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Global research priorities for sea turtles: informing management and conservation in the 21st century

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ABSTRACT: Over the past 3 decades, the status of sea turtles and the need for their protection to aid population recovery have increasingly captured the interest of government agencies, non-governmental organisations (NGOs) and the general public worldwide. This interest has been matched by increased research attention, focusing on a wide variety of topics relating to sea turtle biology and ecology, together with the interrelations of sea turtles with the physical and natural environments. Although sea turtles have been better studied than most other marine fauna, management actions and their evaluation are often hindered by the lack of data on turtle biology, human–turtle interactions, turtle population status and threats. In an effort to inform effective sea turtle conservation a list of priority research questions was assembled based on the opinions of 35 sea turtle researchers from 13 nations working in fields related to turtle biology and/or conservation. The combined experience of the contributing researchers spanned the globe as well as many relevant disciplines involved in conservation research. An initial list of more than 200 questions gathered from respondents was condensed into 20 metaquestions and classified under 5 categories: reproductive biology, biogeography, population ecology, threats and conservation strategies.

KEY WORDS: Sea turtles · Global priorities · Research · Conservation

INTRODUCTION

Over the past 30 years, the status of sea turtles and the need for their protection and population recovery have increasingly captured the interest of many government agencies, non-governmental organisations (NGOs) and the general public (Raustiala 1997, Wright & Mohanty 2006, Campbell 2007). This interest has been matched with increased research attention, which focuses on a wide variety of topics relating to sea turtle biology and conservation, including the interrelations with the physical and biological environments in which they live, and the human dimensions associated with these elements (Avise 2007, Campbell & Cornwell 2008). Indeed, for the last 3 decades there has been an annual symposium dedicated to sea turtle biology and conservation; recently the symposium has had roughly 300 presentations annually, with attendees from over 80 countries across 6 continents (see www.seaturtlesociety.org). The growing body of peer-reviewed literature has equally reflected the increase in sea turtle research, with the ISI Web of Science reporting 813 research items from 2006 to 2009 in a search for 'sea turtle' or 'marine turtle' and 'conserva-

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tion'. However, despite being well studied in comparison to many other marine fauna, management actions and their evaluation for sea turtles are still frequently hindered by lack of key data on turtle biology, human–turtle interactions, turtle population status and environmental threats (e.g. Bjorndal 1999, Amorocho 2002).

Given the heightened interest in sea turtle research, monitoring and management, it is timely to seek opinion from researchers about the most important research questions in order to assist sea turtle conservation. Thus, in a similar fashion to Sutherland et al. (2006, 2009), the opinions of researchers working in fields related to sea turtle biology, conservation and/or their management were assembled into a list of 20 priority questions (Box 1) that can be used to guide future research efforts. This is by no means the first attempt to collate and prioritise pertinent research questions to assist sea turtle conservation, as similar efforts at local, regional and international scales have occurred (IUCN 1995, Bellagio Steering Committee 2004, Mast et al. 2004, 2005, 2006, CPPS 2006). However, several of the early efforts that developed priority research themes were valuable at the time, but were too focused on species or regions, and many are now out of date, especially given the surge in published research, technological advances and the evolving challenges facing sea turtle conservation. The present paper reflects the ideas from an unprecedented collection of researchers from a broad range of backgrounds, and is the first such effort to detail the most relevant conservation-informative research questions in the published literature with regard to sea turtles. Through the listing process we aim to move research and management forward by focusing effort and expertise on what are communally held as priority research questions for sea turtle conservation.

Box 1. Five priority research categories comprising 20 meta-questions relating to sea turtle research and conservation

1. Reproductive biology
1.1. What are the factors that underpin nest site selection and behaviour of nesting turtles?
1.2. What are the primary sex ratios being produced and how do these vary within or among populations and species?
1.3. What factors are important for sustained hatchling production?
2. Biogeography
2.1. What are the population boundaries and connections that exist among rookeries and foraging grounds?
2.2. What parameters influence the biogeography of sea turtles in the oceanic realm?
2.3. Where are key foraging habitats?
3. Population ecology
3.1. Can we develop methods to accurately age individual turtles, determine a population's (or species') mean age-at-maturity, and define age-based demography?
3.2. What are the most reliable methods for estimating demographic parameters?
3.3. How can we develop an understanding of sea turtle metapopulation dynamics and conservation biogeography?
3.4. What are the past and present roles of sea turtles in the ecosystem?
3.5. What constitutes a healthy turtle?
4. Threats
4.1. What will be the impacts from climate change on sea turtles and how can these be mitigated?
4.2. What are the major sources of fisheries bycatch and how can these be mitigated in ways that are ecologically, economically and socially practicable?
4.3. How can we evaluate the effects of anthropogenic factors on sea turtle habitats?
4.4. What are the impacts of pollution on sea turtles and their habitats?
4.5. What are the etiology and epidemiology of fibropapillomatosis (FP), and how can this disease be managed?
5. Conservation strategies
5.1. How can we effectively determine the conservation status of sea turtle populations?
5.2. What are the most viable cultural, legal and socio-economic frameworks for sea turtle conservation?
5.3. Which conservation strategies are working (have worked) and which have failed?
5.4. Under what conditions (ecological, environmental, social and political) can consumptive use of sea turtles be sustained?

METHODS

Four of the authors of this paper (M.H., B.J.G., M.H.G. and J.A.S.) initiated the study. On ISI Web of Knowledge we searched the years 2006 to 2009 for '(SEA TURTLE or MARINE TURTLE) and CONSERVATION' (accessed 4 April 2009). We analyzed the resulting output (813 papers) by author. Among the authors of these papers, 131 had published more than 3 relevant studies over the period. To maximise the geographic/technical experience of panel members, each of the 4 initiating authors independently selected 20 authors from this list, with a key aim being to maximise representation. These names were combined into a new list and those selected by more than 2 of the initiating authors were invited to contribute (n = 40). A total of 35 researchers contributed to this effort, with each proposing up to 10 ranked 'research questions to assist effective sea turtle conservation over the next 10 years'. Responses were 'blind', as questions and compilations were not shared with the wider group until all questions had been submitted.

The 35 participants (10 females and 25 males) are based in 13 countries representing experience in all oceanic basins where sea turtles exist (Eastern Pacific 12%, Central Pacific 9%, Western Pacific 11%, Eastern Atlantic (including Mediterranean) 17%, Central Atlantic 13%, Western Atlantic 21%, Indian Ocean 7% and Southern Ocean 10%). Participants contributed a mean of 8.5 research questions (SD = 2.1, range = 4 to 10), producing a total of 347 questions. M.H., B.J.G., M.H.G. and J.A.S. grouped the questions first into themes/subthemes (n = 14/46) and then into 23 metaquestions. The wording of each metaquestion was based on the most common ideas that occurred in individual questions. In most cases, a submitted question clearly fell into a single theme; with questions that bridged 2 or more themes, a best effort was made to determine the dominant theme of the question—where it was then placed. After compilation into thematic groupings, the final list of metaquestions was circulated to all 35 participants for consensus, and the final 20 questions were selected.

After reaching consensus, teams of 2 or 3 authors drafted the supporting text for the description of each metaquestion. These topical descriptions were written with a focus on those most commonly occurring ideas within each theme while also trying to capture all ideas presented by individual questions. For ease of reporting, the 20 metaquestions were organised into 5 categories after consultation with coauthors (Box 1): (1) reproductive biology, (2) biogeography, (3) population ecology, (4) threats, and (5) conservation strategies. The text of the sections discussed in 'Results' has been left as close as possible to the original provided by the author groups. Metaquestions are not ranked or listed relative to each other in terms of importance.

RESULTS

1. Reproductive biology

This category focuses on research questions related to sea turtles at the nesting beach. Because hatchling production relies on sea turtles laying clutches of eggs in a section of beach above the mean high tide line and because embryo development and phenotype are strongly linked to sand temperatures, beach ecosystems are a critical component of sea turtle lifecycles.

1.1. What are the factors that underpin nest site selection and behaviour of nesting turtles?

Although the minimum criteria for habitat that is suitable for nesting and hatchling production were laid out nearly 2 decades ago (Mortimer 1990), the underpinnings of nest site selection by sea turtles largely remain a mystery. The related questions submitted were linked to breeding behaviour of both adult male and female turtles, with an emphasis on (1) the precision of natal homing, (2) the factors (biotic and abiotic) driving where and when turtles lay their clutches, and (3) what management strategies would help protect or enhance the suitability of nesting habitat for sea turtles. Although natal homing behaviour in both male and female turtles is supported by genetic analyses for nearly all species (Meylan et al. 1990, FitzSimmons et al. 1997), studies have highlighted the flexibility of this behaviour among and within species (Dutton et al. 1999, Shanker et al. 2004, Hilterman & Goverse 2007). Improving our understanding of the level of plasticity in natal homing (see Section 2.1) would assist management, particularly within the context of adaptation and resilience to global climate change and/or coastal development (see Section 4.1), and the possible spatio-temporal changes in availability of suitable nesting habitats for sea turtles (Hamann et al. 2007a, Hawkes et al. 2009). For nest site selection, past studies have indicated that species tend to prefer specific zones of the beach (e.g. Whitmore & Dutton 1985, Hays et al. 1995, Dobbs et al. 1999), although more is known about what specific cues deter nesting than those that encourage it (Miller et al. 2003). Recent studies suggest that individual turtles tend to repeatedly nest at specific sites, although overall nest location may vary across a population (Kamel & Mrosovsky 2004, 2005) and there is likely to be species- and region-specific variation in the magnitude of nest site fidelity (Pfaller et al. 2009). Manipulation of the nesting beach is linked to changes in patterns of placement of sea turtle nests (Salmon et al. 1995, Wetterer et al. 2007), but rarely are these changes linked to increased hatchling production. We need a better understanding of how nesting females respond to situations in which anthropogenic or natural factors render their beaches unsuitable for nesting, and in particular of the limits to their ability to locate an alternate nesting site. To date, management strategies to improve nesting habitat have focused on responding to perceived threats, such as control of nest predators (Engeman et al. 2005), removal of non-native vegetation (Schmid et al. 2008), reduction of artificial lighting visible on the beach (Bertolotti & Salmon 2005), and artificially widening beaches as part of erosion control (Montague 2008). Greater insight into why turtles breed successfully at specific beaches and also specific zones of the beach could lead to management strategies that maximise hatchling production in particular areas. Spatial models (Santana-Garcon et al. 2010) and experimental manipulations (Caut et al. 2006) appear likely routes towards attaining this goal.

1.2. What are the primary sex ratios being produced and how do these vary within or among populations and species?

All species of sea turtle have temperature-dependent sex determination (TSD), with female offspring produced at higher temperatures (Yntema & Mrosovsky 1980). Reviews of the peer-reviewed literature (Wibbels 2003, Hawkes et al. 2009) have summarised studies on sex ratios of hatchling sea turtles; most have reported female-biased sex ratios. The latest review highlighted that overall, relatively few robust datasets on hatchling sex ratios are available that are not laboratory based or based on proxies such as sand temperature or incubation duration (Hawkes et al. 2009). A major reason for the paucity of data is that the only reliable method of sexing hatchlings currently available is histological examination of the gonads from dead hatchlings. Given that most sea turtle species are of conservation concern, studies requiring euthanasia are often hard to justify on an ethical basis, and as a result are generally based on a small number of hatchlings (Mrosovsky et al. 2002), or in the case of sampling from naturally dead hatchlings, there are issues with sample size and biased results (Broderick et al. 2000). As an alternative, studies have focused on estimating hatchling sex ratios from sand temperature (Glen & Mrosovsky 2004, Hawkes et al. 2007), clutch temperature (Godley et al. 2001), incubation duration (driven by temperature; Marcovaldi et al. 1997, Zbinden et al. 2007) and by analysing hormone levels from amniotic fluids (Gross et al. 1995). A recent advance has been the adaptation of surgical laparoscopy to determine sex of post-hatchling turtles (2.5 to 6 mo old; Wyneken et al. 2007). Although there are technical and logistic challenges associated with it, the method has been applied to a variety of species, and data from loggerheads have been used in population models (Wyneken et al. 2003). Therefore, continuing to develop and refine methods to reliably and non-lethally sex hatchlings is crucial to further elucidate the variation that exists and to allow an assessment of the capacity for adaptation to climate change (see Section 4.1). A more indirect approach to assessing sex ratio is to evaluate the juvenile-through-subadult portion of the population on the assumption that it represents a condensation of many years of hatchling production. This can be done by capturing turtles at their foraging habitats and determining sex by using laparoscopy (Limpus et al. 1994), sex steroid concentrations (Owens et al. 1978) and possibly ultrasound (Blanvillain et al. 2008). Whether or not sex ratios persist through age classes is likely to vary within and between species, and while data on hatchling sex ratios are limited, there are even fewer data on sex ratios in other age classes for most species and populations (Limpus 2008a, Conant et al. 2009). If there is excessive feminisation of hatchling sex ratios brought about by climate change, this may result in reduced fertility rates (but see Bell et al. 2009) or, through random drift and loss of genetic variation, compromise a population's ability to respond to selection pressures. As a result, it may be necessary to investigate the development and implementation of mitigation methods to reduce negative impacts in some populations (but see Girondot et al. 1998). Current suggested mitigation techniques include increasing shade on beaches or relocating clutches to sites with cooler temperatures, either within a beach, or at new sites. Pros and cons of these techniques are likely to vary within and among species and locations. Another area worthy of future investigation is to identify new nesting areas, particularly if current nesting sites become unsuitable due to development or climate-driven change (Hamann et al. 2007a, Poloczanska et al. 2009). Identifying these new sites however requires an adequate understanding of factors that are important for nest site selection (see Section 1.1) as well as of factors that determine embryonic development, sex, hatchling dispersal and plasticity of natal homing.

1.3. What factors are important for sustained hatchling production?

Improving knowledge of embryology and hatchling production is a fundamental component of nesting beach management. Knowledge of embryology is needed to improve understanding of hatchling fitness and phenotype, which will become more important with climate change (see Section 4.1). Hatchling production is important because it is a fundamental component of population models (see Section 3.3). Although hatchling production has been a popular area of research over the last 4 decades (Miller 1985, Standora & Spotila 1985, Ackerman 1997), a substantial proportion of research to date has focused on aspects of sex determination (see Section 1.2), and many research and monitoring gaps remain. For example, continued collection of population-scale data on hatching success, fertility rates, egg predation and sex ratios is needed to understand variation in hatchling production. Key areas for future study include embryology (Bell et al. 2004), experimental studies that elucidate environmental effects, including pollutants (see Section 4.4), on embryology, physiology and endocrinology of developing eggs and hatchlings (Hamann et al. 2007b, Booth 2009), developing and evaluating a reliable estimate of hatchling fitness, understanding endocrine influences on embryology, and furthering investigations on nest site selection (see Section 1.1) and its role in hatchling production. Continuing research into these topics will enhance the ability of scientists and managers to better understand the adaptive capacity and resilience of sea turtles to climate change (see Section 4.1) and coastal zone development (see Sections 4.3 and 4.4) and to better model and manage directed and incidental take.

2. Biogeography

Sea turtles are migratory, often travelling great distances between natal beaches and foraging areas, and/or between foraging areas and reproductive sites. Recent technological advances in genetics, telemetry, remote sensing, and biochemical markers are increasing our knowledge of the distribution and behaviour of sea turtles in offshore waters, although many information gaps remain.

2.1. What are the population boundaries and connections that exist among rookeries and foraging grounds?

For many years, sea turtle researchers have recognised the primary importance of defining appropriate 'management units' (MUs). MUs are population segments that exhibit unique demography and can usually be distinguished genetically, behaviourally, or geographically (Moritz 1994) and are the units to which conservation efforts should be directed. Because sea turtles occupy broad geographic ranges including nesting and foraging areas utilised by adults, and in some cases geographically distinct ontogenetic habitats (Musick & Limpus 1997), defining the scale of MUs is challenging. Furthermore, sea turtles exhibit complex population structures often characterised by sex-biased gene flow among nesting stocks, and varying degrees of overlap during post-hatchling migrations, in developmental habitats, and on adult foraging grounds (see Bowen & Karl 2007 for review). Knowledge of the complex relationships among various nesting sites and foraging/nursery areas is crucial for understanding population-level impacts of anthropogenic threats, as well as for designing effective conservation responses to these threats (Bolker et al. 2007). Despite the challenges of collecting data, tremendous advances have been achieved over the past 2 decades to characterise MUs at various spatial scales. A variety of tools including genetic analyses with mitochondrial and nuclear markers (mtDNA sequences, microsatellite polymorphisms, and single nucleotide polymorphisms [SNPs]), mark-recapture studies, and satellite telemetry have permitted determination of nesting and breeding genetic stocks, of mixed genetic stocks on foraging grounds, and of geographic distributions of sea turtle populations around the world (Meylan et al. 1990, FitzSimmons et al. 1997, Polovina et al. 2004, Carreras et al. 2006, Dethmers et al. 2006, Dutton et al. 2008, Godley et al. 2008). Integration of these tools, especially when supplemented with information on the spatial extent and severity of threats plus oceanography and environmental drivers, holds exciting potential for successfully defining MUs for sea turtles globally, thereby facilitating design and implementation of effective, targeted, conservation strategies.

2.2. What parameters influence the biogeography of sea turtles in the oceanic realm?

Questions in this section were divided into the following general topics: (1) geographic location of the oceanic 'hotspots', whether they be migratory pathways or foraging areas; (2) demography of turtles in the oceanic stages, including the duration of oceanic juvenile stages and the cues for turtles to leave the oceanic zone; and (3) physical and biological oceanographic factors driving sea turtle distribution patterns. The oceanic zone, where water depths are greater than 200 m, is a developmental habitat for all species of sea turtles except flatback turtles and is also an adult foraging habitat for leatherback, olive ridley and loggerhead turtles (Hatase et al. 2002a, Bolten 2003, Hawkes et al. 2006, Reich et al. 2007, 2010). The classic paper by Carr (1986) introduced the importance of the oceanic zone as a developmental habitat. Movements of turtles into and out of the oceanic zone are primarily the result of ontogenetic migrations (Bowen et al.1995, Bolten et al. 1998, Boyle et al. 2009, Monzón-Argüello et al. 2009) or reproductive migrations (Hays et al. 2001, James et al. 2005a, Benson et al. 2007a,b). However, recent studies using stable isotope analyses and satellite telemetry suggest that there may be repeated movements between neritic and oceanic habitats (Hatase et al. 2002a,b, Hawkes et al. 2006, McClellan & Read 2007). Demographic parameters derived from empirical studies for oceanic juvenile sea turtles come primarily from loggerhead turtles in the North Atlantic (Bjorndal et al. 2000, 2003a,b, Sasso & Epperly 2007). Bolten (2003) suggested that the selective advantage of ontogenetic habitat shifts from oceanic to neritic zones for juvenile loggerhead turtles may be a maximisation of growth rates. Some oceanic hotspots for sea turtles, particularly juvenile stages, have been identified, and these include sites in the northeast Atlantic (Carr 1986, Bolten et al. 1993), northwest Atlantic/Grand Banks of Canada (Witzell 1999), Mediterranean (Aguilar et al. 1995, Casale

2008), southwest Atlantic/Rio Grande Rise (Sales et al. 2008), North Central Pacific (Wetherall et al. 1993, Balazs & Pooley 1994), southeast Pacific (Alfaro Shigueto et al. 2008) and eastern Pacific (Peckham et al. 2007). Primary physical parameters influencing the spatial distribution of oceanic sea turtles are currents and associated fronts and eddies, bathymetry (particularly seamounts), sea surface temperature and magnetic field (Polovina et al. 2000, 2004, 2006, Lohmann & Lohmann 2003, Luschi et al. 2003, Revelles et al. 2007, Santos et al. 2007, Kobayashi et al. 2008). Currents in particular are likely to influence neonatal dispersal. Biological parameters influencing spatial distribution include the distribution and abundance of prey (primarily gelatinous zooplankton) and possibly predators (Polovina et al. 2000, 2001, 2004, 2006, Hays et al. 2001, 2004, James et al. 2005b, Heithaus et al. 2008, Kobayashi et al. 2008). Anthropogenic disturbances to oceanic food webs and habitats may affect the distribution and abundance of sea turtles (Bjorndal 1997, Mrosovsky et al. 2009, Richardson et al. 2009). Fisheries bycatch, marine debris and pollution are important sources of mortality and may affect sea turtle distribution (Lewison & Crowder 2007, Mrosovsky et al. 2009). Although we have learned much since Carr's (1986) paper, we have only just begun to understand the biology of the oceanic stages. We are a long way from our goal of developing predictive models of sea turtle distribution patterns in the oceanic zone.

2.3. Where are key foraging habitats?

Marine turtles spend the vast majority of their lives in the marine environment, yet much less is known about this component of their life cycle than about the biology of females and hatchlings on the nesting beach. One way to understand where turtles are feeding is to identify the migratory routes that turtles use to move between nesting and foraging areas. Within foraging habitats it is vital to understand what oceanographic and biological parameters determine the home range of a turtle, how the space is used, and what defines an 'optimum' foraging habitat. In addition, it is important to understand the degree of site fidelity to any given foraging area, especially seemingly 'sub-optimal' areas and where, when and why high density aggregations occur. Furthermore, the foraging areas for a given nesting population can be spread over many thousands of kilometers and little is known about why turtles show fidelity to foraging areas distant to a breeding area when presumably suitable foraging areas are often located close to breeding sites, or along migration routes. Current knowledge of turtle spatial ecology comes from tag-recapture studies, and more recently, satellite telemetry (Hendrickson 1958, Limpus et al. 1992, Plotkin 2003, Godley et al. 2008). However, to date, much of this knowledge is incomplete, with many of the above questions only being addressed for some species in a few regions. Future studies should look to incorporate multiple approaches to understand spatial ecology of sea turtles, including genetics (Bowen 1995), intrinsic biomarkers such as stable isotopes (Caut et al. 2008), ultrasonic or VHF radio tags (Seminoff et al. 2002), fisheries interactions (Witt et al. 2008), animal-borne imagery (Heithaus et al. 2002), and ocean current modelling (Godley et al. in press) as accompaniments to more conventional tracking methodologies. Understanding turtle spatial ecology and identifying critical foraging habitats, high and low density areas and migratory pathways is integral in sea turtle conservation and underpins all other facets of sea turtle research. In addition, because turtles travel vast distances and cross international boundaries (Limpus et al.1992, Nichols et al. 2000), their successful management benefits from multinational co-operation (Blumenthal et al. 2006, Shillinger et al. 2008).

3. Population ecology

Sea turtles are late maturing, migratory animals; hence, their life cycles tend to be complex. It has become clear that modelling life history and population dynamics of sea turtles requires information for several life stages, particularly those at sea.

3.1. Can we develop methods to accurately age individual turtles, determine a population's (or species') mean age-at-maturity, and define age-based demography?

A fundamental aspect of sea turtle management and conservation is the use of population models as a basis for making decisions. Because it is imperative that models are based on sound science, there is a fundamental necessity for accurate data on factors such as age-at-maturity and age-based demographic parameters, as model outputs are sensitive to variations in these parameters (Heppell 1998, Heppell et al. 2000). Both age- and stage-based population models have been developed for sea turtles (Crouse et al. 1987, Chaloupka 2002, Heppell et al. 2005), although efforts to model survivorship are often hampered by our inability to accurately determine the age of live turtles. Still, such efforts require adequate distinction between demographic variability and sampling variability (Akçakaya 2000). In order to improve estimates of age, researchers have calculated both growth rates and/or age of sea turtles using skeletochronology (Zug et al. 1995, 2001, Snover 2002, Bjorndal et al. 2003b, Snover et al. 2007, Avens et al. 2009), capture-mark-recapture (Chaloupka & Limpus 1997, Higgins et al. 1997, Limpus & Chaloupka 1997, Braun-McNeill et al. 2008), and length frequency analyses (Bjorndal et al. 2000, 2001). The biases of each of these methods, as well as spatial and temporal variation in the results from each, are still being explored, and methods are being validated. However, there remains a paucity of information on age as it relates to life stage or mortality for many sea turtle populations and we have almost no measures of demographic stochasticity (Chaloupka 2002). In some areas, animals are monitored through their neritic stage to determine the length of time, and possibly age, to reproductive maturation (Limpus 2008a,b), but such studies are rare. In other cases hatchlings or small juveniles were marked and nesting beaches monitored for their return as adults — thus giving an age at first breeding (Zurita et al. 1994, Bell et al. 2007, Limpus 2008a,b); recent advances in genetic markers have the potential to provide this information (Dutton et al. 2005). New techniques to quantify or validate age estimates should greatly contribute to more powerful demographic analyses, e.g. monitoring radioactive decay rates (Andrews et al. 2009), and improved models will strengthen management decisions for the species.

3.2. What are the most reliable methods for estimating demographic parameters?

A number of submissions highlighted the need for reliable estimates of demographic parameters (e.g. clutch frequency, age-specific survivorship, male breeding rates) that could be fed into life history models. Questions fell into 2 broad groups. Approximately half dealt with the estimation of accurate parameter values for life history models, including mortality, and the rest were about the application of models. Several authors have attempted to estimate mortality in sea turtles (Chaloupka & Limpus 2005, Troëng & Chaloupka 2007) but existing models are still not capable of including all the current knowledge from life history stages. Also, improved knowledge of the distribution, variation and estimation of both clutch frequency (Broderick et al. 2003, Briane et al. 2007) and remigration interval (Hays 2000, Rivalan et al. 2005a, Tucker 2010), and technical aspects such as tag loss (Limpus 1992, Bjorndal et al. 1996, Rivalan et al. 2005b) are required for more accurate population models. Estimation of these parameters should be undertaken at the same time as estimation of capture probability and mortality, but no such model has been published. Estimates of juvenile, subadult, adult male, and non-breeding adult female mortality have not been adequately developed for most species/locations. Analyses of stranding and other mortality data sets could be part of a solution, but knowledge is needed as to the true cause of death and the probability of a dead turtle being observed (Epperly et al. 1996). To improve life history models, information is needed on hatchling production, sex ratios and their associated spatial and temporal variation, and sex-specific mortality rates (see Sections 1.2 and 1.3). Another significant gap relates to the role of male turtles within the framework of functional (or operational or adult) sex ratio and how it affects the fertilisation probability or the intrasex competition (Lovich 1996).

3.3. How can we develop an understanding of sea turtle metapopulation dynamics and conservation biogeography?

Sea turtles pose many challenges for understanding population viability and biogeography because a management unit may comprise a single regional breeding area sourced from geographically scattered foraging habitats (Musick & Limpus 1997; see Section 2.1). Demographic trends in foraging areas of the same population can vary significantly (Chaloupka & Limpus 2001), mainly due to local factors affecting somatic growth (Balazs & Chaloupka 2004, Chaloupka et al. 2004a; see Section 3.2). On the other hand, regional environmental forcing can cause spatially synchronised nesting of sea turtle populations by driving food supply dynamics in foraging habitats (Limpus & Nicholls 1988, Chaloupka 2001, Chaloupka et al. 2008a). Importantly, dispersal among nesting sites could help locally depleted subpopulations recover more quickly by immigration from nearby subpopulations and minimise local extinction risk ('rescue effect'). Thus, incorporating spatial variation in demography and nesting fidelity is essential for developing an understanding of the viability of such spatially structured stocks (Akçakaya 2000). Spatially explicit models that account for the population structure are a promising way to address this challenge for sea turtle stocks (Chaloupka 2004). Such models may also be of use for the design and application of effective marine protected areas. However, spatially explicit population models are far more demanding in terms of level of detail for specific demographic inputs (Ruckelshaus et al. 1997), which to date has limited their use for modelling sea turtle dynamics (Chaloupka 2004). For instance, little is known of foraging habitat dispersal or whether dispersal probability is a function of distance between the source-sink populations or whether it is even due to source population abundance (Chaloupka

2004). Nonetheless, developing spatially explicit models of sea turtle demography could provide a mechanistic basis for understanding the impact of climate change on sea turtle distribution (Keith et al. 2008) and the impact of direct and incidental take (see Sections 4.1, 4.2 and 4.3).

3.4. What are the past and present roles of sea turtles in the ecosystem?

For long-term conservation of sea turtles, it is important to acknowledge that they are not just charismatic, anachronistic animals, but vital species for healthy marine ecosystems. 'We envision marine turtles fulfilling their ecological roles on a healthy planet where all peoples value and celebrate their continued survival' is the vision of the IUCN Marine Turtle Specialist Group (MTSG) (www.iucn-mtsg.org/about.shtml). A recovery goal of 'fulfilling ecological roles' appropriately shifts the focus of management away from single-species recovery strategies to restoration of ecosystem function. Recent collapses of marine ecosystems, with dramatic shifts in food webs and trophic cascades, are the result of events both recent and initiated hundreds to thousands of years ago, soon after humans began to exploit marine resources (Jackson et al. 2001, Pitcher 2001, Frazier 2003, Pandolfi et al. 2003). 'Fulfilling ecological roles' is an appropriate, but challenging, goal for recovery. What were the ecological roles of sea turtles, and how many turtles are required to fulfil those roles? To answer these questions, we must combine a historical perspective with a thorough understanding of the current ecological roles of sea turtles. Quantitative models that combine results from observational and experimental studies with extrapolations to past population sizes are needed to reconstruct the roles of sea turtles in the past (Bjorndal & Jackson 2003). We need more information at all levels, from individuals to populations to ecosystems (Bjorndal 2003). The most pressing needs, however, are for studies that address the major roles of sea turtles as ecosystem engineers (Rogers 1989, Preen 1996, León & Bjorndal 2002, Moran & Bjorndal 2005, 2007, Aragones et al. 2006), nutrient transporters (Bouchard & Bjorndal 2000), consumers (Bjorndal 1997), and prey (Heithaus et al. 2007). Quantitative studies are needed; for example, we need to know how much turtles consume, not just what species (Bjorndal & Jackson 2003). Long-term studies are needed that evaluate the responses of turtles to collapsing ecosystems, such as the disintegration of coral reefs killed by bleaching, or the eutrophication of coastal seagrass pastures. Areas where sea turtle populations have not been substantially impacted by humans or have begun to recover and resume their critical roles in marine ecosystems would be valuable study sites. These studies will reveal the importance of sea turtles to the productivity of marine ecosystems, and in turn, the importance to ecological services and economic benefits that marine ecosystems provide to humans (Costanza et al. 1997).

3.5. What constitutes a healthy turtle?

A number of research topics were highlighted that are grouped under this overarching question. These focused on (1) the need for normal baseline physiological (blood work) studies for different species and geographic regions, (2) determining the effects of disease on population viability, (3) elucidating the role of environmental factors in disease and how these will be affected by climate change, (4) developing a better understanding of parasite presence in, and health impacts on, sea turtles and (5) developing a better understanding of the health status of pelagic turtles. Baseline biochemistry and haematology information is available for several sea turtle species, including loggerheads (Lutz & Dunbar-Cooper 1987, Casal & Oros 2007), green turtles (Work et al. 1998), olive ridleys (Santoro & Meneses 2007) and leatherbacks (Deem et al. 2006), although geographic, seasonal and life-stage variation in these values merit further investigation. Little is known about how these physiological parameters vary with health status, although progress is being made using immune function tests in relation to contaminant burdens in loggerheads (Keller et al. 2004) and fibropapillomatosis (FP) in green turtles (Work et al. 2001; see also Section 4.5). The determination of population effects of disease is hampered by lack of long-term disease data, one exception being the case study for FP in Hawaii (Chaloupka & Balazs 2005, Chaloupka et al. 2009). Similarly, little is known regarding the effects of environment or climate change and disease in wild turtles, although it is known that certain diseases such as FP have non-uniform geographic distribution (Work et al. 2004, see Section 4.5). There is a considerable body of literature on parasites of sea turtles that focuses mainly on systematics (Greiner et al. 1980, Aznar et al. 1998) or host response to parasites (Gordon et al. 1998), while the demographics of parasites in sea turtles are less well understood (Work et al. 2005). Importantly, little is known about the health status of oceanic turtles — mainly because this life history stage is often difficult to study. Various strategies (each with inherent limitations) have been used to assess pelagic health, including capture of oceanic immature turtles (Bjorndal et al. 2003a), use of satellite telemetry (Chaloupka et al. 2004b), or necropsy of animals subject to bycatch (Work & Balazs 2002). Finally, a consensus is needed to delineate what constitutes animals suitably healthy for release after long-term captivity or rehabilitation. Ideally, this should be decided on a case by case basis, with emphasis on a sound health history of release stock, preferably including systematic post-mortem exams of all captive mortalities at the same facility to determine causes of death and thus to minimise risks of introducing new pathogens into release habitats.

4. Threats

Sea turtles face a wide variety of threats throughout their complex life histories. More information is needed to elucidate threats and also prioritise responses to such threats which will help drive more effective mitigation strategies.

4.1. What will be the impacts from climate change on sea turtles and how can these be mitigated?

A large number of questions relating to climate change were submitted. The foci of the questions were (1) illuminating what kinds of impacts climate change will have on habitats (developmental, foraging, nesting, etc.; see Section 4.3); (2) monitoring behavioural changes of turtles in response to those changes (see Section 1.1); (3) examining the adaptive capacity of turtles to cope with climate change, and; (4) developing conservation actions in response to climate change. Although signalled as a problem more than 2 decades ago (Mrosovsky et al. 1984, Davenport 1989), recent reviews by Hamann et al. (2007a), Hawkes et al. (2009) and Poloczanska et al. (2009) have highlighted the paucity of data available to accurately predict the impacts of climate change on sea turtles. To date, published studies have looked at impacts of climate change on nesting habitat, including sea level rise (Fish et al. 2005, Baker et al. 2006, Fuentes et al. 2010a), extreme weather events (Pike & Stiner 2007), geomorphology (Fuentes et al. 2010b), as well as anthropogenic development and the management of coastal areas (Rumbold et al. 2001, Kamel & Mrosovsky 2006, Fish et al. 2008). Others have suggested that altered thermal regimes could change life history attributes, such as the timing of nesting seasons (Weishampel et al. 2004), hatchling sex ratios (Glen & Mrosovsky 2004, Fuentes et al. 2009), and survival of incubating eggs (Hawkes et al. 2007). Some researchers have looked at how climate-driven changes to ocean systems may change the locations of developmental and foraging grounds as well as impacting their quality, either negatively or positively (McMahon & Hays 2006, Chaloupka et al. 2008a, Saba et al. 2008, Witt et al. 2010). Applying recent methods of species distribution modelling using global data sets obtained through global data portals is also a promising new direction (Gilman et al. 2009). Although some researchers have emphasised promoting resilience in populations by alleviating other threats (Brander 2008, Robinson et al. 2009), less work has been done on understanding cumulative impacts or developing conservation responses to climate change, both of which are key areas for future research.

4.2. What are the major sources of fisheries bycatch and how can these be mitigated in ways that are ecologically, economically and socially practicable?

The questions on the bycatch of sea turtles focussed on (1) assessing captures and mortality of turtles per area and fishing gear, (2) understanding the impact on populations in terms of both turtle mortality and alteration of marine communities, and (3) developing technical changes to gear and working out policy strategies compatible with socio-economic needs to reduce bycatch impacts on turtle populations. Understanding the bycatch problem is difficult due to intrinsic uncertainties regarding catch levels, socio-economic factors, mortality rates and recovery rates that relate to sea turtle captures (Lewison et al. 2004a). First, the cumulative number of turtle captures cannot be accurately estimated because of (1) substantial variability in capture rates due to a myriad of possible combinations of technical and operational parameters within the same type of gear; (2) the number of unobserved vessels and limited availability of reliable fishing effort data; (3) the high levels of illegal, unregulated and unreported (IUU) fishing (Agnew et al. 2009); (4) the heterogeneous temporal, spatial, and life stage distribution of turtles; and (5) the need to consider species and populations independently (Lewison et al. 2004b, Casale 2008). Second, the mortality resulting from these captures is uncertain; mortality rates vary not only between different kinds of gear but also according to operational and technical parameters within each kind of gear (Sasso & Epperly 2006, Casale et al. 2008). Third, the assessment of the impact of this mortality on populations requires substantial knowledge of population dynamics (Heppell et al. 1999; see Sections 3.1 and 3.2). Measures to mitigate mortality have been proposed mainly as technical changes and mainly to industrial fisheries (Epperly 2003, Gilman et al. 2006, 2010, Cox et al. 2007). Tackling the bycatch of sea turtles in the multitude of small-scale fisheries typical of coastal communities is intrinsically more difficult due to the great diversity of gear used in these fisheries and to the dispersed nature of the fishing communities (Soykan et al. 2008). However, some regional and local programmes dealing specifically with small-scale fishers have begun in recent years and have yielded some noticeable results (Gallo et al. 2006, Hall et al. 2007, Peckham et al. 2007, Abe & Shiode 2009). It is uncertain to what extent specific technical measures can be effective in sea turtle conservation in the long term because they do not usually take into account other possible effects of fishing on the marine ecosystem (Pauly et al. 1998, Richardson et al. 2009). Sea turtle conservation in relation to fisheries should be based on close collaboration with fishers, and should be dealt with in a multidisciplinary way and in the context of population dynamics as well as from an ecosystem-based approach to fishery management (Costanza et al. 1998, Pikitch et al. 2004, Hall et al. 2007, Crowder et al. 2008).

A range of strategies are available that are potentially effective in lessening the impacts of fisheries on sea turtles: awareness and educational programmes, community-based conservation activities, marine protected areas, spatial/temporal closures of fisheries, national legislation and international agreements as well as gear-engineering solutions (Costanza et al. 1998, Hykle 1999, Marcovaldi et al. 2001, 2005, Campbell et al. 2002, Lewison et al. 2003, Food and Agriculture Organization of the United Nations 2005, 2009, Peckham et al. 2007, Witt et al. 2008). Many of these measures, when enacted unilaterally, are proving to be ineffective at promoting recovery of declining populations, because reducing bycatch mortality in one particular fishery or one geographic region does not address the myriad sources of mortality acting on different life stages, nor does it recognize the transboundary nature of sea turtles. A variety of policy instruments should be explored that address the sources of mortality at different life history stages. There is a need to examine the roles played by harvesters and consumers of seafood and the creation of economic incentives through market-based and other policy instruments, as opposed to command-and-control regulations, laws, and adverse incentives. Positive economic incentives help contribute toward a self-enforcing recovery strategy in a multilateral framework, emphasising cooperation and coordination among players (Dutton & Squires 2008). Regardless of policy measures, more focus on the human dimensions associated with fishing and protected species bycatch is needed to improve outcomes of management practices (Marshall 2007, Campbell & Cornwell 2008).

4.3. How can we evaluate the effects of anthropogenic factors on sea turtle habitats?

Human impacts on sea turtle habitats have been recognised for decades (Lutcavage et al. 1997), with efforts to mitigate impacts largely focused on terrestrial habitats (e.g. Witherington & Martin 1996). There has been some progress in protecting and/or restoring marine ecosystems in certain areas (e.g. Molloy et al. 2009), but direct (e.g. disrupting ocean bottom with trawl and dredge fishing gear, Watling & Norse 1998) and indirect (e.g. agricultural runoff, Diaz & Rosenberg 2008; see Section 4.4) anthropogenic impacts to marine ecosystems continue to occur (Halpern et al. 2008). Sea turtle responses to altered terrestrial and marine ecosystems have been documented in some cases, including increased temperatures of hawksbill turtle nesting sites due to deforestation (Kamel & Mrosovsky 2006) and alterations in overall diet of loggerhead turtles in response to changes in prey availability (Seney & Musick 2007). More work is needed to evaluate the condition and status of sea turtle habitats and the threats to those habitats, and to determine how degradation of these habitats affects sea turtle populations. Important research areas related to restoration and mitigation of habitats include (1) developing frameworks to assess risks from cumulative impacts (likelihood and consequences scored across threats, life stages and reproductive value), (2) determining attributes of good quality habitat as well as mechanisms to protect this habitat and to evaluate the success of such measures, and (3) consideration of future threats and their management in decision processes (such as horizontal planning, Sutherland & Woodroof 2009). The carrying capacity of a habitat is an important consideration in habitat restoration (Elliott et al. 2007). Some authors have sought to clarify historical or current carrying capacities of particular ecosystems (Jackson et al. 2001, Girondot et al. 2002), although much more work is needed in this area (see Section 3.4). Overall, improved dialogue across disciplines, and among researchers and end users, will no doubt improve the direction of research in understanding habitat alterations. Additionally, improvements in the availability of, and access to, remotely sensed data coupled with analysis tools such as GIS should provide novel insights about trends and can greatly assist in understanding the impacts of threats and effectiveness of mitigation (Grech & Marsh 2008, Grech et al. 2008).

4.4. What are the impacts of pollution on sea turtles and their habitats?

The questions submitted relating to the impact of anthropogenic pollution on sea turtles suggested the need for accurate evaluation of the effects of pollutants on development, survivorship, health, reproduction, and habitat condition/recovery. Particularly highlighted was the need to evaluate the impact of plastics and other marine debris as well as the need to parameterise sublethal effects (e.g. dietary dilution or chemical absorption; McCauley & Bjorndal 1999). Coastal and marine pollution is increasing dramatically throughout most of the world's coastal and oceanic zones (Laist et al. 1999, Derraik 2002, Moore 2008). In general, pollution in its many forms, such as sound, thermal, photic, plastics, chemical, effluent, and others, poses a threat to marine and terrestrial sea turtle habitats (see Section 4.3). Yet for most pollutants, little is known about critical thresholds and there are often few quantitative data linking them to mortality. Generally speaking, pollution of any type occurring above a certain threshold can render an area uninhabitable. At levels below that threshold, it can significantly degrade habitat quality, carrying capacity and other aspects of ecosystem function. To date, research has begun to elaborate potential effects on turtles (Hutchinson & Simmonds 1991, 1992), in particular of solid debris (Carr 1987, Bugoni et al. 2001, Tomás et al. 2002, Mrosovsky et al. 2009), discarded fishing gear (Chatto et al. 1995, Leitch 2000, Monagas et al. 2008), heavy metals (Godley et al. 1999, Maffucci et al. 2005, Guirlet et al. 2008, García-Fernández et al. 2009), organochlorine pesticides (Keller et al. 2006, Ikonomopoulou et al. 2009), and oil pollution (Chan & Liew 1988). Accumulation of debris at nesting beaches also has the potential to affect female nesting activity, embryo development and hatchling survival (Kasparek et al. 2001) and, *in extremis*, cause adult mortality (Laurance et al. 2008). Pollutants have been associated with the disease FP (Foley et al. 2005; see Section 4.5), immune system suppression (Keller et al. 2006), disruption of endocrine function (Ikonomopoulou et al. 2009), and possibly sex reversal in sea turtles (Bergeron et al. 1994, Stoker et al. 2003). Overall, the questions point towards the need for a better understanding of (1) pollution sources, and especially of non-point sources, (2) the factors influencing pollutant dispersal, (3) toxicology, (4) the vertical transfer from mother to offspring, (5) quantitative links between pollutant and impact, and (6) how to evaluate the use of incentives to minimise pollution

4.5. What are the etiology and epidemiology of FP, and how can this disease be managed?

Contributors were concerned with specifics such as (1) the environmental conditions associated with FP, (2) the cause of FP in sea turtles, (3) the mode of transmission, (4) the need to develop a more systematic assessment of global occurrence of FP in sea turtles, and (5) the need to develop robust diagnostic tests for detection of the herpesvirus (and potentially other viruses) associated with the disease. The presence of FP in sea turtles (mainly in green turtles) has been known since the 1930s (Smith & Coates 1938); however, it was not until the last 15 years that concerted efforts have been made to understand the epidemiology and pathogenesis of this disease. FP is a major cause of stranding in turtles in Hawaii (Chaloupka et al. 2008c) and Florida (Foley et al. 2005) and has a global distribution (Herbst 1994). Unfortunately, compilations of systematic surveys of FP throughout the world do not exist. The pathology of FP has been well documented in the Western Atlantic (Jacobson et al. 1989, Norton et al. 1990) and Central Pacific (Aguirre et al. 1998, Work et al. 2004), but clear geographic differences exist in manifestation of this disease in green turtles (Aguirre et al. 2002), indicating that the pathology of the disease in other regions merits investigations. FP is transmissible experimentally (Herbst et al. 1995), and strong evidence exists of its association with a herpes virus (Lackovich et al. 1999, Quackenbush et al. 2001). Unfortunately, this virus continues to be refractory to laboratory cultivation (Work et al. 2009), thus impeding the development of ante-mortem tests to assess movement of the herpes virus through turtle populations. FP does not have a homogeneous geographic distribution, implicating environmental cofactors associated with disease; however, the role of these is unknown (Work et al. 2004). The mode of transmission is also unknown, although leeches have been implicated (Greenblatt et al. 2004). In terms of recovery and population level impacts, recent analysis of a 26 yr data set in Hawaii has demonstrated that although the disease is a main cause of strandings for the population, long-term tumour regression occurs, even in advanced cases (Chaloupka et al. 2009). Moreover, the Hawaiian green turtle population is recovering despite the prevalence of the disease in the 1980s and 1990s (Chaloupka et al. 2008c). Similar long-term data analyses on recovery rates are warranted for other areas with exposure.

5. Conservation strategies

Sea turtles are susceptible to human impacts at every life stage, from egg to hatchling, juvenile to adult, thereby placing them among the most conservation-dependent of marine taxa. Designing appropriate sea turtle conservation measures relies on sound information on both the biology of sea turtles and the human social and economic dynamics that influence our ability to effect change in the status of sea turtle populations. Understanding the status of sea turtles is critical, as is knowledge of the human dimensions relating to sea turtle mortality. What constitutes effective conservation may vary with each species, and perhaps with each population. This has resulted in a variety of conservation frameworks and direct strategies for conservation that, although different across regions or localities, can be effective for promoting population recovery.

5.1. How can we effectively determine the conservation status of sea turtle populations?

The intentions, processes and outcomes of determining the status of sea turtles at species and/or population level has been debated in both the scientific and public domains since at least the mid 1980s. Central to the initial debates were the classification of hawksbill turtles (see Mrosovsky 1997a,b, 2000, Meylan & Donnelly 1999), and similar arguments for other sea turtle species have followed (see reviews by Godfrey & Godley 2008, Seminoff & Shanker 2008). The dominant issue in these reviews is whether global assessments using the existing IUCN criteria are suitable for sea turtles. Questions in the section fell into 2 broad areas: (1) improvements to life history data availability and analysis for the determination of population/species trends, and (2) determining whether it is possible and useful to conduct status assessments. Clearly, status assessments for all species will benefit from increased data collection at a variety of scales (e.g. population trajectories in foraging as well as nesting aggregations), improved modelling techniques (see Sections 2.2 and 3.3), quantifiable data on threats and assignment of threats to populations (e.g. Sections 4.1 and 5.4) and increased understanding of the social, economic and legal aspects of assessments. To improve the usefulness of status assessments the main areas for future research should include (1) how to best define and classify the extinction risk of species — this would include improved use of population 'forecast' models, a broader threat-based approach and/or development of assessments based on other demographic trends aside from adult female abundance, (2) determining the relevant spatial scale that status assessments should encompass to best enhance conservation action (see Sections 2.1 and 3.3), and (3) determining whether status assessments at global or regional scales are useful conservation tools for designing and implementing national management policy, or in assisting governments and NGOs in their international responsibilities (see Section 2.1).

5.2. What are the most viable cultural, legal and socio-economic frameworks for sea turtle conservation?

Research needs relating to the cultural, political, social, economic, and legal aspects of sea turtle conservation are many and diverse. Questions were broadly categorised as addressing (1) individual behaviour, human values and psychology, and how a better understanding of these can assist conservation education and outreach, and ultimately change human behaviour, (2) broader social, political and economic structures, and actors (e.g. private sector interests, government and non-government organisations, communities) that influence conservation, (3) the costs and benefits of different conservation strategies, and how these are distributed among impacted human populations, and (4) legal and governance structures that can effectively manage migratory species, particularly in international waters. There was some tension within the category regarding the purpose of such research, between those with a utilitarian perspective, concerned with changing values, educating the public, or generating support for conservation, and those with a critical perspective, concerned with the political, cultural, and economic consequences of conservation. Overall, research on these topics has been limited, but is increasing. Much of this has been site specific or case based, and includes research on the role of sea turtles in subsistence culture (Bliege Bird & Bird 1997, Bliege Bird et al. 2001); how conservation objectives impact on and are impacted by local communities (Campbell 1998, 1999, Bird et al. 2003, Campbell et al. 2007, Meletis & Campbell 2009); co-management of sea turtle fisheries and conservation (Granek & Brown 2005, Campbell et al. 2009); the role of science and politics in sea turtle conservation (Campbell 2002, 2007, Jenkins 2002); conflicts associated with sea turtle conservation (Margavio & Forsyth 1996, Santora 2003, Collomb 2009); the economic value of sea turtle based ecotourism (Wilson & Tisdell 2001, Tisdell & Wilson 2005a,b); and the phenomenon of volunteering for sea turtle conservation (Campbell & Smith 2006, Gray & Campbell 2007). Some of this work has been collated to address broader themes, for example, sea turtles as flagship species (Frazier 2005), international instruments (JIWLP 2002), cultural resources (Campbell 2002), direct payment schemes (Ferraro & Gjertsen 2009), and consumptive use of olive ridley sea turtles (Campbell 2007; see Section 5.4). A variety of theoretical concepts from the social sciences (common property, decision analysis, international relations, political ecology, science and technology studies, etc.) are highly relevant to this field. Effectively integrating social science research with ecological or biological research remains a challenge (Campbell 2003), though emerging theoretical frameworks, e.g. social ecological systems theory, offer possibilities for guiding future inter-disciplinary work.

5.3 Which conservation strategies are working (have worked) and which have failed?

Today's sea turtle conservation 'movement' can trace its roots to nesting beaches, where protection efforts started in the 1950s with a handful of projects and have since expanded to hundreds, if not thousands, of nesting beach conservation programmes worldwide (Frazier 2002). Protection of reproductive females at the nesting beach, especially when protection is maintained for 2 or more decades, has led to dramatic reversal in declines of previously over-exploited nesting populations (Mortimer & Bresson 1994, Dutton et al. 2005, Broderick et al. 2006, Chaloupka et al. 2008b, Mortimer & Donnelly 2008). Intervention efforts such as predator abatement and use of hatcheries continue to be widespread, and there is little doubt that these efforts have paid dividends for increasing hatchling production. In recent decades, the detriments of coastal artificial lighting to hatchlings have been mitigated in some areas with expanded use of low-sodium pressure lamps and light shields (Salmon et al. 2000). To meet the growing challenges of fisheries bycatch and marine habitat degradation (see Sections 4.2 and 4.3), there has been a gradual shift toward conservation in the marine realm. The development and proliferation of fishing 'gear fixes' and improved legislation that regulates where and when fishing occurs are 2 management strategies that have proven successful, albeit to varying degrees, depending on the country and fishery in question (Dryden et al. 2008). For example, turtle excluder devices (TEDs) on bottom trawl fisheries and circle hooks in longline fisheries have shown promise for reducing sea turtle bycatch mortality (Epperly 2003). In addition to these tools, bycatch reduction efforts have benefited from technological advances that have resulted in a better understanding of the spatio-temporal habitat requirements of sea turtles (Godley et al. 2008). This science-based approach ensures that fisheries operate in areas with low probability of turtle interactions and has enabled managers to set some areas off limits (e.g. time area closures) during times of peak turtle abundance (central California USA leatherback closure area). Marine protected areas (MPAs) have also been implemented, although with varying success for turtle conservation. While they may not be able to offer protection at ecological scales (i.e. to include all/most of the foraging, migration and nesting areas; Dryden et al. 2008), at smaller scales MPAs may be effective for protecting important foraging, internesting and/or nesting habitat (Dobbs et al. 2007, Dryden et al. 2008). In many cases, habitat protection and fisheries management benefit from national and international instruments and policies (e.g. US Endangered Species Act, IUCN, CITES, Convention on Migratory Species [CMS], Inter-American Convention for the Protection and Conservation of sea turtles [IAC]) that mandate reduction of turtle take or establish the legal framework to minimise the international trade of sea turtle products (Frazier 2002, Bache 2005). In some cases, these instruments have focused exclusively on turtles (e.g. IAC, Indian Ocean and Southeast Asian Memorandum of Understanding [IOSEA]), and provide clear mandates for cooperation among neighbouring countries. As new turtle conservation instruments have come online at the international scale, there has also been increased emphasis on implementation of community-based management and co-management arrangements operating at much smaller scales. Community-based conservation generally places greater recognition on the importance of the 'human element' in wildlife conservation and increased value on knowledge and values of local communities (Jentoft 2000, Pretty & Smith 2004). These 2 approaches (international and local) are widely accepted as sound conservation actions by the wider sea turtle community. However, it is important to note that what constitutes 'effective conservation' has been, and will continue to be, open to debate, and there are inherent tensions between international vs. local approaches to sea turtle conservation (Campbell et al. 2002, Campbell 2007). For decades there have been wide-ranging opinions about the effectiveness of management strategies such as nesting beach hatcheries and headstarting (Frazer 1994), sustainable harvest (Mrosovsky 1997a,b, Campbell 2002; see Section 5.4), direct conservation payments (Ferraro & Gjertsen 2009, see Section 5.2), and ecotourism (Tisdell & Wilson 2005a,b, Campbell & Smith 2006). Additionally, one of the challenges to determining success is that many management projects/ programmes are not designed and implemented with evaluation in mind (Sutherland et al. 2004). Designing management strategies with SMART (specific, measurable, achievable, realistic and time-based) goals that allow evaluation, adaptation and the development of evidence-based conservation will be key to determining management success of current and future projects. While no single conservation 'recipe' is appropriate for all occasions, the debates surrounding effectiveness have resulted in a greater recognition that the 'ethics' of conservation, and effective protection strategies are indeed not universal but may vary with each species, each management unit, and perhaps even each nesting rookery.

5.4. Under what conditions (ecological, environmental, social and political) can consumptive use of sea turtles be sustained?

The issue of consumptive use and whether it is, or could be, sustainable in sea turtle populations is widely debated and challenging to address (Campbell 2002).

Essentially, this is because it intertwines ecological principles, species management, human rights, culture welfare, economic development and animal welfare (Nietschmann & Nietschmann 1981, Campbell 1998, 2002, Kwan et al. 2006, Thiriet 2007, Tisdell et al. 2007, Daley et al. 2008). Historically, consumptive use has ranged from small-scale subsistence and/or cultural use of turtles or eggs through to large-scale systematic commercial take, such as for the turtle soup markets in the latter 19th century or the long-term commercial use of eggs. While there are empirical data linking some consumptive use, particularly commercial use, to population reductions (e.g. green and hawksbill turtles in Seychelles, Mortimer 1984; leatherback turtles in Malaysia, Chan & Liew 1996), data on the level of take, status of the target species/population and socio-economic factors are lacking in most places. Importantly, recent research has indicated that depleted populations can recover, given appropriate management, and management does not necessarily exclude consumptive use (Havemann et al. 2005, Chaloupka & Balazs 2007, Chaloupka et al. 2008b). Determining whether consumptive use is sustainable is challenging because the outcome is likely to vary at social, governance (local/state/country) and biological (species/population) scales and, especially for subsistence use, hunting patterns are strongly tied to the hybrid nature of the coastal economy and other commercial operations such as fishing and tourism (Kwan et al. 2006, Meletis & Campbell 2007). Critical to the sustainability debate from a biological perspective is knowledge of the affected species and populations, and genetic studies such as population characterisation, and mixed stock analysis will be particularly informative here (e.g. Bass et al. 1998). Quantitative data on the size of the population, demography of animals taken and the level of use will be similarly important. Yet these data are absent for most populations and species. In addition, for most geographic areas where consumptive use occurs, data on social, cultural and economical factors related to sea turtles and their use are lacking. Focal areas worthy of research include (1) the sustainability of culture, local economy, health and social networks with and without consumptive use, (2) changes to the dynamics of local economies with and without consumptive use, (3) alternative options — dietary, cultural, economical, environmental offsets, (4) the importance of traditional ecological knowledge in sustaining consumptive use, both historically and currently, and (5) the multi-disciplinary challenges of conserving to consume, especially when there is a legal right to hunt, and the broader environmental consequences of reducing or replacing use. Another important research area, especially in assessing whether consumptive use remains sustainable, lies in understanding and addressing cumulative risk and in understanding the links between legal and illegal use, which are made more problematic by the migratory nature of sea turtles.

DISCUSSION

Recent articles by Sutherland et al. (2006, 2009) highlight the value of expert opinion in identifying pertinent research questions that may facilitate and guide wildlife conservation. Harnessing the ideas of experts is powerful because it generates consensus about current topics as well as areas of research that may become more important in future years — such as improving our understanding of the threats to wildlife, how these threats are managed, and how applied management actions are evaluated. Moreover, the overlap across recommended research actions by individual experts underscores the need to enhance interdisciplinary research, and is an excellent way to highlight 'hotspot' research questions or topics. The synergy created by cross-sectional expert opinion can help focus attention on what is considered to be of immediate importance for conservation. These efforts also provide a baseline with which future assessments of the state of sea turtle conservation research and knowledge can be compared.

Sea turtles are generally regarded as species of conservation concern and in many places throughout world they are impacted by a variety of anthropogenic threats. With increased awareness of their ecological roles and struggles against burgeoning human pressures, coupled with growing enthusiasm for their protection, comes a need for increased knowledge of their biology and human–turtle–management interactions. However, the global distribution of sea turtles, the variety of habitats where they occur and the threats they face, all lead to a large diversity in the biophysical and human elements that influence their life history, ecological role and management.

Through a multinational, multidisciplinary team effort, we distilled what we believe are the most pertinent research themes related to sea turtle conservation into 20 metaquestions. Although there have been previous attempts to collate pertinent research questions related to sea turtle conservation (e.g. compilation of foraging area research priorities; Bjorndal 1999, Richardson 1999), these have either focused on particular issues (e.g. climate change; Hawkes et al. 2009) or have been overly general (e.g. 12 'Burning issues' for sea turtle research, compiled by the IUCN/Species Survival Commission MTSG, see Mast et al. 2006). What sets the current compilation apart is that we sought input from a diverse set of active researchers, allowing us to collate a wide variety of research foci and directions. In many cases, we also linked the research questions to conservation implications, a strategy we believe will encourage research efforts that feed directly into management actions, thus benefiting sea turtles and their habitats.

Despite the fact that sea turtles have been the focus of research and conservation efforts for several decades in various places around the world (Frazier 2003), many of the questions submitted by individual researchers highlighted the need to collect basic life history information. This reflects the ongoing information gaps related to the logistical challenges of studying sea turtles when they are dispersed in the open ocean (see Sections 2.2 and 3.3) and to the long time spans from hatchling to maturity. Our team also identified major knowledge gaps linking terrestrial habitats with the marine. For instance, there is a lack of long-term data on both hatchling sex ratios produced at various beaches worldwide and whether hatchling sex ratios persist into successive age classes over time (see Section 1.2). Overall, the general strategy is that improved collection of basic life history data would then contribute to modelling exercises that could be used to assess impacts and direct conservation efforts, although it is recognised that more effort is needed to develop models pertinent to sea turtle conservation.

There is a clear bias in the underlying questions and metaquestions towards the biological sciences. The bias in focus likely arises as a result of the number of participating authors with 'biology' as their primary interest. Nevertheless, in terms of sea turtle conservation over the next 10 years, there is a substantial need for the involvement of other disciplines and for interdisciplinary work. This need is evident not only in Section 5 which addresses strategies for conservation, but within each of the metaquestions in Section 4 there are key gaps identified that relate to human-threat–turtle links (see Section 4.2). More importantly, the need to understand the human dimensions of threats and impacts not only related to turtles but also to other processes such as ecosystem and economic function are key components of understanding impacts on sea turtles or their habitats and on the impact of management on socio-economic dimensions (Nicholson et al. 2009). Thus, the inclusion of other disciplines will be most important for understanding why threatening processes are occurring (e.g. bycatch and pollution) and assisting in the prioritisation, implementation and evaluation of multidisciplinary frameworks for species and habitat monitoring and management.

Although several participants in the exercise have research backgrounds but are now active in management roles, the approach taken in this exercise has essentially harnessed the expertise of one sector: research. Another exercise could be to expand the process laterally and include input from experts in environmental decision making and/or compare questions derived by experts for other groups of marine wildlife, or in the generalised field of marine conservation (Sutherland et al. 2009). Using data from managers and/or on other species, participants could rank and weight suggested questions to provide a more detailed analysis of questions pertinent to, or perhaps regionally relevant for, both single taxa and/or marine fauna management. Using this process and expanding the scope of the exercise, especially on a regional level, would be valuable as it is likely to provide useful synergies with other disciplines or groups of stakeholders and reduce the gap between science, policy and management. Indeed similar processes, such as horizontal scanning (Sutherland et al. 2008, Sutherland & Woodroof 2009) or a prioritisation exercise used by (Nicholson et al. 2009) have demonstrated the effectiveness of using expert opinions, across a range of disciplines, to highlight a multi-disciplinary list of key current and emerging issues in conservation, plus the technological advances and/or challenges to guide management of the environment.

While the research questions highlighted here are considered to be of upmost priority at the current time, there is little doubt that priorities will change over time, due to both the progressive availability of information and also the dominant themes operating within conservation. For instance, the most frequently repeated question submitted by different authors was related to climate change impacts to sea turtles (28/347 total questions). In contrast, during a meeting of the IUCN MTSG in 2003, climate change was ranked last out of 12 'Burning issues' related to sea turtle research (Mast et al. 2004). Still, other priority research questions appear to remain more constant: bycatch evaluation and mitigation was the second most commonly submitted question in this exercise (27/347 questions) and was also the top 'Burning issue' in 2003 (Mast et al. 2004); bycatch mitigation was also recognised as the top priority for management in the Global Strategy for Sea Turtles (IUCN 1995). In addition, in 2006 the MTSG surveyed its membership to compile a list of the most important unanswered questions related to the natural history of sea turtles (Mast et al. 2006). Each of the 7 unresolved mysteries identified by the MTSG are covered to varying degrees in the 20 metaquestions; some such as ecological role, climate change impacts and FP are specifically contained in both sets.

Effective management of long-lived species such as sea turtles that occur in a broad range of habitats relies upon an appreciation of how biology and management fit within a variety of biophysical and social scales. While the priority question exercise has arrived at 20 independent metaquestions, there are several links within and among them — system-based (individual scale through to populations, multi species and ecosystems), habitat-based (condition, status and threats), spatial scale (site specific through to ecological scale) and temporal scale (from single life stage through to life span). More importantly, it is clear from the descriptions for each question, especially those in Sections 4 and 5 that an appreciation of the links, and their dynamic nature across both space and time is pivotal in terms of prioritising research, monitoring and conservation actions for particular species, populations and/or systems. Therefore, the metaquestions and the descriptive text developed by this exercise should form a useful foundation for future research, management and management evaluation for sea turtle conservation.

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