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Satellite tracking of sea turtles: Where have we been and where do we go next?

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ABSTRACT: The use of satellite tracking for the fundamental and applied study of marine turtles began in the 1980s but has undergone rapid growth in recent years. To provide a background against which to judge the past success and future directions of these research efforts we carried out a comprehensive review of over 130 scientific papers on the use of this technique in this taxon. We show how satellite tracking has changed over time as well as outlining biases in spatial, species and life-stage coverage. Descriptions of migration routes and other habitats have offered novel insights into the basic life history patterns of some species, highlighted focal areas for conservation and reinforced the multi-national nature of the stakeholders of many populations. In foraging areas, knowledge is growing as to how animals move within dynamic seascales, thus facilitating our understanding of 3-dimensional habitat use and seasonal patterns of behaviour. More experimental approaches have elucidated navigational capabilities and post-release survival following fisheries interaction and long-term captivity. In addition, through the Internet and other media, satellite tracking appears to have been effective in engaging public attention in many countries. Finally, we discuss why the use of the technique has increased so markedly over time and point out key areas of concern that we feel should be addressed by the community of researchers and donors who focus on sea turtles.

KEY WORDS: Sea turtles · Satellite tracking · Migration · Conservation · Navigation · Tagging reflex

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OVERVIEW

Many species of marine megavertebrates are of profound conservation concern as the result of a range of past and ongoing impacts such as direct exploitation (Roman & Palumbi 2003, Baum & Myers 2004), indirect take in fisheries (NRC 1990, Hall et al. 2000) and habitat degradation (e.g. Gardner et al. 2003). For effective mitigation of direct threats, there is an acute need to understand how these animals use dynamic seascales. The elaboration of an ever increasing array of tracking technologies has transformed this field of study (Block

2005, Block et al. 2005), with satellite tracking using the Argos system (Argos 1996) having become particularly prevalent in recent decades (Gillespie 2001).

Marine turtle life histories typically span large temporal and spatial scales (Musick & Limpus 1997, Plotkin 2003). Researchers have now extensively utilized satellite tracking to yield a number of insights into the spatial ecology of this group at a range of scales. Recent highlights include demonstrating trans-Pacific migration in leatherback turtles *Dermochelys coriacea* (Benson et al. 2007a), showing high levels of fidelity to foraging areas across multiple years in green

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turtles *Chelonia mydas*, loggerhead turtles *Caretta caretta* and Kemp's ridley turtles *Lepidochelys kempii* (Broderick et al. 2007, Shaver & Rubio 2008, this Theme Section [TS]), recording juvenile hibernation of loggerhead turtles (Hochscheid et al. 2005), unlocking the adult life histories of the more enigmatic species (leatherback turtles: James et al. 2005a,b,c; hawksbill turtles *Eretmochelys imbricata*: van Dam et al. 2008, this TS), as well as questioning some of the established life-history models for other better studied species (loggerhead turtles: Hatase et al. 2002b, Hawkes et al. 2006; green turtles: Hatase et al. 2006, Seminoff et al. 2008, this TS).

There are a number of reasons why workers have sought to track turtles using the Argos system. Firstly, given its global coverage, satellite tracking allows us to follow turtles in near real time and find out what routes they take, no matter how far they go. This does not mean to devalue the seminal work of the pioneering turtle taggers (e.g. Hendrickson 1958, Balazs 1976, Carr et al. 1978, Limpus et al. 1992) who discovered a great deal about turtle dispersion using modified farm animal markers backed up by thousands of painstaking hours on the beach and years of patiently waiting for results. The main problems with using flipper tags to unlock spatial movements are that large numbers must be deployed to ensure sufficient recaptures and biases are present in the likelihood of recapture and reporting (Godley et al. 2003b). Although animals can be tracked with flipper tags over long durations, possibly up to decades (Limpus et al. 1992, C. J. Limpus pers. comm.), little is known of the intervening route and speed. In contrast, satellite tagging, when carried out effectively, yields significant information regarding each study individual, including routes and speeds and, above all, this information can be gathered quickly, albeit for a typical maximum duration of several months to a few years, with a fiscally dictated sample size.

In order to provide a detailed background against which to judge the past success and future directions of such research efforts, we carried out a comprehensive review of >130 peer-reviewed research publications that have used this technique in this taxon (Appendix 1; see also reviews by Papi & Luschi 1996, Luschi et al. 2003a, 2006, Plotkin 2003, Morreale & Standora 2005).

THE RISE OF THE SATELLITE TAG

The first published results of successful satellite tracking of sea turtles were of post-nesting loggerhead turtles in the USA (Stoneburner 1982, Timko & Kolz 1982) followed by that of a single leatherback turtle tracked after nesting in French Guiana (Duron-Dufrenne 1987). Following a gap of several years,

results were published on additional loggerhead and green turtles tracked in Greece (Hays et al. 1991) and Japan (Baba et al. 1992). These latter publications marked the start of an exponential rise (Fig. 1a, Appendix 1), with as many as 24 scientific papers utilising the technique in 2006 alone (at time of writing, this total has already been surpassed for 2007). The

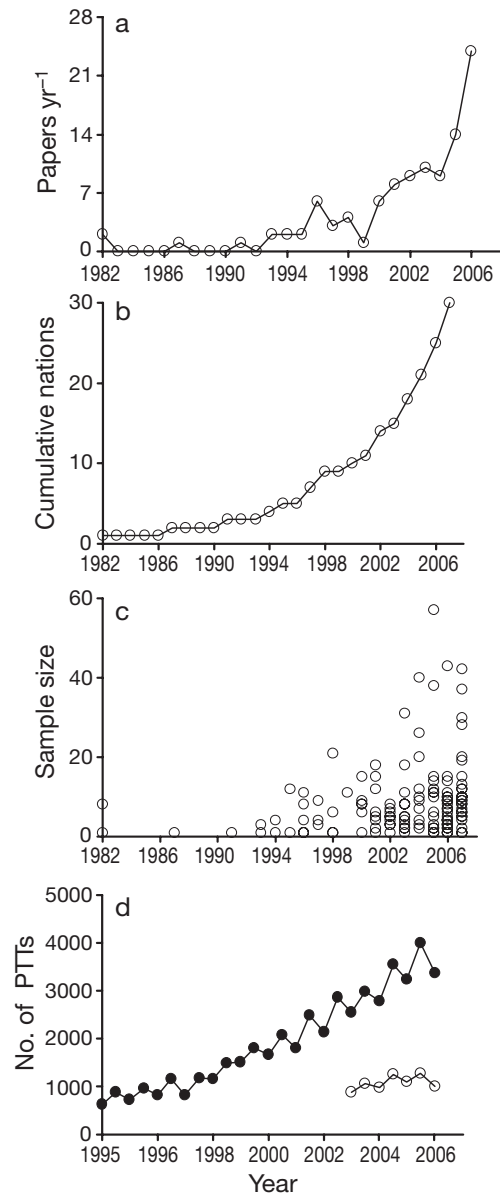


Fig. 1. Growth of satellite tracking in sea turtles. (a) Number of peer-reviewed papers involving satellite tracking published per year (1982–2006). (b) Cumulative total number of geopolitical units as deployment sites of satellite tracking in the published literature (1982–2007). (c) Temporal pattern in species-specific sample size in peer-reviewed publications (1982–2007). (d) Temporal pattern in number of active platform terminal transmitters for marine animals in each half year (●: 1995–2006) and marine turtles (○: 2004–2006). PTT: platform terminal transmitter. Note that Panels (a–c) have a longer timescale than (d)

number of peer-reviewed publications, however, does not truly reflect how prolific the use of this technique has become for sea turtles. Further insight can be obtained from data gathered by CLS, the company that operates the Argos system. Tags recorded as being deployed on marine animals (fish, turtles, pinnipeds and cetaceans; excluding seabirds or archival fish tags) make up approximately one third of tags tracking animals (Fig. 1d). Of these marine animal deployments, since 2004, the 7 species of sea turtles have accounted for approximately 20% of the total (mean number of active sea turtle platforms per 6 mo period = 252 ± 68 (SD), range 140–355; Philippe Gros, CLS, pers. comm.). It should be noted that some tags may have been deployed multiple times and/or on species for which they were not initially intended. These numbers are, however, likely to be indicative.

Biases inherent in work to date

The number of countries of deployment of these published studies has also grown (Fig. 1b) but significant geographic biases remain. By the time of writing, publications reviewed had included transmitters deployed in only 30 geopolitical units, with an uneven distribution across the globe. (Atlantic Ocean: Western 35%, Central 9%, Eastern 4%; Mediterranean 11%; Indian Ocean 15%; Pacific Ocean: Western 16%, Central 1%, Eastern 14%; Appendix 1; NB some papers provide data on more than one species/ocean basin. Overall species-specific datasets published: $n = 141$). Much of this bias is likely related to differential funding for research among regions but is one that is gradually being addressed, partly as a result of strategic international funding by intergovernmental organisations and governments/non-governmental organisations in wealthier nations.

Perhaps more profound, however, are the species and life stage biases. To date, 82% of studies have featured only 3 species (Appendix 1: loggerhead turtle: $n = 38$; green turtle: $n = 39$; and leatherback turtle: $n = 39$) with much less effort expended thus far on 3 other species (Appendix 1: olive ridley *Lepidochelys olivacea* $n = 12$; Kemp's ridley turtle $n = 8$; hawksbill turtle $n = 6$). Finally, although there are no publications as yet on the flatback turtle *Natator depressus*, studies are underway (K. Pendoley pers. comm., S. Whiting pers. comm.). Given the ease of access at the rookery and the fact that their relatively large size is more conducive to device attachment, it is perhaps not so surprising that over 75% of the published tracking studies have featured adult females. Even within this life stage, however, there may be some bias in selecting individuals (see next subsection).

Tracking females at the nesting grounds

Although adult sea turtles are perhaps most vulnerable on the nesting beach, these habitats are relatively well known and, given the will and the means, solutions to many threats are relatively more tractable than those at sea. The inwater breeding/internesting habitat is also a point of relatively high risk where dense aggregations of adult turtles are found in limited areas during the periods prior to and between multiple clutch depositions. It is, therefore, of interest to define these areas and the level of nest site fidelity shown by individuals during multiple breeding attempts within the same season. However, the internesting habitat is also one where transmitters might fail as a result of mating, internesting resting behaviour e.g. under rocky ledges, nesting behaviour including sand excavation and terrestrial locomotion, or increased fisheries risk (Georges et al. 2007, Hays et al. 2007, Fossette et al. 2008, this TS) and many authors, ourselves included, have often taken the safer option and deployed transmitters in the latter part of nesting seasons to increase the likelihood of imminent departure, transmitter survival and thus successful tracking of migration (e.g. Luschi et al. 1998, Hays et al. 2002, 2004c, Godley et al. 2002). As well as having the potential to introduce artefacts into the ecological patterns of post-nesting movements described (e.g. if all individuals at the breeding colony late in the season had travelled from farther away), choosing individuals nesting at the end of the season tells us very little about space use prior to post-reproductive migrations. Satellite tracking studies have, however, whether by serendipitous coverage or design, still afforded a significant body of knowledge regarding behaviour in the internesting period.

Leatherback turtles have been shown to use extensive areas between successive nesting activities (Eckert 2006, Eckert et al. 2006, Georges et al. 2007, Hitipeuw et al. 2007). Although this usually only encompasses waters of the continental shelf, movements can be up to several hundred kilometres and encompass nesting at various beaches across different geopolitical units (Keinath & Musick 1993). It is clear that the magnitude of spatial use in this species poses a significant impediment to designing effective marine protected areas or other mitigation measures for threatened breeding colonies (Witt et al. in press).

For some hardshell sea turtles, females typically remain within the vicinity of the nesting beach in the internesting period (loggerhead turtles: Stoneburner 1982, Godley et al. 2003a; green turtles: Hays et al. 1999, Craig et al. 2004, Troëng et al. 2005b, Fuller et al. 2008, this TS; hawksbill turtles: Troëng et al. 2005a, Whiting et al. 2006; Kemp's ridley turtles: Seney &

Landry 2008, this TS, Shaver & Rubio 2008). As a result of gathering extensive, spatially explicit interesting data in the vicinity of the rookery, Zbinden et al. (2007) were able to make a series of recommendations regarding the management of the Marine Park at Zakynthos, Greece.

Exceptions to the rule of staying nearby the nesting sites have been found, however. Some loggerhead and green turtles have undertaken oceanic loops during the interesting period (Blumenthal et al. 2006). In hawksbill turtles, subsequent nesting in the Dominican Republic was thought to have been described in 1 out of 7 females tracked from Puerto Rico (van Dam et al. 2008). Olive ridley turtles in Australia moved offshore from the nesting site (McMahon et al. 2007), remaining in neritic waters (Whiting et al. 2007). Earlier studies of this species in Costa Rica (Plotkin et al. 1995) did not receive sufficient locations to reconstruct tracks, although the turtles seemed to stay in the vicinity but may, in some cases, have moved offshore into oceanic habitat between breeding attempts.

Post-nesting movements of adult females

Recent reviews of long distance movements in sea turtles (Luschi et al. 2003b, Plotkin 2003) suggested that, with exceptions, there were 2 main patterns of movement: Firstly, departure from the breeding site, swimming directly towards a fixed feeding area, generally in the neritic (hereafter 'Type A') and secondly, departure to oceanic habitats followed by wandering movements, often over great distance ('Type B'). Through satellite tracking, ever-increasing insight has been gathered for 6 of the 7 species of sea turtle in a relatively short period of time. This has allowed us to suggest a 4 point classification framework (Types A1 to A3, and Type B) to describe patterns in post-nesting movements in adult turtles. Although we follow the distinction between 'oceanic' and 'pelagic' as in Bolten (2003a), our classification framework for adult movement should not be confused with the 3-part classification of development pattern proposed by Bolten (2003b).

Type A1 — oceanic and/or coastal movements to neritic foraging grounds

All green turtle populations so far tracked have exhibited this pattern, at least in part, whether they nest on islands (e.g. Pacific: Cheng 2000, Craig et al. 2004, Yasuda et al. 2006; Atlantic: Luschi et al. 1998, Blumenthal et al. 2006; Mediterranean: Broderick et al. 2007) or the continental shelf (Kennett et al. 2004,

Troëng et al. 2005b). Routes are often relatively direct but can involve coastal sections that mean a greater migratory distance but perhaps afford interim foraging possibilities en route to preferred foraging areas (Cheng 2000, Godley et al. 2002) or may facilitate navigation (Hays et al. 2002).

Loggerhead turtles that nest on continental nesting beaches typically undertake coastal migrations to foraging grounds and in some populations appear to demonstrate long-term residency (e.g. Limpus & Limpus 2001, Luschi et al. 2006, Broderick et al. 2007), whilst others undertake seasonal latitudinal shuttling (see Type A2 below). Some populations nesting on oceanic islands have demonstrated dichotomous behaviour with larger adult animals displaying Type A1 behaviour and smaller adult animals foraging pelagically generally in oceanic habitats (see Type B below).

Given some of the controversy that has surrounded the ecology and status of hawksbill turtles (Mrosovsky 1997, Meylan 1998) it is somewhat surprising that very few data have been published in only 4 studies of adult migrations to date. In the insular Caribbean (Horrocks et al. 2001, van Dam et al. 2008), individuals crossed oceanic areas and moved through other neritic areas to their final foraging grounds (Fig. 2a). In Costa Rica (Troëng et al. 2005a) and the Gulf of Carpentaria, Australia (Whiting et al. 2006) continentally nesting hawksbills moved along the coastal shelf to discrete foraging areas.

Recent studies of olive ridley turtles in Australia (McMahon et al. 2007, Whiting et al. 2007) have highlighted that although some turtles do live pelagically, others move through continental shelf waters to locations where they forage benthically, sometimes at rather greater depths than had previously been thought (McMahon et al. 2007). Post-nesting tracks of Kemp's ridley turtles took them through coastal waters, where they established coastal home ranges (Seney & Landry 2008, Shaver & Rubio 2008).

Type A2 — coastal shuttling between summer foraging and wintering sites

For turtles at temperate latitudes, seasonal oscillations in climate may mean that it is essential or beneficial to move to lower latitudes or other areas with higher water temperatures during the winter season. It should be noted that this is demonstrably the case for leatherback turtles within their Type B movements (Hays et al. 2006, James et al. 2005a, 2006b) but within the hardshell turtles in neritic habitats, this has only been shown in 2 species that are regularly found in temperate waters. It is the predominant strategy for loggerhead turtles in North America (Plotkin &

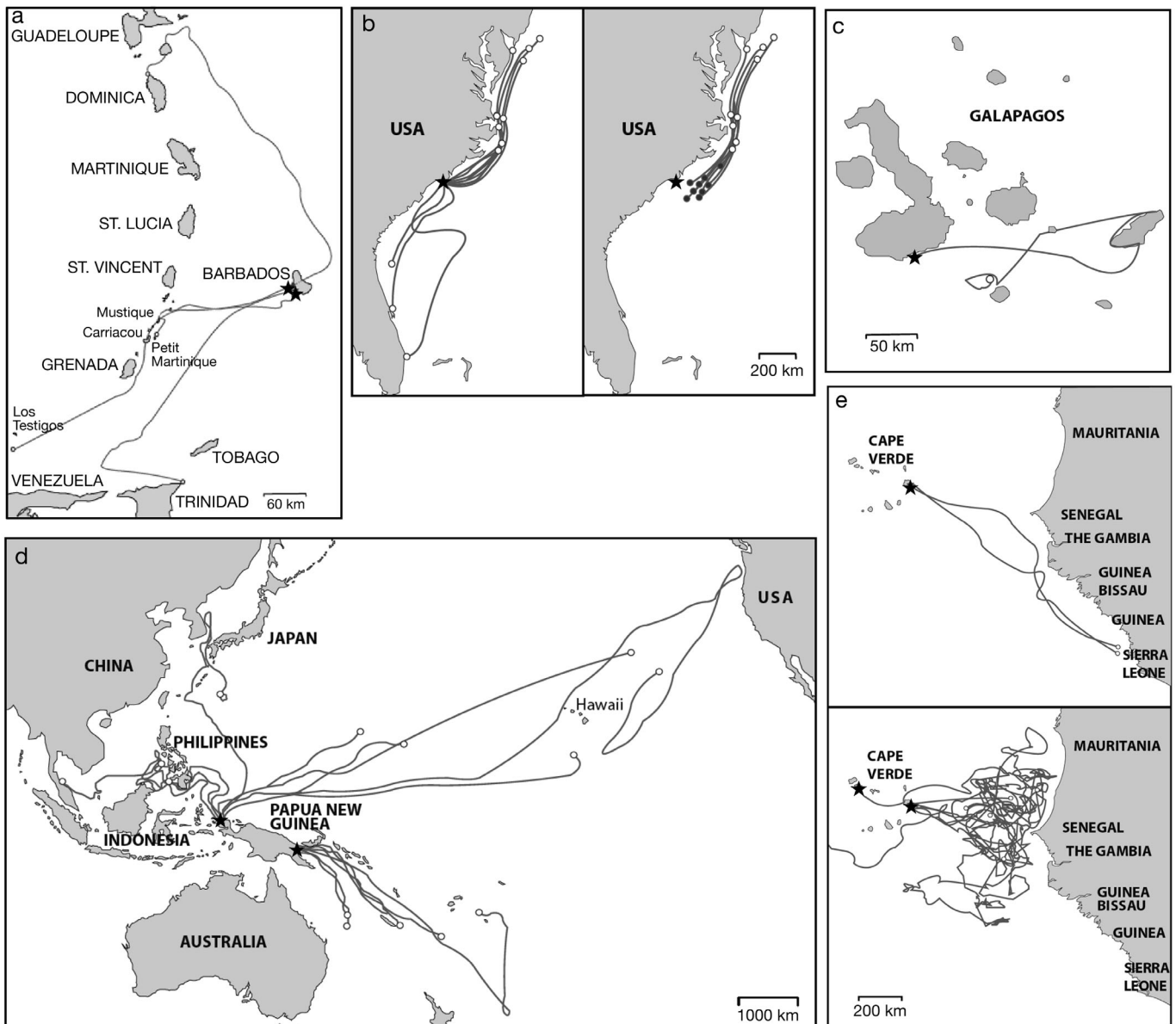


Fig. 2. Diversity of post-nesting dispersal patterns in adult female turtles. ★: tagging location; ○: last known location (except in b). (a) Type A1 — coastal and/or oceanic movements to neritic foraging grounds. Hawksbill turtles following nesting in Barbados (Horrocks et al. 2001; $n = 4$; courtesy of authors and Allen Press). (b) Type A2 — coastal shuttling between summer foraging and wintering sites. Loggerhead turtles following nesting at Bald Head Island, North Carolina, USA. Left panel: post nesting migration to summer/autumn foraging grounds (○); right panel: southward autumn migration to overwintering grounds (●) (Hawkes et al. 2007; $n = 9$ with an additional 3 staying resident in southern areas; courtesy of authors and Blackwell Publishing). (c) Type A3 — local residence. Short range movements of a female green turtle following nesting in Galapagos Islands, Ecuador (Seminoff et al. 2008; $n = 1$; courtesy of authors and Inter-Research Science Publishers). (d) Type B — pelagic living. Leatherback turtles following nesting in Indonesia and Papua New Guinea (Benson et al. 2007a,b; $n = 28$, courtesy of authors and Allen Press). (e) Mixed strategy (Type A1 and B) of loggerheads following nesting in Cape Verde (Hawkes et al. 2006; $n = 9$; 2 Type A1 and 7 Type B; courtesy of authors and Elsevier Publishing)

Spotila 2002, Morreale & Standora 2005, Hawkes et al. 2007; our Fig. 2b). Although some Kemp's ridley turtles that have been tracked using satellite appear to undertake some form of seasonal shuttling (Morreale & Standora 2005, Renaud & Williams 2005, Gitschlag 1996), this does not seem to be a prevalent

pattern among adult females tracked to date (Shaver & Rubio 2008). It should be noted that although thermal conditions are not necessarily the proximate cue for such movements, it is likely that temperature and its ecological correlates will, in part, be the ultimate drivers of such behaviours.

Type A3—local residence

Satellite tracking has confirmed past flipper tagging results (Limpus et al. 1992, Green 1984) in that not all individual sea turtles are profoundly migratory, with some individuals staying in the neritic areas in the vicinity of the nesting colony, migrating only short distances. This has been demonstrated in green turtles in the Galapagos Islands (Seminoff et al. 2008; our Fig. 2c) and loggerhead turtles in the Mediterranean (Broderick et al. 2007), hawksbill turtles in Australia (Whiting et al. 2006) and Kemp's ridley turtles in USA (Shaver & Rubio 2008). Definition of movements in this category is confounded by the difficulty posed by a lack of a clear threshold between Types A1 and A3. Although it is likely to be population-specific, a putative threshold would be the extent of normal internesting movement.

Type B—pelagic living

The leatherback turtle typifies the pelagic sea turtle, and adult females have been shown to undertake dramatic transoceanic movements. Much of their time is spent in oceanic habitats and, although neritic waters are often used (James et al. 2005c, Eckert et al. 2006), it is likely that they feed epipelagically (Hays et al. 2004b,c). In the eastern Pacific, females nesting in Costa Rica (Morreale et al. 1996) and Mexico (Eckert & Sarti 1997) were subsequently tracked southwards across the equator into international waters and those of the Galapagos, Peru and Chile. Morreale et al. (1996) suggested the presence of an important migratory corridor, whilst Eckert & Sarti (1997) raised concern that the coincidence of turtles in a global fishery hotspot may be causal in the declines in leatherbacks observed in the eastern Pacific. More recent tracking of stocks nesting in the Western Pacific has demonstrated that postnesting females undergo a variety of migration routes, including south into the South Pacific, east into coastal waters off North America, north into waters off Japan, and west into waters of the Philippines and Malaysia (Fig. 2d; Benson et al. 2007a,b). In the Atlantic, following seminal work with limited tracking duration (Duron-Dufrenne 1987, Keinath & Musick 1993), more recent tracking has shown adult females from western Atlantic stocks nesting in French Guiana and Suriname (Ferraro et al. 2004), Grenada (Hays et al. 2004c), the USA (Eckert et al. 2006) and Trinidad (Eckert 2006) disperse widely throughout the north Atlantic, often using the productive waters associated with the Gulf Stream. In the Indian Ocean, only turtles from South Africa have thus far been tracked (Hughes et al. 1998, Luschi et al. 2003c, 2006). These individuals have typically stayed in oceanic habitats undertaking convo-

luted routes associated with strong current systems within 1000 km of the African continent in both the Indian and Atlantic Oceans.

Although it is generally felt that post-hatchlings and small juveniles of all sea turtle species except the flat-back turtle use oceanic habitats (Carr 1987, Musick & Limpus 1997, Bolten 2003a,b) it appears that adults of several hardshell species are also to be found in the open ocean. Limited studies of adult female olive ridley turtles suggest that many individuals move directly to oceanic areas following nesting (Plotkin et al. 1995, Plotkin 1998, Pandav & Choudhury 2006) but mixed strategies may be involved (McMahon et al. 2007, Whiting et al. 2007) including some neritic habitat utilisation. Although loggerhead adults have long been thought to be primarily benthic feeders, description of migration routes by satellite tracking in some populations has demonstrated apparent size-related dichotomous migration strategies with smaller animals undertaking Type B lifestyles and larger individuals the more typical Type A1 (Hatase et al. 2002b, Hawkes et al. 2006). Additionally, Luschi et al. (2003b) showed that, following experimental displacement, adult loggerheads could live in the open ocean. The green turtle, long thought to be a near obligate herbivore and therefore tied to benthic habitats, has recently been tracked and observed showing behaviours highly suggestive of oceanic feeding after nesting in Japan (Hatase et al. 2006) and the Galapagos (Seminoff et al. 2008).

Finally, there appear to be some individuals who in the midst of, or prior to, a sequence of Type A1 coastal movements, undertake oceanic loops (green turtle: Troëng et al. 2005b, Cheng 2000; loggerhead turtle: Dodd & Byles 2003, Hawkes et al. 2007). Based on the increasing records of this type of behaviour, the weight of evidence of prevalence and timing suggests that this might sometimes represent a form of facultative habitat switching, including change of feeding mode, rather than simply orientation behaviour (Papi et al. 1997).

Unifying patterns

As tracking studies increase in the number of populations covered and individuals tracked, a number of general patterns are becoming clear.

Firstly, patterns of dispersal in adults of every hardshell turtle population thus far studied appear to encompass only a relatively discrete part of an ocean basin, e.g. green turtles from Costa Rica (Troëng et al. 2005b) and hawksbill turtles from Puerto Rico (van Dam et al. 2008) appear confined to the Caribbean. Loggerhead turtles from the Cayman Islands (Blumenthal et al. 2006) and Cape Verde (Hawkes et al. 2006)

were tracked only to their proximate region of the Atlantic. This was also true in studies of loggerhead turtles tracked from nesting sites in the USA, where further substructuring is apparent when multiple sites are compared (Plotkin & Spotila 2002, Dodd & Byles 2003, Hawkes et al. 2007). This informs the generalised life history model for hardshell turtles where hatchlings are thought to disperse at the level of oceanic gyres (Musick & Limpus 1997). The first phase of hatchlings and small juveniles is an oceanic one; this is typically followed by settling out into one of a series of neritic foraging habitats. Upon maturation, adult turtles undertake cyclical reproductive migrations from the foraging ground to the rookery of origin (Bowen & Karl 1997, Musick & Limpus 1997). Molecular evidence (Bowen et al. 2004, Bolker et al. 2007) suggests sub-regional natal homing in larger juveniles that we suggest is mirrored by adult distribution patterns as demonstrated by tracking. Indeed, Nichols et al. (2000) and Cejudo et al. (2006) appear to illustrate homing to the natal region in animals following captivity.

Secondly, it is becoming clear that there can be a diversity of strategies used by individuals within populations. There is more behavioural plasticity in sea turtles than might previously have been imagined. Clear examples of mixed strategies include those demonstrated by loggerhead turtles nesting in Japan (Type A1/B; Hatase et al. 2002b), the USA (Type A1/A2/B; our Fig. 2b; Hawkes et al. 2007) and Cape Verde (Type A1/B; our Fig. 2e; Hawkes et al. 2006); green turtles in Japan (Type A1/B; Hatase et al. 2006) and Galapagos (Type A1/A3/B; Seminoff et al. 2008); olive ridley turtles nesting in Northern Australia (Type A1/B; Whiting et al. 2007). Perhaps less clear are the differences within Type B movement patterns made by leatherbacks in the Western Atlantic (Ferraro et al. 2004, Hays et al. 2004b, Eckert 2006, Eckert et al. 2006). Although there may be a degree of subregional fidelity shown by individuals to areas such as north, northeast or tropical Atlantic (James et al. 2005b, Hays et al. 2006), leatherbacks appear to generally disperse widely across most of the ocean basin but have not yet been tracked across the equator. Time and additional studies with larger sample sizes and of longer duration will further elaborate the ecological correlates of the different strategies used by females and also allow us to compare how closely these patterns of movement compare with conspecific adult males from the same populations.

Tracking of adult females in the foraging grounds

Description of behaviour of adults in foraging grounds is a fundamental part of most post-nesting

tracking studies, although this is often achieved with limited success, typically with simple descriptions of the endpoint of tracks. This is particularly true when animals reach neritic locations and are thought to damage their transmitters, thus ending transmissions (loggerhead turtles: Stoneburner 1982, Godley et al. 2003a; green turtles: Luschi et al. 1998, Cheng 2000, Hays et al. 2002, Kennett et al. 2004). In addition, biofouling may also play a role in transmitter failure or intermittent function (Troëng et al. 2006, Broderick et al. 2007, Hays et al. 2007). Nevertheless, a growing body of studies can boast tracking datasets with durations in the foraging sites approaching a year or more, thereby yielding significant insights into aspects such as variable levels of foraging site fidelity among populations (e.g. loggerhead turtles: Blumenthal et al. 2006 vs. Broderick et al. 2007; green turtles: Troëng et al. 2005b, Broderick et al. 2007). Additionally, wintering patterns and Type A2 movements have now been described in great detail as a result of these long-term tracking studies (Hawkes et al. 2007). For leatherbacks, tremendous insights have been gained into foraging ground usage and seasonal shuttling (James et al. 2005b, Eckert et al. 2006, Hays et al. 2006, Seminoff & Dutton 2007).

Tracking migration to nesting grounds

How sea turtles relocate their nesting grounds, particularly at remote insular locations, is one of the great mysteries of animal navigation, and experimentally testing hypotheses as to how they undertake their travels has become a focussed area of research (see 'Experimentation' below). So far, few transmitters deployed in the nesting grounds have lasted sufficiently long to have demonstrated return migrations, as this is typically a period in excess of 2 yr. Some individuals, however, have been tracked on their return migration after an interval of ca. 1 yr (loggerhead turtles to each of Cape Verde and Northern Cyprus: Godley et al. unpubl. data; Kemp's ridley turtles: Shaver & Rubio 2008). Transmitters have been deployed in the foraging grounds and allowed females to be tracked to the nesting sites (loggerhead turtle: Limpus & Limpus 2001; Kemp's ridley turtle: Renaud et al. 1996). In these cases, animals moved through coastal habitats to nesting sites in parallel with post-nesting migration strategy typical for each species.

The under-represented majority

What, however, of the under-represented majority of sea turtles i.e. the males and the far more numerous juveniles? Slowly the number of studies of adult

males of 6 species has been building. With slight variations, it appears that one generality is that males display migration patterns broadly similar to those observed in adult female conspecifics and could be classified according to the 4 part classification detailed above. Reproductively active male olive ridley turtles tagged off Costa Rica dispersed to oceanic habitats upon the completion of reproduction (Plotkin et al. 1996) in a manner comparable with, albeit earlier than, females from the same site. An additional male olive ridley turtle collected in the Eastern Tropical Pacific was tracked for several months in the open ocean (Beavers & Cassano 1996). Adult male green turtles at Ascension tracked using experimental transmitters with internal antennae (Hays et al. 2001c) provided enough data to suggest an extended mating period followed by a post-breeding migration pattern broadly similar to that previously described for conspecific females from the site (Luschi et al. 1998). The first published studies on the movements of male hawksbill turtles (van Dam et al. 2008) showed that although both sexes of the same population stayed within the same region, males travelled to more proximate foraging areas. Additionally, 2 males were recorded as returning to the breeding site within 1 yr in comparison to the multi-year inter-breeding intervals typically demonstrated by conspecific females. Tracking of male Kemp's ridley turtles captured off the main nesting site for the species suggested that males did not disperse as far as conspecific females, generally residing in the vicinity of the nesting beach, and all stayed within Gulf of Mexico waters (Shaver et al. 2005). For the loggerhead turtle, limited tracking of males in the Pacific (Sakamoto et al. 1997, Hatase et al. 2002a) suggests the possibility of neritic and oceanic habitat use. Tracking of male leatherback turtles from high latitude foraging grounds (James et al. 2005a,b,c) has demonstrated that males also travel south to breeding grounds across a similarly diffuse range of paths as females; possibly with a greater frequency. Once in the vicinity of breeding sites, they remain closer to shore than internesting females.

We also have a long way to go before we have an adequate understanding of juvenile movement patterns. All leatherbacks tracked to date have been adult or near adult sized, likely related to the relative lack of observations and captures of live juvenile leatherbacks in the wild (Eckert 2002). Despite physical size constraints there is a small but slowly building literature on the movements of juveniles of all hardshell species apart from the flatback turtle.

Within oceanic habitats, loggerhead turtles have so far received the most attention. Cardona et al. (2005) and Revelles et al. (2007a,b) suggested that pelagic juvenile loggerheads in the Mediterranean generally

avoided coastal areas and remained resident in relatively discrete oceanic areas for considerably longer than predicted by simulations based on passive drifting in ocean currents. Cejudo et al. (2006) showed near transatlantic movement of juveniles released at the Straits of Gibraltar. In the Pacific, Polovina et al. (2000, 2004, 2006) and Swimmer et al. (2002, 2006) have tracked relatively large numbers of juvenile loggerhead and olive ridley turtles, demonstrating clear inter-specific differences in habitat utilisation, association with specific oceanic features and active swimming against currents.

For large juvenile loggerhead turtles, movements have ranged from extensive (Bentivegna. 2002, Hochscheid et al. 2005) to relatively short range (Renaud & Carpenter 1994) with individuals, although spending a majority of the time in the neritic, having the potential to move into oceanic habitats (Morreale & Standora 2005, McLellan & Read 2007). Tracking of juvenile green turtles (Godley et al. 2003b) demonstrated a range of behaviours from extreme site fidelity to movements over extended areas of coastline. Whiting & Koch (2006) demonstrated the facultative shift of a juvenile hawksbill turtle in the Cocos Islands between habitats >1000 km apart. Juvenile Kemp's ridley turtles have been shown to undertake seasonal migrations (Schmid & Witzell 2006).

There is clearly room for much additional information to be gathered through further satellite tracking of males and immatures, particularly those juveniles in oceanic habitats where it is difficult to gather data by other means. Specifically, tracking of increased numbers of wild juveniles that are likely to be free from any anthropogenic influence is recommended, because although satellite tracking of rehabilitated or longline captured animals is a valid method of testing fates of these individuals, it is questionable how typical the behaviour of these animals is likely to be. Technology has yet to offer effective mechanisms of tracking individual hatchlings and other early life stages for extended periods, but in the terrestrial realm animals as small as dragonflies have been subject to radio tracking (Wikelski et al. 2006). Although aspirational, it seems plausible that technology may be developed that would allow tracking turtles in their first few years. This would seem a worthy target for future technological innovation.

TECHNOLOGICAL ADVANCES

As outlined above, a great deal has been uncovered from analysis of horizontal movement of marine turtles. These data have been significantly augmented by 2 major spheres of development: (1) the advancement of

dive logging capability and (2) the integration of movements with oceanographic data.

Time-space specific dive logging

Rather than having to infer submergence patterns from Argos data (Hatase & Sakamoto 2004) or simple dive summary data (Hays et al. 1999, Godley et al. 2002), incorporation of complex dive logging capabilities has now allowed individual dive profiles to be transmitted. Satellite-linked dive data are often sent in concatenated format (Fedak et al. 2001) and this system has recently been validated in sea turtles using traditional time depth recorders (Myers et al. 2006). Findings have shown how animals use the water column (Hays et al. 2004b,c, Sale et al. 2006, McMahon et al. 2007) and allowed elaboration of seasonal patterns in behaviour such as hibernation (Godley et al. 2002, Hochscheid et al. 2005, 2007, Broderick et al. 2007, Hawkes et al. 2007). Such data have allowed the suggestion of fisheries bycatch mitigation steps (Polovina et al. 2003). Linkage of dives with thermal profiles has facilitated postulation as to the thermal niche and possible future range under scenarios of climate change (James et al. 2006a, McMahon & Hays 2006), and dive durations have even been used to infer field metabolic rates (Bradshaw et al. 2007).

Integration with oceanography

Inferences from movement patterns can be taken to a higher level once incorporation of oceanographic information starts to yield information as to how animals move within dynamic seascapes. Analysis of currents has given significant insights into oceanic movements of sea turtles (Polovina et al. 2000, Luschi et al. 2003a,c, Gaspar et al. 2006, Hawkes et al. 2006, 2007, Sasamal & Panigraphy 2006, Bentivegna et al. 2007, Revelles et al. 2007b). Inferred chlorophyll levels have shown how some populations are feeding in relation to oceanic productive zones (Polovina et al. 2000, Hawkes et al. 2006, Seminoff et al. 2008). For an integrated view including sea turtles and fisheries see Polovina et al. (2001). Interpretation of thermal conditions experienced by individual animals has facilitated a growing understanding of the physiological ecology of overwintering (Godley et al. 2002, Hochscheid et al. 2005, 2007, Broderick et al. 2007, Hawkes et al. 2007) and also the conditions that may trigger migration (Sherrill-Mix et al. in press) or be experienced during extended movements (Hays et al. 2001d, Seminoff et al. 2008). In a recent analysis of a long-term data series of gelatinous zooplankton across the North Atlantic it

became clear that areas used by leatherback turtles tracked in previous published studies were among the clear hotspots of potential prey (Witt et al. 2007). A significant point in the consideration of past studies of movements and oceanographic variables is that comparisons have been largely qualitative; there is significant room for the development of techniques to allow more quantitative and dynamic comparisons. Further, the potentially exciting role of animal-borne sensors has been advocated within operational oceanography (Fedak 2004), and McMahon et al. (2005) have recently demonstrated that thermal data gathered by diving leatherbacks were reliable when compared with those gathered using the ARGO buoy system.

ADDITIONAL AREAS OF ADVANCEMENT

Several additional spheres of activity are worthy of highlighting as growing areas within the field.

Experimentation

Although the majority of studies to date have been descriptive, some studies, however, have taken a more experimental approach yielding significant insights into navigational capabilities of loggerhead (Papi et al. 1997, Luschi et al. 2003b) and green turtles (Papi et al. 1995, 2000, Luschi et al. 1996, 2001, 2007, Papi & Luschi 1996, Åkesson et al. 2001, 2003, Hays et al. 2003a, Girard et al. 2006). Attaching high resolution time depth recorders to experimentally displaced individuals tracked by satellite facilitated the first detailed analysis of dive profiles during oceanic movement (Hays et al. 2001a).

Inferring fates

Hays et al. (2003b) reviewed a number of studies and data from previously unpublished tracks and suggested that satellite tracking could be used to infer capture in fisheries and thus generate an index of at-sea survivorship, although this met with some controversy (Chaloupka et al. 2004b, Hays et al. 2004a). Others have used satellite tracking to describe the behaviour of animals immediately following bycatch (Swimmer et al. 2002, 2006, Chaloupka et al. 2004a, Revelles et al. 2007a,b), following rehabilitation and release (Bentivegna 2002, Cejudo et al. 2006) or after extended periods in captivity (Pelletier et al. 2003, Polovina et al. 2006). This includes the year-long, transpacific tracking of the captive-raised loggerhead turtle from Mexico to Japan (Nichols et al. 2000) and a

comparison of wild adult females and those which had been headstarted (Shaver & Rubio 2008).

Sharing science

There is tremendous public interest in marine vertebrates, especially taxa that exhibit spectacular migrations. Through near real-time tracking on the Internet, often associated with a media campaign, a number of organizations including our own have been highly successful in engaging large numbers of the public in turtle tracking projects (Coyne & Godley 2005, Halpin et al. 2006). It is not possible to track the true impact of this interest, but as a value-added aspect of research efforts it must be considered positive.

CATALYSIS

There has been an acceleration of the use of satellite tracking of sea turtles, but how has this come about? We suggest that this development has been multifactorial. Over the last 25 yr, the technology has moved from an experimental to a far more operational phase. Transmitters and attachment methods have improved, with durations well in excess of a year no longer uncommon (Hays et al. 2006, Broderick et al. 2007, Hawkes et al. 2007, van Dam et al. 2008). Argos itself has improved, with the initiation of Argos service plus and improved global satellite coverage. Complemen-

tary tools have also developed in parallel enabling easier handling and interpretation of data (Geographic Information Systems, remote sensing technologies and the Internet).

Although initially designed for turtle researchers, the Satellite Tracking and Analysis Tool (STAT; Coyne & Godley 2005) has sought to bring all these electronic technologies together in an open access format for researchers of all taxa. Providing standard tools and formats, automated downloading and effective data preservation to maximize value from tracking data, STAT aims to foster collaboration and data sharing. This is especially powerful when combined with the open-access mapping suite Maptool (www.seaturtle.org/maptool/). The number of platforms stored within STAT continues to rise ($n = 1976$, as of 1 Aug 2007) as do the taxa included: marine turtles, 7 spp.; sharks, 1 sp.; birds, 18 spp. (11 marine, 7 terrestrial); marine mammals, 6 spp. The global footprint of these endeavours has also increased with sea turtle deployments in 41 geopolitical units (Fig. 3). These include 25 nations not yet represented in the published literature.

Additional exciting innovations in the STAT portfolio are a new data-clearing house mechanism and geographically explicit viewing tools that allow managers to view all data within a geopolitical region from all data-sharing projects within the system (Coyne & Godley 2007). Although the sample size in some studies has increased in recent years (Fig. 1c), given that >68% of studies to date have involved species-specific sample sizes <10 and only 10% of studies were based

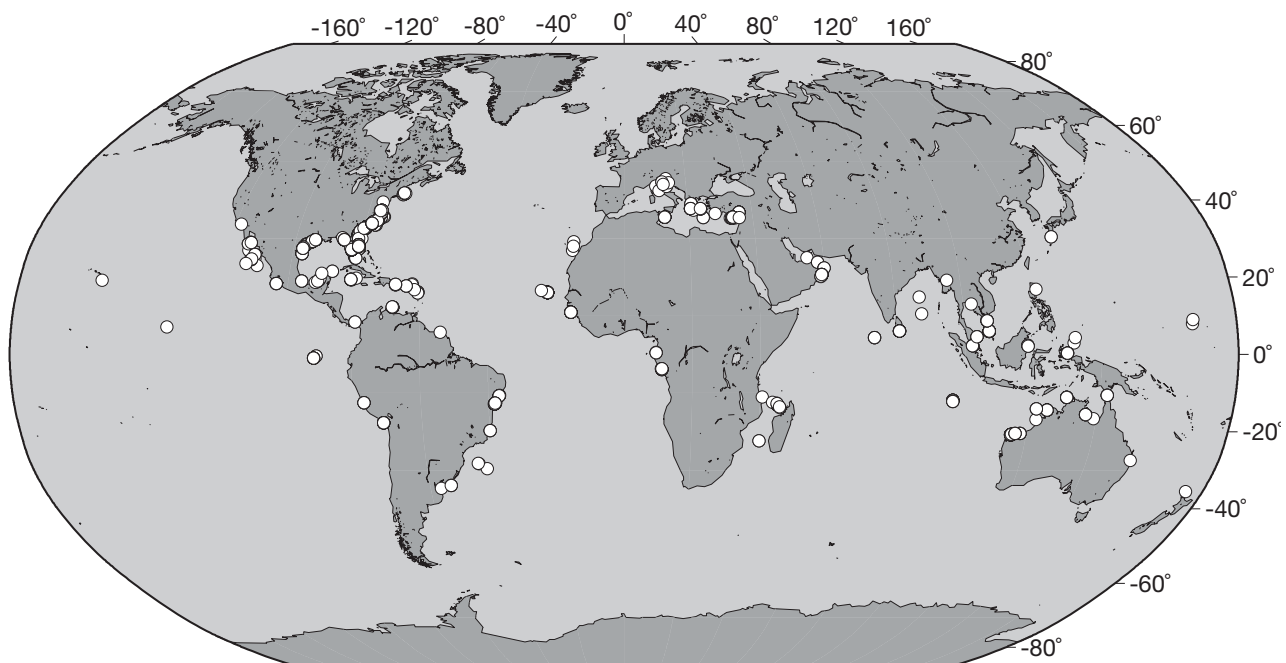


Fig. 3. Spatial footprint of STAT (Satellite Tracking and Analysis Tool, see Coyne & Godley 2005) turtle tracking projects. Circles denote the launch point of marine turtle tracking with data managed within the STAT system

on sample sizes >20, there is clear need to extend our work into collaborative data-sharing and meta-analyses. It is hoped that innovations such as this nascent clearing house will greatly facilitate needed progress.

A 21ST CENTURY (SATELLITE) TAGGING REFLEX?

Intrinsically, satellite tracking is exciting and the arguments for potential research dividends outlined above are compelling, while the benefits in terms of public relations and education can also be substantial. The technology has improved and is now available to all workers with access to an online computer and sufficient fiscal resources to buy transmitters, limited consumables and satellite time (ca. US\$5000–10 000 per unit depending on transmitter model and longevity). If sea turtle researchers are deploying in the order of 250 to 500 transmitters per year (see Fig. 1d), at the estimated costs above, the costs of the high-tech consumables are between US\$1.25–5.0 million per annum. On top of this are a great deal of associated salary and travel costs that, if they could be calculated, would likely dwarf the above figure. Is sea turtle biology and conservation benefiting enough from this investment? Are we now partaking in a 21st century version of Mrosovsky's (1983) 'tagging reflex'? We must be more self-reflective on a number of issues to ensure that limited resources are used most effectively.

Animal welfare

Several workers have correctly highlighted the need for a strong ethical standpoint in studies such as animal tracking (Frazier 2000, Hawkins 2004, Wilson & McMahon 2006, Cooke 2008, this TS). Some questions must be continually asked. Are deployment package compactness and attachment methods sufficient to minimise hydrodynamic drag (cf. Watson & Granger 1998), weight, buoyancy, physical damage or impingement of natural movement or mating? Are we sure we are not increasing chances of entanglement? Is there potential for magnetic interference e.g. from transmitters placed on the head? We need to share both our failures and successes as we improve our methodologies.

In general, leatherback tracking has proven difficult as one cannot attach transmitters using the standard techniques for hardshell turtles (cf. Renaud et al. 1993); hence the development of a variety of tethers (Morreale et al. 1996), harnesses (Eckert & Eckert 1986) and direct carapacial attachment procedures (Lutcavage et al. 1999, Fossette et al. 2008, Doyle et

al. 2008, this TS). Techniques have clearly improved over the years (for an early example of an excessive transmitter package, see illustration in Duron-Dufrenne 1987) but given recent concern expressed regarding harnesses (Troëng et al. 2006), it is timely that Fossette et al. (2008) show that, albeit based on a very small sample size, turtles equipped using direct attachment techniques may swim faster and dive deeper than conspecifics equipped with harnesses. Sherrill-Mix & James (2008, this TS) also investigate potential tagging effects. Given the ever-increasing number of leatherbacks being tracked, this is a topic worthy of much more attention. Although turtle workers have sought to minimize deleterious impacts from the start, we are now entering a phase in our discipline where we can start to empirically test for even quite subtle impacts on our study animals and we must join forces to adequately test for these possibilities.

Scientific rigour

The topics of experimental design and data analysis and interpretation have been highlighted as concerns that should be given close attention (Frazier 2000). We must constantly ask ourselves whether our sample sizes are sufficient to generate meaningful results. Authors have begun to explicitly target transmission performance and accuracy (Plotkin 1998, Hays et al. 2001b, 2007) and the array of statistical techniques and treatments to improve the robustness of data interpretation is increasing (Flemming et al. 2006, Jonsen et al. 2006, 2007). There is, however, a clear need for more easily accessible and reliable techniques to help workers describe home ranges and key areas of occupancy that will allow satellite tracking to feed more easily into spatially relevant management. Additionally, tools to allow the quantitative comparison of movement with oceanographic variables need to be refined and made accessible before maximal benefit will be extracted from tracking data.

Is satellite tracking the best technique?

Although the technique has offered much, it is not a panacea for research needs. It has not yet matured to the point that we can track the smallest of turtles and there is still much to be gained from direct observation, molecular and other forensic methods and oceanographic modeling approaches. For many neritic juveniles, who move short distances for long periods and do not generate many high quality locations (e.g. Godley et al. 2003b), satellite tracking may not be the best

technique. Indeed, sonic and radio tracking in addition to traditional mark and recapture methods offer greater insight and value for money in some cases (Seminoff et al. 2002, Avens et al. 2003). Standard GPS tracking offers potential but requires reliability of recapture (Schofield et al. 2007). Developing satellite-linked GPS capabilities (Yasuda & Arai 2005) will hopefully provide significant insights into the movement of all animals, including those that move only short distances without the need for recapture. This is especially true for tags using Fastloc technology that have recently been trialed on loggerhead turtles off North America (M. S. Coyne et al. unpubl.) and shows great promise for the remote gathering of high precision location data. Although not satellite linked, another technique which offers promise is geolocation (GLS) using light levels which, although offering lower spatial resolution and requiring recapture, is relatively inexpensive per animal and may allow the tracking of larger sample sizes (Fuller et al. 2008). Additionally, although currently necessitating recapture, datalogging technologies are now reaching an unparalleled level of breadth, precision and resolution and the advent of the 'Daily Diary' promises to unlock many unknowns about spatial ecology of animals such as turtles (Wilson et al. 2008, this TS).

Publish or be damned!

We have largely restricted ourselves to the peer-reviewed literature in this review although there is an additional wealth of data that has been presented only in arcane technical reports or in symposium proceedings (over 220 non peer-reviewed abstracts in the proceedings of the International Sea Turtle Symposia by 2007; B. J. Godley pers. obs.). The total of papers reviewed here does not compare favourably with this massive total, especially given that many published papers are of the same study individuals featured in previous publications, sometimes repeatedly. Acknowledging that there will always be a delay between tracking and effective publication, it is clear that only the minority of satellite tracking data have been published in the peer-reviewed literature. Although presentation at any venue may be better than no dissemination at all, data that are not fully analysed and presented in the public domain are more liable to be damaged, lost or forgotten and although they can be used by their custodians, this utility is limited. For the greater good, should we (workers and donors) consider time-limited tenure over data before they are shared on the global commons? In the meantime, are your data safe? Are they in a format that will facilitate sharing in the future? In

some cases, data may already be lost. Donor organizations and researchers share a responsibility to ensure positive steps are made in this regard.

Seeking outcomes

This research area offers a great deal of management-relevant information, and is constantly feeding into management plans (e.g. Western Pacific Regional Fishery Management Council 1994, Turtle Expert Working Group 2007) but to date clear documented policy changes as a result of findings are few. For instance, multiple studies have highlighted Nicaragua as holding foraging grounds for adults of 3 species from multiple origins (Troëng et al. 2005a,b, Blumenthal et al. 2006, van Dam et al. 2008), yet largely unmanaged harvesting of adult turtles continues in the coastal waters there (Lagueux 1998). Researchers studying leatherback migration have used satellite tracking data to highlight key areas for leatherback conservation (Eckert 2006, James et al. 2005c) but it is clear that mitigation of threats in these areas is not simple. Perhaps the exception, Shaver & Rubio (2008) outline how tracking, in addition to nesting and stranding data were instrumental in the development of a time-area fisheries closure in Texas, USA to protect Kemp's ridley turtles.

Much of the sea turtle tracking literature claims to inform conservation but why the apparent lack of clear policy changes? What does it really mean if turtles migrate across international boundaries? What does it mean if there are hotspots for turtles? How can we translate these data into positive outcomes? Are managers and policy makers prepared to make decisions on an $n = 8.5$ (our overall average number of conspecific turtles per study) or on an $n = 9.9$ turtles (our average since 2005)? Are we presenting results in a clearly understandable format and suggesting suitable management changes? Are tracking data perhaps simply one investigative strand that needs to be integrated with multiple lines of evidence to generate a synthetic understanding before the long slog of effecting change can begin? Additionally, unless molecular profiling progresses to a point where individuals can be individually identified for very little cost with no time delay, there is likely always going to be a valid research need to permanently or semi-permanently mark study individuals. This facilitates upfront hypothesis testing (e.g. behaviour of neophytes versus remigrants) and acts as post-hoc backup of identity following loss of satellite tags (Sherrill-Mix & James 2008).

We suggest that the major scientific breakthroughs in this field are likely to come from increased sample

size, most easily attained through data-sharing and through inter-disciplinary synergy with others such as ecological modelers, oceanographers, statisticians and fisheries scientists. Such partnerships will help us to progress from the qualitative to the quantitative with regard to integration of movements with dynamic environmental variables, both physical and anthropogenic e.g. fishing effort. It is time for us all to embrace such approaches, perhaps facilitated through mechanisms such as the clearing house outlined above (Coyné & Godley 2007). In addition, with appropriate intellectual safeguards, data can (and we suggest should) be shared for management purposes prior to the production of scientific papers (e.g. Turtle Expert Working Group 2007).

In closing, we hope that we have highlighted the obvious need for a clearer strategy to address inadequate sample size and the species, life stage and geographic imbalance of many past studies. We need to participate in a shift in the way we carry out our work for maximal benefit to ensure we can counter any allegations of a 'tagging reflex' (Mrosovsky 1983). Finally, it is our observation that much of the tracking work to date has been funded and acted upon in such a manner that has so far failed to ensure translation of the research into tangible outputs and management benefits. It is the responsibility of all who purport to be carrying out research in the name of sea turtle conservation to work to have our research published, disseminated, built upon and translated into positive conservation action.

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Appendix 1. Summaries of published studies of satellite tracking in 6 species of marine turtles. Ocean: ocean basin (W: west; C: central; E: eastern); F: adult female; M: adult male; J: juvenile; U: sex/maturity status unknown

Ocean	Country (state/s)	F	M	J	U	Total	Reference
Loggerhead turtle <i>Caretta caretta</i>							
W Atlantic	USA (Georgia)	8	0	0	0	8	Stoneburner (1982)
W Atlantic	USA (Mississippi)	1	0	0	0	1	Timko & Kolz (1982)
Mediterranean	Greece	1	0	0	0	1	Hays et al. (1991)
Atlantic	USA (Texas)	0	0	4	0	4	Renaud & Carpenter (1994)
Indian	South Africa	4	0	0	0	4	Papi et al. (1997)
W Pacific	Japan	2	1	0	0	3	Sakamoto et al. (1997)
E Pacific	Mexico	0	0	1	0	1	Nichols et al. (2000)
E Pacific	High seas	0	0	9	0	9	Polovina et al. (2000)
W Pacific	Australia (Queensland)	6	0	0	0	6	Limpus & Limpus (2001)
Mediterranean	Italy	3	1	0	0	4	Bentivegna (2002)
W Pacific	Japan	0	1	0	0	1	Hatase et al. (2002a)
W Pacific	Japan	5	0	0	0	5	Hatase et al. (2002b)
W Atlantic	USA (Georgia)	5	0	0	0	5	Plotkin & Spotila (2002)
W Atlantic	USA (Florida)	4	0	0	0	4	Dodd & Byles (2003)
Mediterranean	Northern Cyprus	5	0	0	0	5	Godley et al. (2003a)
Indian	South Africa	11	0	0	0	11	Hays et al. (2003b)
Indian	South Africa	5	0	0	0	5	Luschi et al. (2003b)
E Pacific	USA (Hawaii)	0	0	0	2	2	Polovina et al. (2003)
E Pacific	USA (Hawaii)	0	0	40	0	40	Chaloupka et al. (2004a)
W Pacific	Japan	2	0	0	0	2	Hatase & Sakamoto (2004)
E Pacific	High seas	3	0	23	0	26	Polovina et al. (2004)
Mediterranean	Spain (Balearic Islands)	0	0	5	0	5	Cardona et al. (2005)
Mediterranean	Italy	0	0	1	0	1	Hochscheid et al. (2005)
Mediterranean	Italy, Tunisia	0	0	0	13	13	Hochscheid et al. (2005)
W Atlantic	USA (New York)	0	0	3	0	3	Morreale & Standora (2005)
W Atlantic	UK (Cayman)	3	0	0	0	3	Blumenthal et al. (2006)
E Atlantic	Spain	0	0	2	0	2	Cejudo et al. (2006)

Appendix 1. continued

E Atlantic	Cape Verde	10	0	0	0	10	Hawkes et al. (2006)
Indian	South Africa	8	0	0	0	8	Luschi et al. (2006)
W Pacific	High seas	0	0	43	0	43	Polovina et al. (2006)
Mediterranean	Italy	3	1	4	0	4	Bentivegna et al. (2007)
Mediterranean	Northern Cyprus	10	0	0	0	10	Broderick et al. (2007)
Mediterranean	Cyprus	2	0	0	0	2	Fuller et al. (2008)
W Atlantic	USA (North Carolina)	12	0	0	0	12	Hawkes et al. (2007)
W Atlantic	USA (North Carolina)	0	0	30	0	30	McLellan & Read (2007)
Mediterranean	Spain (Balearic Islands)	0	0	10	0	10	Revelles et al. (2007a)
Mediterranean	Spain (Balearic Islands)	0	0	10	0	10	Revelles et al. (2007b)
Mediterranean	Greece	6	0	0	0	6	Zbinden et al. (2007)
Green turtle <i>Chelonia mydas</i>							
E Pacific	USA (Hawaii)	3	0	0	0	3	Anonymous (1993)
Indian	Malaysia	1	0	0	0	1	Anonymous (1994)
W Pacific	Malaysia	1	0	0	0	1	Papi et al. (1995)
W Pacific	Malaysia	4	0	0	0	4	Luschi et al. (1996)
C Atlantic	UK (Ascension)	6	0	0	0	6	Luschi et al. (1998)
Indian	Australia (West Australia)	1	0	0	0	1	Spring & Pike (1998)
C Atlantic	UK (Ascension)	11	0	0	0	11	Hays et al. (1999)
W Pacific	Taiwan	8	0	0	0	8	Cheng (2000)
Indian	Malaysia	8	0	0	0	8	Liew et al. (2000)
C Atlantic	UK (Ascension)	15	0	0	0	15	Papi et al. (2000)
C Atlantic	UK (Ascension)	15	0	0	0	15	Åkesson et al. (2001)
C Atlantic	UK (Ascension)	0	2	0	0	2	Hays et al. (2001a)
C Atlantic	UK (Ascension)	1	0	0	0	1	Hays et al. (2001b)
C Atlantic	UK (Ascension)	12	0	0	0	12	Hays et al. (2001c)
C Atlantic	UK (Ascension)	5	0	0	0	5	Hays et al. (2001d)
C Atlantic	UK (Ascension)	18	0	0	0	18	Luschi et al. (2001)
Mediterranean	North Cyprus	6	0	0	0	6	Godley et al. (2002)
C Atlantic	UK (Ascension)	7	0	0	0	7	Hays et al. (2002)
W Pacific	China (Guangdong)	3	0	0	0	3	Song et al. (2002)
W Pacific	China (Guangdong)	3	0	0	0	3	Wang et al. (2002)
C Atlantic	UK (Ascension)	18	0	0	0	18	Åkesson et al. (2003)
W Pacific	China (Hong Kong)	1	0	0	0	1	Chan et al. (2003)
W Atlantic	Brazil (Ceara)	2	0	6	0	8	Godley et al. (2003b)
C Atlantic	UK (Ascension)	6	0	0	0	6	Hays et al. (2003a)
Indian	France (La Reunion, Tromelin, Moheli)	2	0	6	0	8	Pelletier et al. (2003)
Mediterranean, W Pacific, E Pacific, C Atlantic	Cyprus, Malaysia, Mexico, UK (Ascension)	31	0	0	0	31	Hays et al. (2003b)
W Pacific	American Samoa	7	0	0	0	7	Craig et al. (2004)
W Pacific	Australia (Northern Territory)	20	0	0	0	20	Kennett et al. (2004)
E Pacific	Costa Rica	0	0	1	0	1	Swimmer et al. (2006)
W Atlantic	Costa Rica	10	0	0	0	10	Troëng et al. (2005b)
Indian	Thailand	1	0	0	0	1	Yasuda & Arai (2005)
W Atlantic	UK (Cayman Islands)	7	0	0	0	7	Blumenthal et al. (2006)
Indian	France (Europa)	3	0	0	0	3	Girard et al. (2006)
W Pacific	Japan	4	0	0	0	4	Hatase et al. (2006)
Indian	Thailand	7	0	0	0	7	Yasuda et al. (2006)
Mediterranean	North Cyprus	10	0	0	0	10	Broderick et al. (2007)
Indian	France (Mayotte)	20	0	0	0	20	Luschi et al. (2007)
E Pacific	Ecuador (Galapagos)	12	0	0	0	12	Seminoff et al. (2008)
Mediterranean	Cyprus	4	0	0	0	4	Fuller et al. (2008)
Leatherback turtle <i>Dermochelys coriacea</i>							
W Atlantic	France (French Guiana)	1	0	0	0	1	Duron-Dufrenne (1987)
W Atlantic	USA (USVI)	1	0	0	0	1	Keinath & Musick (1993)
E Pacific	Costa Rica	8	0	0	0	8	Morreale et al. (1996)
E Pacific	Mexico (Michoacán)	9	0	0	0	9	Eckert & Sarti (1997)
Indian, E Atlantic	South Africa (KwaZulu-Natal)	1	0	0	0	1	Hughes et al. (1998)
Indian	South Africa (KwaZulu-Natal)	3	0	0	0	3	Luschi et al. (2003b)
E Pacific, Indian	Mexico, South Africa	8	0	0	0	8	Hays et al. (2003b)
W Atlantic	France (French Guiana)	12	0	0	0	12	Ferraroli et al. (2004)

Appendix 1. continued

W Atlantic	Grenada	4	0	0	0	4	Hays et al. (2004a)
W Atlantic	Grenada	9	0	0	0	9	Hays et al. (2004b)
W Atlantic	Puerto Rico	3	0	0	0	3	Lutcavage et al. (1999)
W Atlantic	Canada	0	11	0	0	11	James et al. (2005a)
W Atlantic	Canada	9	3	3	0	15	James et al. (2005b)
W Atlantic	Canada	21	11	6	0	38	James et al. (2005c)
W Atlantic	Grenada	6	0	0	0	6	McMahon et al. (2005)
W Atlantic	Trinidad and Tobago	9	0	0	0	9	Eckert (2006)
W Atlantic	USA (Florida)	10	0	0	0	10	Eckert et al. (2006)
W Atlantic	Canada (Nova Scotia)	0	0	0	0	3	Flemming et al. (2006)
W Atlantic	France (French Guiana)	1	0	0	0	1	Gaspar et al. (2006)
W Atlantic	Grenada	9	0	0	0	9	Hays et al. (2006)
W Atlantic	Canada	3	2	0	0	5	James et al. (2006a)
W Atlantic	Canada	0	0	0	15	15	James et al. (2006b)
W Atlantic	Canada	8	3	3	0	14	Jonsen et al. (2006)
W Atlantic	Grenada	9	0	0	0	9	McMahon & Hays (2006)
Indian	South Africa (KwaZulu-Natal)	4	0	0	0	4	Sale et al. (2006)
W Atlantic	Grenada	1	0	0	0	1	Myers et al. (2006)
Indian	South Africa	11	0	0	0	11	Luschi et al. (2006)
W Atlantic	Grenada	9	0	0	0	9	Bradshaw et al. (2007)
W Pacific	Indonesia	9	0	0	0	9	Benson et al. (2007a)
W Pacific	Papua New Guinea	19	0	0	0	19	Benson et al. (2007b)
W Pacific	Indonesia	10	0	0	0	10	Hitipeuw et al. (2007)
E Pacific	USA (California)	0	1	0	0	1	Seminoff & Dutton (2007)
W Atlantic	France (French Guiana)	5	0	0	0	5	Fossette et al. (2008)
W Atlantic, E Atlantic	France (French Guiana), Gabon, Grenada, Suriname	37	0	0	0	37	Georges et al. (2007)
W Atlantic	Canada	0	0	0	5	5	Jonsen et al. (2007)
W Atlantic	Costa Rica	2	0	0	0	2	Troëng et al. (2007)
E Atlantic	Gabon	7	0	0	0	7	Witt et al. (in press)
W Atlantic	Eire	1	1	0	0	2	Doyle et al. (2008)
W Atlantic	Canada	20	8	14	0	42	Sherrill-Mix & James (2008)
Hawksbill turtle <i>Eretmochelys imbricata</i>							
W Atlantic	Barbados	4	0	0	0	4	Horrocks et al. (2001)
W Atlantic	Costa Rica	2	0	0	0	2	Troëng et al. (2005a)
na(captivity)	Thailand	0	0	2	0	2	Yasuda & Arai (2005)
Indian	Cocos Islands	0	0	1	0	1	Whiting & Koch (2006)
W Pacific	Australia (Northern Territory)	2	0	0	0	2	Whiting et al. (2006)
W Atlantic	Puerto Rico	7	8	0	0	15	van Dam et al. (2008)
Kemp's ridley turtle <i>Lepidochelys kempii</i>							
W Atlantic	USA (Louisiana)	1	0	0	0	1	Renaud et al. (1996)
W Atlantic	USA (Georgia)	1	0	0	0	1	Gitschlag et al. (1996)
W Atlantic	USA (Texas, Louisiana, North Carolina)	0	0	0	57	57	Renaud & Williams (2005)
W Atlantic	Mexico (Tamaulipas)	0	11	0	0	11	Shaver et al. (2005)
W Atlantic	USA (New York)	0	0	12	0	12	Morreale & Standora (2005)
W Atlantic	USA (Florida)	0	0	6	0	6	Schmid & Witzell (2006)
W Atlantic	USA (Texas)	28	0	0	0	28	Shaver & Rubio (2008)
W Atlantic	USA (Texas)	6	0	0	0	6	Seney & Landry (2008)
Olive ridley turtle <i>Lepidochelys olivacea</i>							
E Pacific	Costa Rica	12	0	0	0	12	Plotkin et al. (1995)
E Pacific	High seas	0	1	0	0	1	Beavers & Cassano (1996)
E Pacific	Costa Rica	0	11	0	0	11	Plotkin et al. (1996)
E Pacific	Costa Rica	21	0	0	0	21	Plotkin (1998)
E Pacific	USA (Hawaii), Costa Rica	0	0	8	0	8	Swimmer et al. (2002)
E Pacific	USA (Hawaii)	0	0	0	2	2	Polovina et al. (2003)
C Pacific	High Seas	0	0	10	0	10	Polovina et al. (2004)
E Pacific	Costa Rica	0	0	1	13	14	Swimmer et al. (2006)
Indian	India (Orissa)	4	0	0	0	4	Pandav & Choudhury (2006)
Indian	India (Orissa)	4	0	0	0	4	Sasamal & Panigraphy (2006)
W Pacific	Australia (Northern Territory)	4	0	0	0	4	McMahon et al. (2007)
W Pacific	Australia (Northern Territory)	8	0	0	0	8	Whiting et al. (2007)