

#### *Loggerhead turtle (Caretta caretta)*

The initial mtDNA data supported the natal homing hypothesis for green turtles, but the generality of this conclusion for all species of sea turtles was unknown. The next tests of natal homing focused on loggerhead turtles. Of particular interest are the geographic clusters of nesting beaches in the Mediterranean and along the continental coastline of the Northwest Atlantic, which reveal the geographic scale of natal-site fidelity. The latter area hosts a very large rookery in southern Florida (USA), flanked by major nesting areas in Yucatan (Mexico), Georgia, South Carolina, and North Carolina (USA; Fig. 2).

Through a series of papers, mtDNA data resolved eight nesting habitats that differed significantly in haplotype frequencies: (i) Bahia, Brazil; (ii) Quintana Roo, Yucatan, Mexico; (iii) northwest Florida in the Gulf of Mexico, USA; (iv) South Florida, USA; (v) northeast Florida to North Carolina, USA, combining discrete nesting habitats in



**Fig. 2** Loggerhead nesting colonies and feeding aggregates of the western Atlantic and Mediterranean with estimated contributions from regional nesting colonies (Bolten *et al.* 1998; Laurent *et al.* 1998; Rankin-Baransky *et al.* 2001; Bowen *et al.* 2004). Consult the original papers for standard errors. Nesting colonies are indicated with boxes and abbreviations are: NFL, northern Florida along the Gulf of Mexico coast; EFL, northeastern Florida to North Carolina; SFL, southern Florida; DT, Dry Tortugas; YU, Yucatan Peninsula; BR, Brazil; GR, Greece; TU, Turkey; MED, combines six nesting beaches in the eastern Mediterranean (see Laurent *et al.* 1998). Feeding aggregation abbreviations are: EFL, northeastern Florida to North Carolina; TMP, temperate zone; SFL, southern Florida; PAN, Panama; AZO/MAD, Azores and Madera; WMD, western Mediterranean; EMD, eastern Mediterranean; and EGP, Egypt. Note that the region designated EFL includes both nesting and feeding habitats. Pelagic and benthic columns refer to early- and late-stage juveniles, respectively, distinguishing the habitat switch from feeding in the water column to feeding on the bottom.

northeast Florida, Georgia, South Carolina, and North Carolina; (vi) Dry Tortugas off the Florida peninsula, USA; (vii) Greece; and (viii) Turkey (Bowen *et al.* 1993; Laurent *et al.* 1993; Schroth *et al.* 1996; Bolten *et al.* 1998; Encalada *et al.* 1998; Laurent *et al.* 1998; Bowen *et al.* 2004). Estimates of population structure include  $\Phi_{ST} = 0.42$  ( $P < 0.001$ ) for nesting colonies along the southeast coast of the USA (Bowen *et al.* 2005), and  $\Phi_{ST} = 0.33$  ( $P < 0.001$ ) for nesting habitats in the Mediterranean (Laurent *et al.* 1998). The conclusion of female-mediated population structure and corresponding natal homing in Atlantic and Mediterranean loggerheads is robust, and is corroborated by parallel studies of Pacific loggerhead turtles (FitzSimmons *et al.* 1996; Hatase *et al.* 2002a).

On the finest scale, nesting populations in south and northeast Florida, separated on a scale of 50–100 km, are distinct in terms of mtDNA haplotype frequencies. These data indicate that loggerhead females are capable of homing on a scale of tens of kilometres; however, exceptions to

this pattern provide lessons about the influence of climate on sea turtle population structure. First, the Mediterranean nesting populations share two haplotypes with the Western Atlantic nesting aggregates. While these regions are highly distinct in terms of haplotype frequencies, the shared haplotypes indicate recent contact. Second, the nesting aggregates in northeastern Florida, South Carolina, and North Carolina, spread across 1000 km, are indistinguishable and nearly fixed for a single haplotype.

Loggerhead eggs require a minimum of 60 days of incubation above 25 °C to hatch, such that thermal conditions in the Mediterranean may have precluded nesting during the recent glacial maxima (18 000–12 000 years BP; Buckley *et al.* 1982). During the same glacial interval, loggerheads may have nested in southern Florida, but present-day rookery locations in Georgia, South Carolina, and North Carolina were too cold (see Hedgpeth 1954). Thus the contemporary distribution of nesting beaches in the southeast USA is likely the product of colonization events, sufficient

to extend the northern limits of nesting by 1000 km within the last 10 000 years. This pattern of postglacial expansion is apparent in Japanese nesting cohorts as well (Hatase *et al.* 2002a). Turtles from the western Atlantic apparently colonized the Mediterranean during the same interglacial interval.

#### *Hawksbill turtle* (*Eretmochelys imbricata*)

In contrast to the colonial nature of most sea turtle nesting populations, the hawksbill turtle is regarded as a solitary nester in some locations. This observation, however, may be a modern artefact of vastly reduced numbers relative to historical levels. Do female hawksbills return to their natal beach? Broderick *et al.* (1994) found nearly fixed differences in the distribution of mtDNA haplotypes between nesting areas in northeast and northwest Australia, but pairs of nesting beaches within each region were similar in terms of haplotype frequencies. Bass *et al.* (1996) documented significant haplotype frequency shifts between seven West Atlantic rookeries, demonstrating strong population structure within the Caribbean basin ( $\Phi_{ST} = 0.64$ ,  $P < 0.01$ ). These data are consistent with expectations of natal homing. Both Broderick *et al.* (1994) and Bass *et al.* (1996) report that some nesting aggregates separated by a few hundred kilometres are not distinct in terms of haplotype frequencies. Lack of differentiation may be attributed in part to historical colonization events, but tagging studies indicate a low level of relocation between adjacent nesting habitats (Limpus *et al.* 1983). The combined evidence from tagging data and mtDNA data indicate that natal homing predominates, but breeding populations may encompass several proximal nesting sites.

#### *Olive ridley turtle* (*Lepidochelys olivacea*)

Olive ridley nesting populations have strong population structure on a global scale (Bowen *et al.* 1998; Shanker *et al.* 2004), but modest structure within regions. Across the 3000 km of nesting habitat between Baja California (Mexico) and Costa Rica, Lopez-Castro & Rocha-Olivares (2005) report low but significant population structure (mtDNA  $\Phi_{ST} = 0.048$ ,  $P = 0.006$ ). A similar survey of three mass nesting sites in Orissa (India), spread across 320 km, reveals no population structure (Shanker *et al.* 2004). This nesting zone (with nesting aggregates in excess of 100 000 females), however, is highly isolated from the nesting colonies in Sri Lanka ( $\Phi_{ST} = 0.58$ ,  $P < 0.001$ ) and northern Australia ( $\Phi_{ST} = 0.90$ ,  $P < 0.001$ ). Overall, these data support a natal homing scenario. The shallow population structure observed on the continental coastlines of Central America and eastern India indicate low site specificity in nesting females. It is notable in this regard that olive ridleys are the only Cheloniid sea turtles with a predominantly pelagic adult

phase, in which feeding habitat for a nesting population may encompass vast tracks of open ocean (Polovina *et al.* 2004). Perhaps site fidelity is less important for animals with a large oceanic feeding range.

#### *Flatback turtle* (*Natator depressus*)

The flatback turtle was long regarded as a West Pacific variant of the green turtle (*Chelonia depressus*), until red-descriptions by Limpus *et al.* (1988) and Zangerl *et al.* (1988). This species occurs only on the North and East coasts of Australia and adjacent New Guinea. In the single available study, FitzSimmons *et al.* (1996) surveyed nesting populations in the southern Great Barrier Reef, northern Great Barrier Reef, and western Australia. Flatbacks showed low mtDNA variation and no population structure in terms of haplotype frequencies; however, a survey of six microsatellite loci showed significant divergence between the three regions. FitzSimmons *et al.* (1996) conclude that the low mtDNA variation may have limited inferences, and that with more variation, the two classes of markers might be concordant. Based on this evidence, and the nesting site fidelity documented with tagging studies (Limpus *et al.* 1984), the paradigm of natal homing provisionally applies to the flatback turtle.

#### *Leatherback turtle* (*Dermochelys coriacea*)

This species is known for remarkably long feeding migrations and an oceanic existence that confers the broadest animal distribution on earth (Hays *et al.* 2004). Nesting occurs on tropical islands and continental coastlines, but feeding habitat ranges from the tropics to the Arctic Circle (Goff & Lien 1988). In a global mtDNA survey of leatherback turtles, Dutton *et al.* (1999) found a shallow gene genealogy, strong population structure worldwide ( $\Phi_{ST} = 0.42$ ,  $P < 0.001$ ), as well as within the Atlantic Ocean ( $\Phi_{ST} = 0.25$ ,  $P < 0.001$ ) and Indian-Pacific Ocean ( $\Phi_{ST} = 0.20$ ,  $P < 0.001$ ). These data again support the natal homing hypothesis. Some geographically distant populations, however, were indistinguishable, including Florida, Atlantic Costa Rica, Surinam/French Guiana, and South Africa (Dutton *et al.* 1999). Nesting populations from Indonesia to Vanuatu, spread across 4000 km of the West Pacific, also proved indistinguishable in an mtDNA survey (Dutton *et al.* 2007). These findings indicate that, like the oceanic olive ridley, the leatherback females may be less nest-site specific, or more prone to nest-site relocation.

#### *Conclusion*

Natal homing is the dominant paradigm for sea turtle migrations, although the geographic specificity of homing apparently varies widely. Haplotype frequencies in

loggerhead nesting populations can differ significantly on a scale of 100 km (Bowen *et al.* 2005), green turtles on a scale of 500 km (Dethmers *et al.* 2006, but see Lee *et al.* 2007), while olive ridley and leatherback nesting populations may encompass thousands of km (Lopez-Castro & Rocha-Olivares 2005; Dutton *et al.* 2007). A prominent caveat to the natal homing conclusion is highlighted by the findings that vagrants from Brazil recently (on a scale of thousands of years) founded the green turtle nesting colony at Ascension Island, and the Mediterranean loggerhead rookeries recently were colonized from the western Atlantic. Among the thousands of female sea turtles tagged on the beach, a tiny percentage are observed nesting far outside the range of their previous nesting site (e.g. LeBuff 1974), and mtDNA surveys also indicate occasional nest-site shifts (Reece *et al.* 2005). These 'gravid waifs' are probably essential to the prosperity of sea turtles, as absolute natal homing, over the 100-million-year history of this group, would be a strategy for extinction. The habitats that were appropriate for nesting in the Cretaceous, Eocene, or Miocene are not the same ones that are appropriate today. As Carr *et al.* (1978) observed, 'Strays and wandering must occur, and are no doubt adaptively advantageous aberrations, necessary for colony proliferation'. The mtDNA surveys of nesting beaches are the alpha level examination of population structure, but leave open the issue of population structure of feeding cohorts, to be examined in the next section.

### Population overlap: mixed stocks in feeding habitats

Many nesting habitats have been identified, but the feeding habitats (as noted above), where turtles spend the vast majority of their lives, are little studied or unknown. Mark and recapture studies have revealed links between nesting and feeding populations in a few cases (Carr 1975; Limpus *et al.* 1992), but the contribution of each regional rookery to a feeding area remains unknown in most cases.

The mtDNA haplotype frequency differences among nesting populations afford an opportunity to link feeding populations back to their rookery of origin. The corresponding methodology, known as mixed-stock analysis, employs a maximum likelihood or Bayesian algorithm to estimate the contribution of source (rookery) populations that provides the best fit to the genotype frequencies observed in the 'mixed' feeding aggregate (Pella & Milner 1987; Okuyama & Bolker 2005). Mixed-stock methods were originally developed to assess the composition of salmon feeding cohorts in coastal waters, which can include contributions from several riverine spawning sites (Grant *et al.* 1980). These methods, however, have proven quite adaptable to marine turtles. Here, we review four case histories that illustrate the applications of mixed-stock methods to sea turtle biology.

### North Atlantic loggerhead turtle

Over the last 50 years, researchers have identified most of the loggerhead nesting habitats in the North Atlantic and Mediterranean regions. In addition to the nesting populations in Yucatan, southeastern USA, Greece, Turkey, and elsewhere, researchers discovered a large aggregate of juvenile loggerheads on the eastern margin of the North Atlantic (Brongersma 1972). Based on this observation and ocean circulation patterns, Carr (1986) suggested that these pelagic juveniles were derived from the rookeries of the West Atlantic, rather than the adjacent Mediterranean Sea. Data in support of this theory were scarce, but a few turtles tagged in the eastern Atlantic were subsequently recovered in the western Atlantic (Bolten *et al.* 1992). Encalada *et al.* (1998) provided an mtDNA control region survey of West Atlantic nesting colonies, plus a Mediterranean nesting colony (Kiparissia Bay, Greece). These data provided the genetic foundations for testing the origin of eastern Atlantic juveniles.

Bolten *et al.* (1998) analysed juvenile loggerheads from the waters of the Azores and Madeiras, using the same mtDNA control region segment as the nesting population surveys. Among these juvenile specimens, 92% had haplotypes that matched those in the nesting colony, indicating a strong basis for conclusions. It was also clear, however, that there may be additional, unsurveyed nesting colonies in the North Atlantic. One of the limitations of mixed stock analyses is 'orphan' haplotypes in the feeding aggregate that have no known source population and therefore cannot be assigned back to a location of origin.

Contributions to the pelagic juvenile aggregate were estimated with a maximum-likelihood method (Xu *et al.* 1994; Pella & Milner 1987). The highest estimated contribution came from the very large rookery in South Florida (71%), while the contributions from Brazil and Mediterranean nesting colonies were zero (Fig. 2). These data support the hypothesis that juvenile loggerhead turtles are riding the North Atlantic gyre from West Atlantic nesting habitat to East Atlantic feeding habitat as proposed by Carr (1986). The estimated contribution to Azores/Madeiras feeding habitat from the nesting habitat in northwest Florida (Gulf of Mexico) also was zero, but the size of this population (two orders of magnitude smaller than the South Florida nesting population) may prohibit detection within the accuracy of this analysis. This highlights a second consideration in mixed-stock analyses — nesting colony size is an important variable that may confound the analyses.

How accurate are these estimated contributions? The standard deviations in this analysis range from about 20–40%, indicating that values should not be over interpreted, but instead provide useful qualitative estimates, and definitive hypothesis tests for the origin of turtles in feeding habitats. An interesting and reassuring comparison is

**Table 1** The estimated mixed-stock composition of a feeding population in the northeast Atlantic based on mtDNA haplotype distributions (Bolten *et al.* 1998), compared to the proportion of nesting effort at northwest Atlantic rookeries estimated from nesting beach surveys (Murphy & Hopkins-Murphy 1989; Zurita *et al.* 1993; Meylan *et al.* 1995)

Nesting habitat	MLC	PNE
NFL, USA	0.00	0.01
South Florida, USA	0.72	0.88
EFL, USA	0.17	0.08
Yucatan, Mexico	0.10	0.03

Abbreviations: MLC, maximum likelihood estimated contribution; PNE, proportion of nesting effort based on field surveys; NFL, northwest Florida in the Gulf of Mexico; EFL, northeast Florida to North Carolina along the east coast of the USA.

available in the sizes of the West Atlantic nesting colonies (Table 1). Here, we see a strong rank-order agreement between the estimated contributions to feeding habitat, and the estimated size of the source populations. These data indicate that North Atlantic nesting populations contribute juveniles in approximate proportion to reproductive output (Bolten *et al.* 1998).

The temporal stability of these patterns is generally unknown. In the only survey explicitly testing temporal variation, Bass *et al.* (2004) found no significant differences in a North Carolina, USA loggerhead feeding habitat sampled across 3 years.

#### *Mediterranean loggerhead turtle*

In the Mediterranean Sea, there appear to be more juvenile loggerhead turtles than can be produced by regional nesting colonies (Laurent 1990). One explanation is an extension of Archie Carr's pelagic juvenile hypothesis; perhaps West Atlantic juveniles enter the Mediterranean (Groombridge 1990). Laurent *et al.* (1993, 1998) surveyed feeding populations in the eastern and western Mediterranean, using specimens from the longline fisheries (pelagic juveniles averaging about 50 cm curved carapace length) and benthic trawl fisheries (advanced benthic juveniles averaging about 65 cm). Laurent *et al.* (1998) reported that approximately 47% of pelagic juveniles are derived from West Atlantic nesting colonies, and 53% from Mediterranean nesting colonies. In the larger benthic size class, however, no contribution was detected from the West Atlantic (Fig. 2). Maffucci *et al.* (2006) detected a small West Atlantic contribution (about 7%) to benthic feeding habitat around southern Italy, but also concluded that most of the West Atlantic turtles depart the Mediterranean before switching to benthic habitat. Evidently, the older juveniles are

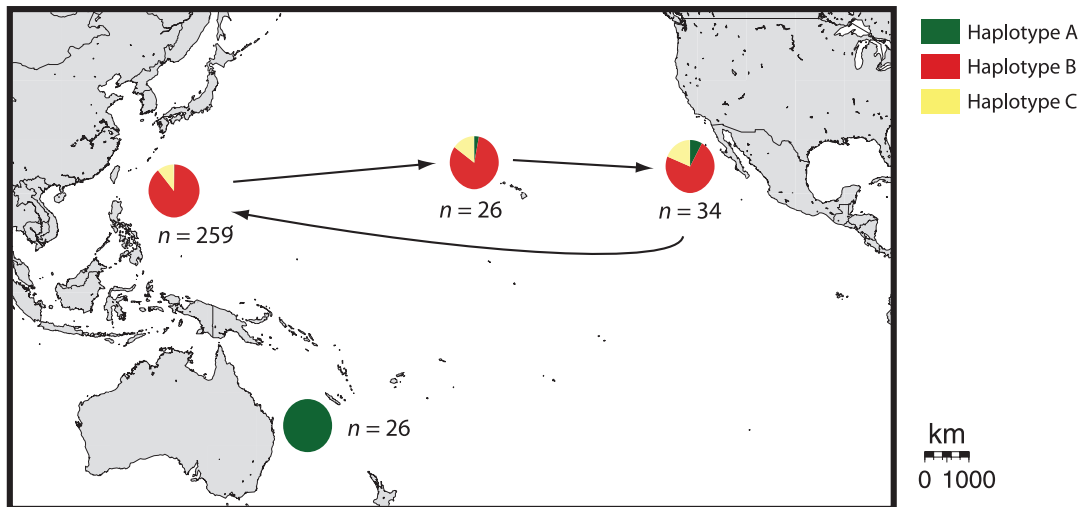
returning to coastal feeding habitats in the West Atlantic (see Complex population structure below).

These juveniles are a conservation concern, because Mediterranean fisheries capture an estimated 20 000 turtles per year (Groombridge 1990), and perhaps 20–50% of these animals perish (Aguilar *et al.* 1995). Furthermore, these data indicate that approximately half of the turtles killed in Mediterranean fishery are from the West Atlantic nesting beaches. These findings highlight the problem of jurisdiction over endangered species that do not recognize international boundary designations.

#### *North Pacific loggerhead turtle*

About 40 years ago, a large feeding aggregate of juvenile loggerheads (10 000+ individuals) was discovered off Baja California (Bartlett 1989). This finding posed a fascinating enigma because the nearest nesting beaches are in Japan and Australia, over 10 000 km distant. Where do the Baja California loggerheads come from? For several decades, it was assumed that a loggerhead nesting beach lay undiscovered somewhere on the West coast of the Americas. Extensive surveys along this coastline, however, failed to reveal a loggerhead nesting colony. Based on the finding of a juvenile turtle tagged in Japan and recaptured in the eastern Pacific, Uchida & Teruya (1991) suggested that Baja California loggerheads are coming from Japan. This suggestion was dismissed in the scientific community as physiologically impossible. In the early 1990s, an international team, including scientists from Japan, Australia, Mexico, and the USA, surveyed the West Pacific nesting beaches and East Pacific feeding habitats to address this issue. During this period, juvenile loggerhead turtles were discovered in driftnet fisheries in the central North Pacific, and Hawaiian sea turtle biologist G.H. Balazs contributed specimens from this fishery.

When samples from North Pacific driftnet mortalities and the Baja California feeding aggregate were compared to the West Pacific nesting beach haplotypes, 95% of these individuals matched the two common haplotypes observed at Japanese nesting beaches (Fig. 3; Bowen *et al.* 1995). The remaining 5% may include a contribution from Australian nesting beaches, although Japanese nesting populations contain the 'Australian' haplotype at very low frequency (Hatase *et al.* 2002a). Once dismissed as impossible, it is now clear that Japanese loggerhead turtles traverse the entire Pacific Ocean, about one third of the planet, during juvenile migrations. The route from Japan to the Americas is apparently through the Kuroshio Current, an extension of the North Pacific gyre. Subsequent satellite tracking studies demonstrate that the return route is not via prevailing currents, but a directed migration from Baja California to Japan (Nichols *et al.* 2000). This stands as one of the greatest navigational feats in the animal kingdom.



**Fig. 3** Haplotype distributions at nesting populations, migratory cohorts, and juvenile feeding aggregates for the North Pacific loggerhead turtle (Bowen *et al.* 1995; Hatase *et al.* 2002a). Haplotype A is in a frequency of 0.4% in Japan (i.e. 1 individual) but does not show in the pie chart.

#### *Caribbean hawksbill turtle*

The hawksbill turtle is heavily exploited for the translucent scales (bekko), which may be worked into jewelry, figurines, and a variety of artworks. Many nesting populations are greatly reduced or extinct as a result of this exploitation. Meylan (1989) estimated that no more than 10 000 nesting females remain in the Caribbean, greater than a 10-fold reduction from historical levels. At the same time, the Caribbean harvest (including males, juveniles, and females) may have exceeded 10 000 turtles/year in recent decades (Canin 1989). In view of the alarming depletion of this species, international trade has been prohibited under the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) agreement, and this species is listed as Critically Endangered by the International Union for the Conservation of Nature and Natural Resources (IUCN, Meylan & Donnelly 1999). Local commerce, however, continues throughout the tropics, and there is interest in reopening the lucrative international trade. The government of Cuba petitioned at the CITES meetings in 1997 and 2000 to resume international trade with commercially harvested hawksbills from the reefs within Cuban territorial waters (Ottenwalder & Ross 1992; Carrillo *et al.* 1999). The proposed harvest on foraging habitat is based on a fishery model that assumes that hawksbill turtles are nonmigratory (Heppell & Crowder 1996). This is an important point: if only turtles from local nesting beaches are taken on Cuban reefs, then no other countries are affected by this harvest.

To test the assumptions of this fishery model, Bowen *et al.* (1996) compared mtDNA control region haplotypes from the nesting beach at Mona Island (Puerto Rico) to

samples from an adjacent feeding aggregate. If hawksbill turtles are nonmigratory, as assumed in the Cuban fishery model, then the Mona Island nesting population and feeding aggregate should be similar in terms of haplotype composition. Contrary to predictions of the fishery model, feeding population specimens were significantly different from the adjacent nesting population ( $P < 0.005$  in a  $G$  test of independence).

Subsequently, Bowen *et al.* (2007) analysed 10 West Atlantic nesting populations, and compared these to eight feeding aggregates in the Caribbean basin. Nesting colonies differ significantly in the frequencies of mtDNA haplotypes ( $\Phi_{ST} = 0.588$ ,  $P < 0.001$ ), corroborating earlier conclusions about nesting site fidelity. There is also low but significant structure among feeding aggregates ( $\Phi_{ST} = 0.089$ ,  $P < 0.001$ ), indicating that foraging populations are not homogenous across the Caribbean Sea. This data set shows a significant correlation between the contribution to feeding populations and proximity to the corresponding nesting areas ( $r = 0.394$ ,  $P = 0.003$ ). This preference for feeding near the natal nesting site is not absolute, as mixed-stock analyses indicate connectivity between feeding and nesting habitats across the Caribbean basin (Fig. 4). This study also detected a single mtDNA sequence in foraging habitat that matches a market sample from Sao Tome (Gulf of Guinea), invoking occasional transoceanic migrations (Bellini *et al.* 2000). As with loggerhead turtles, the survey of Caribbean hawksbills feeding populations yields significant correlation with nesting population sizes ( $r = 0.378$ ,  $p = 0.004$ ), indicating that larger rookeries contribute more individuals to feeding aggregates.

The mixed-stock analyses of hawksbill turtles show that a harvest on Caribbean feeding habitats will deplete nesting



populations throughout the region. As a result of genetic analyses and other considerations, the CITES petitions to resume international trade were voted down in both 1997 and 2000. The interest in international trade continues, however, and may be a subject of debate at the next CITES meeting.

### Conclusion

Mixed-stock analyses are now widely employed to resolve sea turtle movements. In addition to the cases described above, mixed-stock analyses have revealed the composition of feeding aggregates in several other species and regions:

- Green turtles in the West Atlantic (Bass *et al.* 1998; Lahanas *et al.* 1998; Luke *et al.* 2004; Bass *et al.* 2006; Naro-Macieli *et al.* 2007)
- Loggerhead turtles in the West Atlantic and Mediterranean (Rankin-Baransky *et al.* 2001; Engstrom *et al.* 2002; Witzell *et al.* 2002; Bass *et al.* 2004; Roberts *et al.* 2005; Carreras *et al.* 2006; Reece *et al.* 2006)
- Hawksbill turtles in the West Pacific (Broderick *et al.* 1994) and Caribbean (Díaz-Fernández *et al.* 1999)
- Leatherback turtles in the Pacific (Dutton *et al.* 2007)

The mixed-stock methodology is valuable but has limitations, most notably in obtaining all the source (nesting) populations. An oft-repeated observation in sea turtle biology is that if you sit on a tropical beach long enough, you will see a turtle nest. This anecdote emphasizes that an unknown proportion of sea turtle nesting is solitary females on long tracts of tropical beach, and is utterly refractory to the orderly collection of genetic specimens. A second consideration is that major nesting populations continue to be discovered in under-surveyed areas. A third limitation is that nesting colonies are not always differentiated in haplotype frequencies. All three factors may contribute to the large confidence intervals that typically accompany mixed-stock analyses of sea turtles. While precise estimates of feeding aggregate composition continue to elude scientists in most cases, the answers that this methodology provides are compelling when applied at the appropriate scale: do hawksbill feeding populations contain turtles from multiple rookeries? Do West Atlantic loggerheads enter the Mediterranean? Do Japanese loggerheads cross the Pacific Ocean? On these issues, the mixed-stock analyses provide compelling affirmatives that are highly relevant to conservation.

### Complex population structure

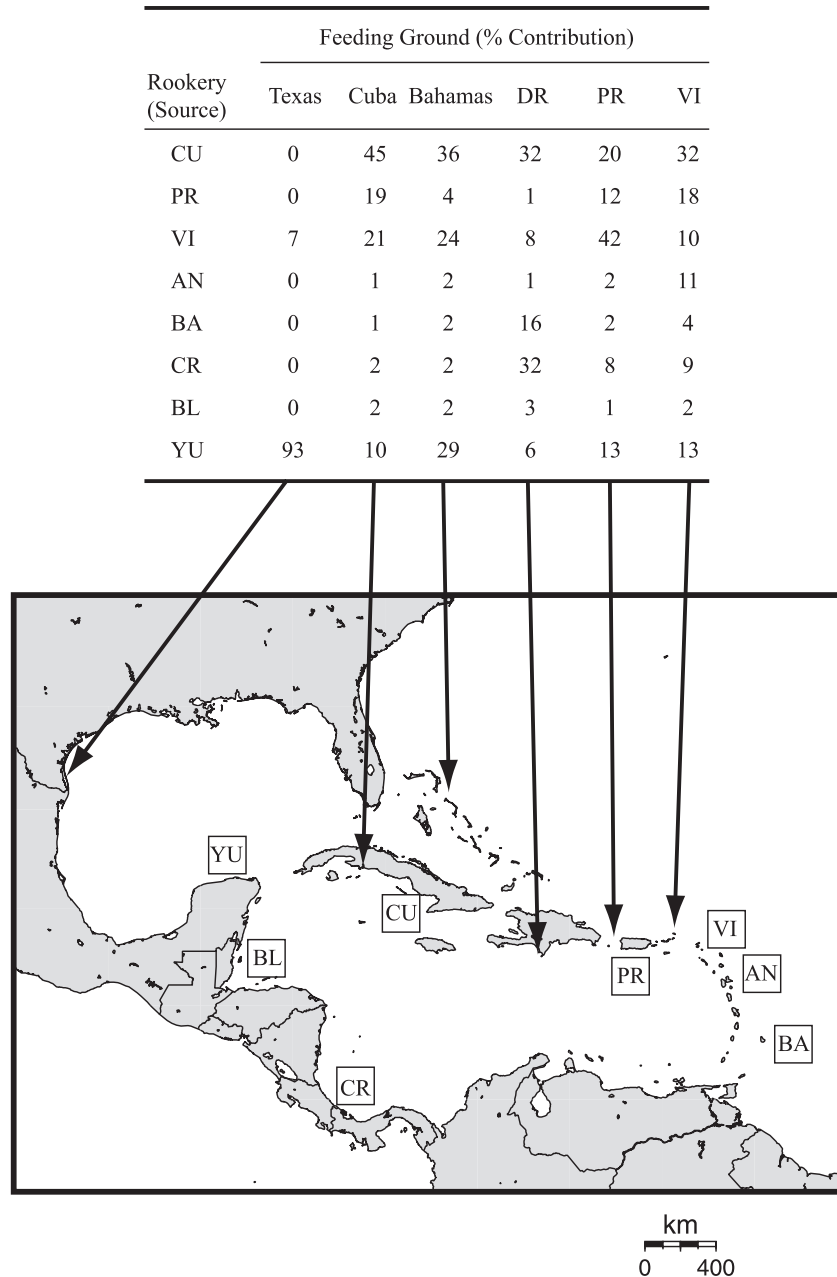
The mixed-stock studies outlined above demonstrate that juvenile loggerheads cross entire ocean basins in passive

migrations, and satellite tracking shows an active migration by advanced juveniles back to their region of origin (Nichols *et al.* 2000). This poses a challenge to conventional definitions of stock structure. How can we define stocks when reproductive populations are thoroughly mixed at one life stage, and strongly segregated at another? A second challenge is apparent when maternally inherited mtDNA provides a different image of population structure than biparentally inherited nDNA. Both these issues apply to sea turtles, fishes (Pardini *et al.* 2001), marine mammals (Baker *et al.* 1994), and are a ubiquitous feature of terrestrial mammals (Lawson Handley & Perrin 2007). These two issues fall under the heading of complex population structure, and sea turtles are instructive on both fronts. In this section, we consider the changes in population structure between juveniles and adults, and the implications of discordance between nDNA and mtDNA surveys.

### Juvenile vs. adult stages

The mixed stock analyses of loggerhead juveniles indicate that cohorts from genetically distinct rookeries extensively mix on oceanic feeding habitats. Surveys of these pelagic-stage juveniles indicate no population structure among locations across the North Atlantic ( $\Phi_{ST} < 0.001$ ,  $P = 0.919$ ; Bolten *et al.* 1998; LaCasella *et al.* 2007). At the end of this pelagic stage, juveniles apparently migrate from the Mediterranean and East Atlantic to coastal zones of the West Atlantic, switching to a benthic (bottom feeding) niche. Mixed-stock analyses of these older juveniles indicated an elevated contribution from nearby rookeries, prompting several researchers to suggest that benthic stage juveniles feed in the vicinity of their natal rookery (Witzell *et al.* 2002; Bass *et al.* 2004; Roberts *et al.* 2005; Reece *et al.* 2006). To address the issue of juvenile homing behaviour, Bowen *et al.* (2004) analysed specimens from 10 juvenile feeding zones across the northwest Atlantic and compared these samples to potential source (nesting) populations in the Atlantic Ocean and Mediterranean Sea. While the nesting colonies of the Northwest Atlantic have strong population structure ( $\Phi_{ST} = 0.42$ ,  $P < 0.001$ ; Bowen *et al.* 2005), the feeding populations of benthic juveniles have low but significant mtDNA haplotype frequency shifts ( $\Phi_{ST} = 0.0088$ ,  $P = 0.016$ ). In addition, haplotype frequencies at coastal feeding populations are significantly correlated with the haplotype composition of adjacent nesting populations ( $R^2 = 0.52$ ,  $P = 0.001$ ). These analyses are consistent with homing behaviour by juvenile loggerhead turtles.

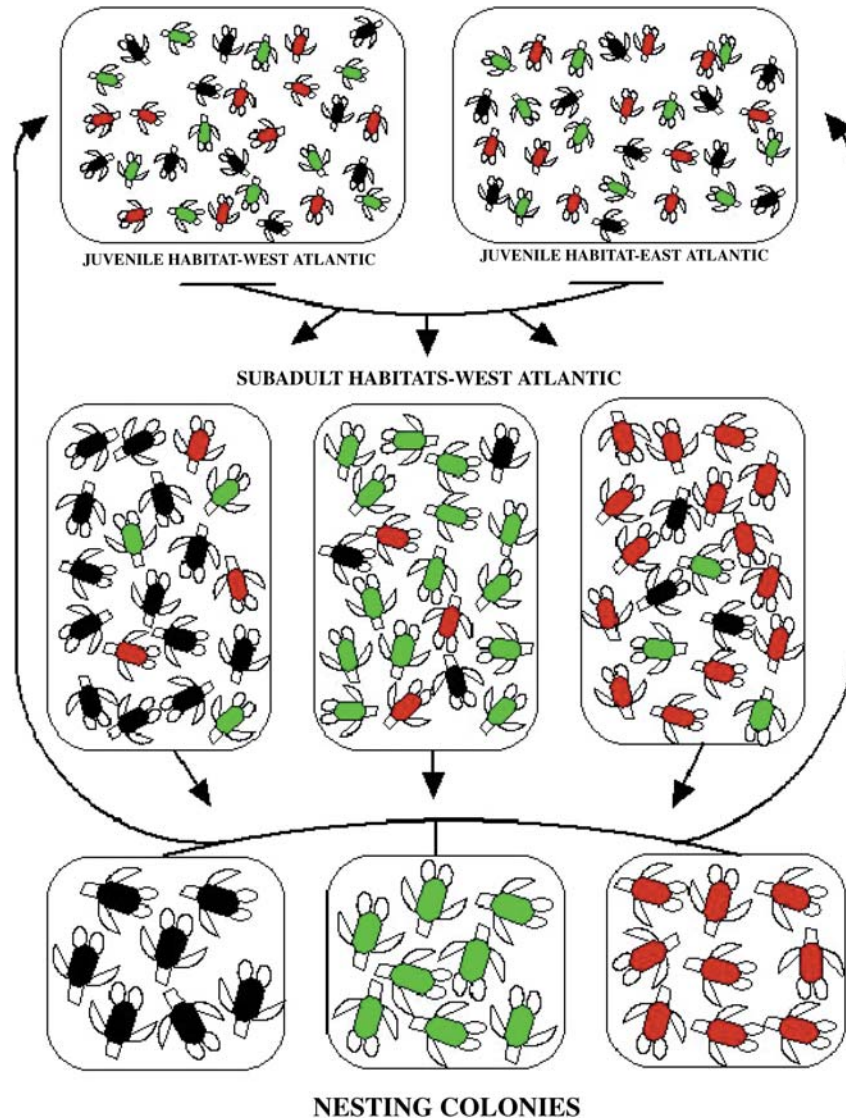
Loggerhead turtles have progressively greater population structure as they advance in age and development (Fig. 5). The pelagic juvenile populations have no genetic structure, and are composed of cohorts from regional nesting colonies in approximate proportion to the size of the nesting population (Table 1). The corresponding conservation



**Fig. 4** Caribbean hawksbills nesting and feeding habitats, with estimated contributions from regional nesting colonies to feeding populations (Bowen *et al.* 2007). Consult the original paper for standard errors. Rookery abbreviations are: CU, Cuba; PR, Puerto Rico; VI, US Virgin Islands; AN, Antigua; BA, Barbados; CR, Costa Rica; BL, Belize; and YU, Yucatan Peninsula. Feeding ground abbreviations are: DR, Dominican Republic; PR, Puerto Rico; and VI, US Virgin Islands.

concern is that oceanic fisheries (longlines and driftnets), which capture tens of thousands of turtles per year, will deplete nesting colonies throughout the region. The advanced benthic juveniles make a directed migration from oceanic habitat to coastal habitat in the vicinity of their natal rookery. The switch from pelagic to benthic habitat is not immutable, and both advanced juveniles and adults can switch back to

pelagic feeding (Hatase *et al.* 2002b; Witzell 2002). Hence, the advanced juveniles have some degree of flexibility. Nonetheless, perhaps half of the subadults feed near their natal rookery, so coastal hazards here will have a strong impact on the nearby nesting population. Corresponding conservation strategies may prioritize coastal habitat in the vicinity of small and dwindling nesting colonies. Finally,



**Fig. 5** A model illustrating population structure at three life stages of the loggerhead turtle. Turtles originate at three rookeries indicated by red, green and black icons. In the pelagic juvenile stage, turtles intermingle in oceanic habitat and no population structure is apparent between eastern, central, and western Atlantic. In the advanced (benthic) juvenile stage, turtles recruit to coastal feeding habitat near their natal rookery, inducing modest but significant population structure. In the breeding adults, females (and possibly males) have high site fidelity to breeding/nesting habitat, inducing strong population structure. Figure reprinted from Bowen *et al.* (2005) with permission of *Molecular Ecology*.

disturbance to adult stage nesting females will yield specific reductions to the corresponding reproductive population. Clearly, at each life-history stage, there are different threats and different consequences.

#### *Nuclear vs. mtDNA structure*

Karl *et al.* (1992) provided the first comparison of genetic results from mtDNA and nDNA, allowing the resolution of maternal and paternal influences on population genetic structure. Recall the test of natal homing with Ascension Island and Surinam nesting populations of green turtles,

in which none of the mtDNA haplotypes are shared between populations, and estimates of maternal gene flow are near zero (Bowen *et al.* 1992). Based on five nDNA loci, the two populations are indistinguishable, and corresponding estimates of nuclear gene flow indicate current or recent exchange. Overall, Karl *et al.* (1992) reported low population structure in nDNA (Atlantic  $F_{ST} = 0.130$ , Indo-Pacific  $F_{ST} = 0.126$ ), compared to mtDNA (Atlantic  $G_{ST} = 0.63$ , Indo-Pacific  $G_{ST} = 0.71$ ; Bowen *et al.* 1992). Microsatellite surveys across the same range corroborate this finding (Atlantic  $F_{ST} = 0.038$ , Indo-Pacific  $F_{ST} = 0.024$ ; Roberts *et al.* 2004). These studies demonstrate significant male-mediated gene

flow between green turtle nesting colonies, a finding supported by surveys of mtDNA and microsatellites in the West Pacific (FitzSimmons *et al.* 1997b).

As noted above, loggerhead nesting colonies have strong population structure in the northwest Atlantic ( $\Phi_{ST} = 0.42$ ,  $P < 0.001$ ). In contrast, a survey of five (biparentally inherited) microsatellite loci indicates no significant population structure ( $F_{ST} = 0.002$ ,  $P > 0.05$ ) across the same nesting colonies (Bowen *et al.* 2005). Males apparently provide an avenue of gene flow between regional nesting colonies (but see Carreras *et al.* 2007).

This pattern of strong maternal population structure and low nuclear population structure is surprisingly common in migratory marine vertebrates. In a comparison of white sharks (*Carcharodon carcharias*) between South Africa and Australia, the mtDNA haplotypes reveal strong structure ( $F_{ST} = 0.81$ ) while microsatellites reveal no significant structure (Pardini *et al.* 2001). In global surveys of the sperm whale (*Physeter macrocephalus*), mtDNA sequence comparisons demonstrate significant structure ( $G_{ST} = 0.03$ ,  $P < 0.001$ ; Lyrholm & Gyllenstein 1998), but microsatellite comparisons show no structure ( $G_{ST} = 0.001$ ,  $P = 0.232$ ; Lyrholm *et al.* 1999). A similar pattern is apparent in humpback whales (*Megaptera novaengliae*; Baker *et al.* 1994; Palumbi & Baker 1994).

Male-mediated gene flow in sea turtles can be conducted by two general mechanisms; males are not homing to natal sites, or mating occurs where adult populations overlap in feeding areas and migratory corridors. FitzSimmons *et al.* (1997a) evaluated the first possibility in a survey of male and female green turtles at the breeding site in the southern Great Barrier Reef. The males had the same haplotype composition as the females, indicating natal homing by both genders.

In evaluating the second possibility, consider the nesting populations of the West Atlantic loggerheads (Fig. 2). A female coming from the south, with a destination of nesting habitat in Georgia, South Carolina, or North Carolina, will pass through the breeding area for the large rookery in South Florida. Given the aggressive proclivities of breeding males (see Multiple paternity below), it seems likely that males from South Florida will mate with these females and gene flow will occur even if both sexes are homing to natal breeding sites.

### Conclusion

The genetic discordance between mtDNA and nDNA surveys provides two lessons about population structure relevant to wildlife management of sea turtles and other migratory marine animals:

- 1 Nesting populations are independent management units regardless of the level of male-mediated gene flow.

To illustrate this point, consider the extremes of gender-specific extirpation. If males were eliminated from the breeding habitat adjacent to the nesting beach, the nesting population would continue, because some of the females are inseminated on feeding grounds or migratory corridors. In contrast, if the females are eliminated then the nesting population is extinct. Females transmit the genetic threads of life across generations (Avice 1995), and the natal homing behaviour of females defines breeding populations, regardless of male behaviour.

- 2 Either nDNA or mtDNA alone could provide incomplete and misleading conclusions about population structure. The mtDNA surveys of North Atlantic juvenile turtles, taken alone, would indicate a single panmictic population, obscuring the true structure of subadults and nesting adults. Most genetic surveys of large migratory fishes (tunas, billfishes) are based on adults sampled on feeding habitat, and these surveys indicate low or no population structure. When reproductive or nursery populations are sampled, however, fine-scale population structure can emerge (Carlsson *et al.* 2007). For regional nesting colonies of sea turtles, nDNA data alone could indicate a single management unit, a disastrous premise. To resolve management units of migratory marine animals, an optimal strategy is to survey all life stages with both mtDNA and multiple nuclear loci. It is especially important to survey at breeding sites. Only at these locations will the essential population structure be revealed.

### Multiple paternity: a new paradigm emerges

Microsatellites have revolutionized the study of breeding behaviour, and sea turtle research in this arena has been fruitful. Although intense male competition for females and sperm storage have long been recognized, an accurate picture of male mating success is slow in coming. Female reproductive success is readily estimated in terms of the numbers of hatchings, but estimating the male's contribution is nearly impossible. Male breeding success can, however, be estimated through genetic analyses. The results of several microsatellite analyses indicate that multiple paternity is a dominant paradigm in turtle reproduction (Pearse & Avice 2001; Moon *et al.* 2006). Estimates of multiple paternity across sea turtle clutches range from 0 to 100%, but most of the studies with robust sample sizes provide estimates in the range of 30–90% (Table 2). The leatherback turtle seems to have the lowest incidence (0–16%), while the ridley turtles provide some of the highest estimates (20–92%). Regardless of the specific frequency, it is clear that multiple paternity is the norm for all species.

The advantages of multiple paternity are still debated, but most authorities agree that it should occur where males do not contribute parental care, and there is little opportunity for females to evaluate male fitness before copulation.

Species	Location	No. of clutches	Percentage of multiple paternity	Citation
Leatherback	Pacific Costa Rica	4	0	Rieder <i>et al.</i> 1998
<i>Dermochelys coriacea</i>	Virgin Islands	17	0	Dutton <i>et al.</i> 2000
	Pacific Costa Rica	50	16	Crim <i>et al.</i> 2002
Green	Pacific Costa Rica	8	63	Peare <i>et al.</i> 1998
<i>Chelonia mydas</i>	Great Barrier Reef	22	9	FitzSimmons 1998
	Ascension	3	100	Ireland <i>et al.</i> 2003
	Ascension	18	61	Lee & Hays 2004
Flatback				
<i>Natator depressus</i>	Queensland Aus.	16	69	Theissinger <i>et al.</i> 2006
Loggerhead	Queensland Aus.	45	33	Harry & Briscoe 1988
<i>Caretta caretta</i>	Florida USA	3	33	Bollmer <i>et al.</i> 1999
	Florida USA	70	31	Moore & Ball 2002
	Greece	16	94	Zbinden <i>et al.</i> 2006
Olive ridley	Surinam	10	20	Hoekert <i>et al.</i> 2002
<i>Lepidochelys olivacea</i>	Pacific Costa Rica	13	92*	Jensen <i>et al.</i> 2006
	Pacific Costa Rica	13	31†	Jensen <i>et al.</i> 2006
Kemp's ridley				
<i>Lepidochelys kempi</i>	Atlantic Mexico	26	58	Kichler <i>et al.</i> 1999

\*Arribada; †solitary.

Both conditions apply to sea turtles, for which there is no paternal investment in offspring and copulatory events are brief encounters off the nesting beach (and possibly elsewhere). In cases where female investment is high, and male investment is low, the indirect advantages of multiple paternity may include fertility insurance (Orsetti & Rutowski 2003), increased fitness through sperm competition, receiving good genes (Kempenaers *et al.* 1992; Otter & Ratcliffe 1996), increased genetic variation among offspring (Madsen *et al.* 1992; Byrne & Roberts 2000), and higher survivorship of hatchlings (reviewed in Pearse & Avise 2001). The last possibility has been demonstrated in a freshwater turtle (McTaggart 2000), but none of these benefits have been demonstrated in sea turtles.

An alternative explanation that incorporates sea turtle behaviour has emerged in two recent studies: multiple paternity in sea turtles may be a consequence of male aggressiveness rather than female choice. Jensen *et al.* (2006) assessed multiple paternity in olive ridleys on the Pacific coast of Costa Rica. There and elsewhere, ridleys have a unique nesting strategy when population densities are high: they mass offshore and nest simultaneously in huge numbers, in a phenomenon known as an arribada (arrival). Tens of thousands of turtles can come ashore in a matter of hours, a behaviour that is believed to provide predator saturation for eggs and hatchlings. Perhaps half of the nesting of olive ridleys, however, is by solitary females, coming ashore at low density. Jensen *et al.* (2006) compared multiple paternity in arribada nests and solitary nests, and found that 92% of arribada nests have multiple sires, whereas only 31% of solitary females lay clutches

**Table 2** Studies of multiple paternity in five species of sea turtles, modified and updated from Pearse & Avise (2001). All assessments were made with microsatellites, except Harry & Briscoe (1988; allozymes)

with multiple sires. The authors attribute the difference between arribada nesters and solitary nesters to the abundance of individuals, a density effect on the rate of multiple paternity.

The second observation is by Lee & Hays (2004), who find no fitness benefits to multiple paternity in green turtles at Ascension Island, where the environmental variables have a much greater influence on clutch survival. While the evidence is limited to hatchling success as a measure of fitness, these authors suggest that multiple paternity is the outcome of male coercion, where females allow extra matings 'to make the best of a bad job' in response to male harassment. Both of these studies are consistent with the aggressive mating behaviour reported for male sea turtles, summarized in Karl *et al.* (1995) and Bowen (2007). In at least two fisheries, male turtles are harvested by offering a wooden disk or barrel in the water as a potential mate. The male mounts the decoy and will not release it when hauled to a fishing vessel. On the Atlantic coast of Florida, human swimmers are occasionally subject to amorous advances by male loggerheads. In one of these attempts, the turtle 'made good its mating attack on this luckless individual' (Epstein 1989). Hence, the phenomenon of multiple paternity may be guided more by male density and proclivity, rather than the theoretical goals of female fitness and fecundity.

### Hybridization

Hybrid sea turtles have been reported for over 100 years. The earliest documented example is a loggerhead × hawksbill hybrid, known to Caribbean fishermen as a

**Table 3** Marine turtle hybrids identified by morphology and genetics

Species	Location	Marker	Age of separation	Reference
<i>Chelonia mydas/Eretmochelys imbricata</i>	Surinam	allozymes	50+ Ma	Wood <i>et al.</i> 1983
	Surinam	DNA		Karl <i>et al.</i> 1995
	Mexico	DNA/morphology		Seminoff <i>et al.</i> 2003
<i>Chelonia mydas/Caretta caretta</i>	Canada	DNA/morphology	50+ Ma	James <i>et al.</i> 2004
	Australia	morphology		C. Limpus, personal communication
	Brazil	DNA		Karl <i>et al.</i> 1995
<i>Chelonia mydas/Lepidochelys olivacea</i>	Brazil	morphology	50+ Ma	M. Marcovaldi, personal communication
<i>Caretta caretta/Eretmochelys imbricata</i>	Bahamas	morphology	10–20 Ma	Garman 1888
	Japan	morphology		Kamezaki <i>et al.</i> 1983
	USA	morphology		Greenblatt <i>et al.</i> 2005
	China	morphology		Frazier 1988
	Brazil	DNA/morphology		Lara-Ruiz <i>et al.</i> 2006
	Brazil	allozymes		Conceicao <i>et al.</i> 1990
	USA	DNA		Karl <i>et al.</i> 1995
<i>Caretta caretta/Lepidochelys kempi</i>	USA	DNA	10–20 Ma	Karl <i>et al.</i> 1995
<i>Eretmochelys imbricata/Lepidochelys olivacea</i>	Brazil	DNA/morphology	10–20 Ma	Lara-Ruiz <i>et al.</i> 2006
	USA	DNA		Barber <i>et al.</i> 2003
	Brazil	DNA, morphology		Lara-Ruiz <i>et al.</i> 2006

'McQueeggie' (Garman 1888). Since then, there have been numerous documented cases of hybridization among species in the family Cheloniidae (Table 3). If we exclude the geographically localized Kemp's ridley and flatback turtles, almost every hybrid combination in Cheloniidae has been documented. What is most surprising is the age of the species producing hybrids, as the Cheloniidae includes three deep lineages separated by 50+ million years (Dutton *et al.* 1996). By comparison, mammal species generally lose the ability to hybridize in less than ~3 million years, and birds and frogs in less than ~20 million years (Wilson *et al.* 1974; Fitzpatrick 2004). Marine turtles maintain reproductive compatibility over a much longer interval, and constitute the oldest bastards known to science. One factor may be the slow rate of molecular evolution in turtles (Avisé *et al.* 1992). A second factor is the indiscriminate mating behaviour of males noted above, and a third factor may be the maintenance of identical chromosomal number and structure (Bickham 1981). Additional genomic features, yet to be resolved, are surely involved.

The phenomenon of sea turtle hybridization, initially identified by aberrant morphology, is now robustly documented. It is less clear what conditions promote the phenomenon, and to what extent hybridization occurs. Lara-Ruiz *et al.* (2006) estimate that ~44% of putative hawksbills in Bahia, Brazil are hybrids, so this phenomenon is not merely a rare by-product of overlap in breeding areas, but may have some evolutionary manifestations. Hybridization in other vertebrate groups appears when either habitat or life history are disturbed; Karl *et al.* (1995) speculate that a *Lepidochelys kempi* × *Caretta caretta* hybrid captured in the West Atlantic may be the product of a headstart (captive rearing

and release) programme for *L. kempi*. Given that all species of sea turtles are listed by IUCN as Endangered or Threatened, and that human disturbances can induce hybridization in other vertebrates, the conditions that promote this phenomenon should be more fully explored.

### Comparative phylogeography

Two primary geographic barriers separate the tropical marine fauna of the Atlantic and Indo-Pacific, and they strongly influence patterns of speciation and biodiversity. The Isthmus of Panama closed off the Pacific–Atlantic connection about 3.5 million years ago. This is an immutable barrier for marine species except for the few that can tolerate freshwater conditions of the Panama Canal (McCosker & Dawson 1975). Southern Africa is the other barrier, where warm waters of the Indian Ocean (Aghulas Current) collide with the cold upwelling (Benguela Current) in the Atlantic. The thermal regime of the Benguela Current is believed to be a death sentence for tropical organisms, and the primary barrier to Atlantic–Indian exchange. This barrier is not, however, insurmountable. Sediment cores reveal a hiatus in upwelling at the end of Pleistocene glacial periods, with corresponding intrusions of warm water into the Atlantic (Peeters *et al.* 2004). Contemporary dispersal also may be possible via warm-core gyres from the Agulhas Current that become entrained in the northward moving Benguela Current (Penven *et al.* 2001). These gyres occasionally transport tropical species into the Atlantic, as indicated by mtDNA comparisons of Atlantic and Indian Ocean reef fishes (Rocha *et al.* 2005; Bowen *et al.* 2006) and large pelagic fishes (Graves & McDowell 2003; Castro *et al.* in press).

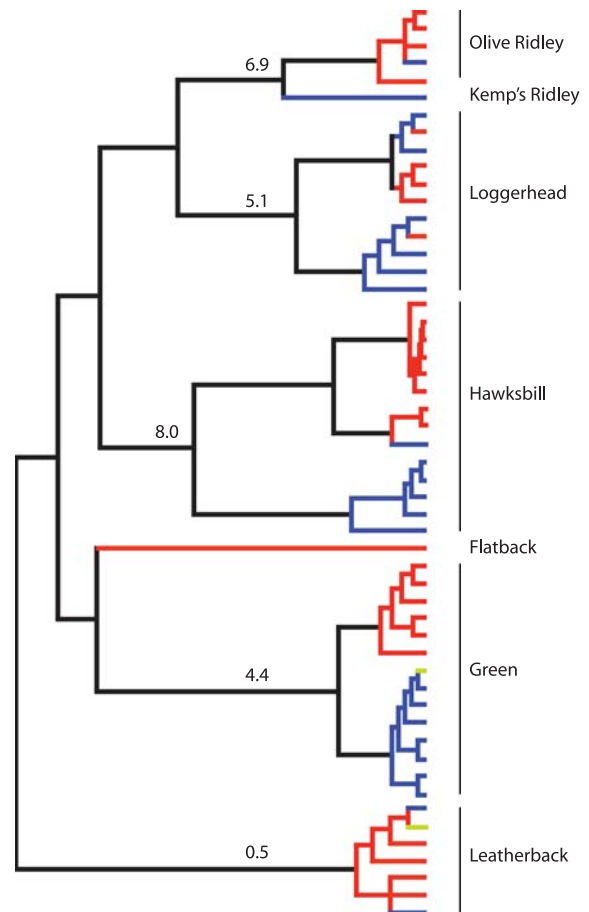
Sea turtles nest primarily in the tropics, but there is extensive variation in the latitudinal limits of nesting and feeding habitat. The hawksbill and green turtle have the most tropical distributions, with little nesting outside the 25° latitudes north and south. The olive ridley nests primarily in the tropics but can feed at higher latitudes. The loggerhead turtle nests as high as 35° in the North Atlantic, and near 40°N in the Mediterranean. The leatherback nests in the tropics and subtropics, but has been observed feeding in boreal (0 °C) waters above 50°N (Goff & Lien 1988).

The mtDNA phylogeny for sea turtles shows a rank-order agreement between thermal preference and evolutionary exchange between Indo-Pacific and Atlantic Oceans. The green turtle has an ancient separation ( $d = 4.4%$  in control region sequences; Encalada *et al.* 1996), but recent leakage of an mtDNA lineage from the Atlantic to the southwestern corner of the Indian Ocean (Bourjea *et al.* 2007). The hawksbill turtle also has two distinct lineages, corresponding to Atlantic and Indo-Pacific ( $d = 8.0%$ ; Okayama *et al.* 1999; D. Broderick; unpublished data), but with a younger lineage in the East Atlantic that is affiliated with the Indian Ocean (D. Broderick, personal communication; Fig. 6). Hence, an ancient isolation is indicated in both species, followed by a rare dispersal event.

The loggerhead phylogeny also has two primary lineages ( $d = 5.1%$ ; Encalada *et al.* 1998), but with less geographic partitioning. The distribution of this species includes a rookery in the Indian Ocean (Natal, South Africa) within a few hundred kilometres of the South Atlantic Ocean, indicating that the southern Africa barrier may be less formidable to interoceanic gene flow in *Caretta caretta*. The mtDNA phylogeny shows two effective transfers of matrilineal lineages between the Atlantic and Indian Oceans (Fig. 6). One of these appears to be very recent, as indicated by the sharing of haplotypes between South Africa and the West Atlantic (Bowen *et al.* 1994).

The olive ridley and Kemp's ridley may have initially been isolated by the Isthmus of Panama, a theory advanced by Pritchard (1969) based on morphological similarity and biogeographic evidence. The divergence between species ( $d_{\max} = 6.9%$ ; Bowen *et al.* 1998) matches the timeframe for the closure of the Pacific–Atlantic seaway, based on a molecular clock of 2% per million years. Subsequently, the olive ridley colonized from the Indian Ocean into the Atlantic. A single control region polymorphism distinguishes Atlantic and Indian haplotypes, demonstrating that the dispersal event was recent. Most olive ridley haplotypes are separated by  $d < 0.5%$ , indicating a shallower evolutionary history than green, hawksbill, and loggerhead turtles. Based on these patterns, Shanker *et al.* (2004) proposed a late Pleistocene radiation from the Indian Ocean into both the Pacific and Atlantic Oceans.

In contrast, the leatherback shows no geographic segregation of lineages, and an extremely shallow topography in



**Fig. 6** Matriarchal phylogenies for seven species of sea turtle based on mtDNA control region sequences (Ridleys, Bowen *et al.* 1998; loggerhead, Encalada *et al.* 1998; green, Bowen *et al.* 1992; Encalada *et al.* 1996; Bourjea *et al.* 2007; leatherback, Dutton *et al.* 1999). Indo-Pacific lineages are shown in red, Atlantic lineages are blue, and lineages observed in both oceans are green. The hawksbill phylogeny is an unpublished maximum-likelihood analysis of genetic distances using the HKY + I + G model of evolution and mtDNA control region sequences from GenBank (accession nos EF546379, DQ924961, EF191013, EF546379, EF191014, EF587752, AJ421797, AJ421796, DQ479344, DQ177341, DQ479339, DQ479342, DQ479335, DQ479341 top to bottom OTU in phylogeny, respectively). This phylogeny is a composite of intraspecific phylogenies grafted onto a species-to-family level tree in Dutton *et al.* (1996). Relationships within species were configured to impart two classes of information; the relative depth of intraspecific partitions (numbers above nodes are average nucleotide diversities) and their classification as Atlantic or Indo-Pacific lineages. We excluded closely related and in some cases rare haplotypes that provided little additional topological information. The branch lengths above the species level are not proportional to evolutionary depth, and are only intended to depict the branch order for deep evolutionary separations per Dutton *et al.* (1996).

phylogenetic analyses ( $d = 0.5%$ ;  $d_{\max} = 1.4%$ ; Dutton *et al.* 1999). This is remarkable in a species 100+ million years apart from the other sea turtles. Nonetheless, findings are consistent with the theme that thermal tolerance has a strong

influence on intraspecific phylogeography. The tropical green and hawksbill have ancient separations between Atlantic and Indo-Pacific, the more temperate loggerhead and olive ridley show evidence of recent interocean movement, and the leatherback shows the shallowest genealogy and the weakest geographic structuring.

While the mtDNA data show a rank-order agreement with thermal regime, caution is indicated in using a single locus to reach these conclusions. A nuclear DNA analysis of green turtles indicates that some Indo-Pacific to Atlantic exchange has occurred (Roberts *et al.* 2004). This is consistent with greater male dispersal in sea turtles (Casale *et al.* 2002), and highlights the need for multiple gene genealogies before phylogeographic conclusions are made with finality.

The Mediterranean populations of green and loggerhead turtles are the product of recent colonization, probably after the last glacial interval (12 000 years BP; Bowen *et al.* 1992, 1994). Likewise, the available evidence indicates that East Pacific populations of sea turtles are all recent arrivals. Green turtles in this region share an mtDNA haplotype with Hawaii (Bowen *et al.* 1992) and do not appear to be a distinct evolutionary entity in terms of nDNA (Karl & Bowen 1999). East Pacific leatherback turtles share a haplotype with the West Pacific (Dutton *et al.* 1999), and olive ridleys in this region are two control region mutations removed from a common Indo-West Pacific haplotype (Bowen *et al.* 1998). In all cases, the East Pacific haplotype networks coalesce in the late Pleistocene, within a quarter million years and possibly much more recently (Lopez-Castro & Rocha-Olivares 2005). These data are consistent with climate records in indicating that the tropical regime in the East Pacific is ephemeral. Under contemporary conditions, cold upwelling along this coast extends across the equator. During glacial intervals, many tropical faunas may be extirpated from the East Pacific, apparently including sea turtles.

The pattern of ancient isolation between tropical oceans, and recent connections in more temperate species, appears to have a strong influence on the phylogeography of sea turtles, and ultimately on the evolution of this group. Allopatric speciation, characterized by long-term isolation without gene flow, is believed to be the predominant mode of speciation (Coyne & Orr 2004). A model of allopatric speciation is consistent with phylogeographic patterns in the ridleys. The hawksbill and green turtle have Indo-Pacific–Atlantic divergences of several million years (perhaps confounded by occasional migrants), justifying recognition of subspecific evolutionary entities. Yet these divergences are not sufficient to generate reproductive isolation and speciation, if lineages separated by 10–50 million years can interbreed. Furthermore, what are the opportunities for geographic isolation in the leatherback, with a global distribution from the tropics to the Arctic Circle? This may explain why the leatherback has flourished for tens of millions of years, but exists as a single lineage across deep evolutionary

time. In the previous sections, we showed how natal homing, behaviour, habitat preference, and life history have left indelible signatures on the distribution of genetic diversity. Here, we conclude that climate, geography, and oceanography likely have a greater influence on evolution and speciation.

### Summary and prospectus

The DNA assays reveal much about the hidden lives of sea turtles, including homing behaviour in juveniles and adults, male-mediated gene flow and complex population structure, feeding aggregates that nourish several regional nesting colonies, multiple paternity that may be density dependent, hybridization with potential evolutionary significance, and global phylogeographic patterns that influence speciation. What are the future directions of these genetic studies?

Sea turtles are mobile islands of life, with a variety of symbionts, commensals and parasites (Frick *et al.* 1998; Bugoni *et al.* 2001). The species composition of these hitch-hiking animals and plants can reveal migratory pathways (Caine 1986; Eckert & Eckert 1988), and their population genetics will yield additional insights. Some tantalizing clues about life history have emerged from population genetic studies of commensal barnacles, including a strong genetic break between East and West Pacific cohorts that inhabit the loggerhead turtles migrating between these two regions (Rawson *et al.* 2003).

In terms of phylogeography and evolution, there appears to be sufficient leakage between ocean basins to prevent long-term isolation and allopatric speciation (Roberts *et al.* 2004; Bourjea *et al.* 2007). Hence, the most important evolutionary phenomenon may be the loggerhead/ridley/hawksbill hybrid swarm in Brazil. This hybrid complex is a large component of nesting effort and is probably far beyond the  $F_1$  stage (Lara-Ruiz *et al.* 2006). Whether similar levels of hybridization are occurring elsewhere is an open question. Documenting the filial generation of the hybrids (e.g.  $F_1$  or later, backcrosses, etc.) will indicate whether the hybrid swarm is stable and persistent.

On the subject of nesting population structure and female fidelity, surveys of major rookeries are ongoing, and continue to yield surprises (Chassin-Noria *et al.* 2004; Lopez-Castro & Rocha-Olivares 2005; Formia *et al.* 2006). This effort is likely to culminate in comprehensive worldwide coverage in the next decade. Researchers have also begun to apply recent advances in population genetic theory, especially coalescence approaches, to estimate population ages and historical trends in abundance (Reece *et al.* 2005; Rivalan *et al.* 2006). On another front, the fine-scale assignment tests of Ascension Island nesters (Lee *et al.* 2007) indicate a new tool for evaluating the precision of female homing behaviour. This methodology may effectively close the gap between contemporary tagging studies and



the more historical approaches based on haplotype (and genotype) frequencies.

Male migrations and homing are largely unknown, because of the difficulty in studying turtles in the off-shore breeding habitat. Recall the innovative study by FitzSimmons *et al.* (1997a), in which male green turtles in breeding habitat had the same mtDNA haplotype frequencies as their female counterparts. A decade later, this study has not been replicated elsewhere to our knowledge. Are the males of other species homing to their natal site? This is a notable gap that can only be resolved with thorough sampling of male breeders, as is planned for the large loggerhead population off southeast Florida, USA (R. Carthy, personal communication).

Mixed-stock analyses of feeding populations have advanced in recent years, including new methodologies motivated by sea turtle cases (Bolker *et al.* 2003, 2007; Okuyama & Bolker 2005). These studies reveal aspects of migratory behaviour that are largely refractory to direct observation (Carreras *et al.* 2006; Maffucci *et al.* 2006). After the shore-based studies that define management units in terms of nesting beaches, these ocean-based studies may have the highest conservation impact. When industrial fishing methodologies are applied to sea turtles, the consequences for regional nesting habitats can be elucidated with mixed-stock analyses (Bolten *et al.* 1998; Bowen *et al.* 2007).

The long generation time and terrestrial life stages of sea turtles make them especially vulnerable to depletion, and their vast cartographic ranges make them especially difficult to manage. Two species are Critically Endangered, the hawksbill and the range-restricted Kemp's ridley (<http://www.iucnredlist.org/>). Other species are subject to severe regional depletions, including the Mediterranean and Caribbean green turtles, Mediterranean and South Pacific loggerheads, and Pacific leatherbacks. The news is not all bleak, however (Hays 2004). Signs of recovery, at least for individual nesting colonies, are apparent in Caribbean leatherbacks, green, and hawksbills (Dutton *et al.* 2005; Troëng & Rankin 2005; Richardson *et al.* 2006), Hawaiian greens (Balazs & Chaloupka 2004), and even the critically endangered Kemp's ridley (TEWG 2000). In all cases, the recovery is attributed to long-term protection. Decades are the units by which we can measure sea turtle recovery. While this time frame exceeds the scope of most regulatory plans, the recovery of sea turtles has urgency far beyond the status of individual populations. Sea turtles are a key species in many coastal ecosystems (Jackson *et al.* 2001). They are also a focus of public concern, and therefore a flagship species (Frazier 2005) for ecosystem restoration, for fishery management, for conservation of resources on the high seas. Like the panda, gorilla, and great whales, they symbolize the hope that endangered species can recover, that ecosystems can heal, and that humanity can turn back from the abyss.

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