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REVIEW

Are we working towards global research priorities for management and conservation of sea turtles?

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ABSTRACT: In 2010, an international group of 35 sea turtle researchers refined an initial list of more than 200 research questions into 20 metaquestions that were considered key for management and conservation of sea turtles. These were classified under 5 categories: reproductive biology, biogeography, population ecology, threats and conservation strategies. To obtain a picture of how research is being focused towards these key questions, we undertook a systematic review of the peer-reviewed literature (2014 and 2015) attributing papers to the original 20 questions. In total, we reviewed 605 articles in full and from these 355 (59%) were judged to substantively address the 20 key questions, with others focusing on basic science and monitoring. Progress to answering the 20 questions was not uniform, and there were biases regarding focal turtle species, geographic scope and publication outlet. Whilst it offers some meaningful indications as to effort, quantifying peer-reviewed literature output is obviously not the only, and possibly not the best, metric for understanding progress towards informing key conservation and management goals. Along with the literature review, an international group based on the original project consortium was assigned to critically summarise recent progress towards answering each of the 20 questions. We found that significant research is being expended towards global priorities for management and conservation of sea turtles. Although highly variable, there has been significant progress in all the key questions identified in 2010. Undertaking this critical review has highlighted that it may be timely to undertake one or more new prioritizing exercises. For this to have maximal benefit we make a range of recommendations for its execution. These include a far greater engagement with social sciences, widening the pool of contributors and focussing the questions, perhaps disaggregating ecology and conservation.

KEY WORDS: Sea turtle · Marine conservation · Evidence-based conservation · Systematic review · Research prioritisation

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INTRODUCTION

The key research question approach has been used effectively to engage ecologists with priority topics determined by policy makers or the researchers themselves (Sutherland et al. 2006, 2009). The approach draws on the knowledge of a broad range of targeted experts to set out their priority questions for the subject matter. The individual questions are then discussed and synthesised to generate a number of priority questions that, if addressed, would have the greatest impact (Cooke et al. 2010). This approach has been used on a range of subject areas, from global conservation and biodiversity issues (e.g. Sutherland et al. 2009) to taxon specific initiatives, such as for sea birds (Lewison et al. 2012) and cetaceans (Parsons et al. 2015).

The status of sea turtles and the need for conservation to aid population recovery have captured the interest of government agencies, non-governmental organisations (NGOs) and the general public, worldwide. This has facilitated increased research focusing on a wide variety of topics relating to sea turtle biology and conservation. However, management actions are often hindered by the lack of data on turtles themselves, human–turtle interactions, turtle population status and threats or the effectiveness of conservation interventions. In an effort to inform effective sea turtle conservation, Hamann et al. (2010) compiled a list of priority research questions based on the opinions of 35 sea turtle researchers from 13 nations. A list of more than 200 questions was condensed into 20 metaquestions that were classified under 5 categories: reproductive biology, biogeography, population ecology, threats and conservation strategies (see Fig. 1). Now, more than 5 years later, we set out to critically appraise the progress that has been made towards informing these key research priorities in this taxon.

METHODS

Reviewing the literature

To determine how published research has been focused towards informing sea turtle management and conservation, we evaluated the peer-reviewed literature. We undertook a systematic review using Web of Science (v.5.22.3; 21 June 2016). In order to ensure capture of all relevant texts we used the topic search '*sea turtle*' or '*marine turtle*' or '*loggerhead turtle*' or '*green turtle*' or '*leatherback tur-*

tle' or '*olive ridley*' or '*Kemps ridley*' or '*hawksbill turtle*' or '*flatback turtle*' in 'All databases' for the 2 most recent complete years (2014 and 2015), which resulted in a list of 707 articles. We then removed duplicates, spurious hits, generic texts (such as references to entire proceedings) and non-peer-reviewed 'grey' literature based on title and abstract, or main text if relevance was unclear from the abstract.

Literature analysis

For each article, 2 authors (A.F.R. and B.J.G.) independently reviewed and ascribed its application to the original 20 questions highlighted in Hamann et al. (2010). These assignments were compared, and where differences occurred they were resolved through discussion. As a further check, input on the assignment of articles was sought from the other co-authors. Papers were, where possible, classified by sea turtle species and ocean basin.

Expert opinion

A total of 63 publishing sea turtle researchers were invited to contribute to this initiative. Those that responded positively (n = 42) were requested to indicate the 3 most relevant questions in Hamann et al. (2010) that matched their expertise. Based on their indications, they were then assigned to groups of 2 or 3 to compile summaries on recent progress towards answering each of the 20 questions. These summaries were then shared among all co-authors for comment, cross-linkage, internal review and refinement.

RESULTS

In total, 605 articles were reviewed in full and from these 355 (59%) were judged to substantively address the 20 key questions in sea turtle conservation and management (Fig. 1 and Appendix). A total of 40 (11%) of these papers cited the Hamann et al. (2010) paper. Papers on palaeontology (n = 21; 3%) were excluded. Publications on fundamental science (n = 74; 12%) and novel techniques (n = 36; 6%) not yet linked with conservation or management questions were not included here, although we stress the importance of such work in leading innovation that can underpin significant advancement. Baseline

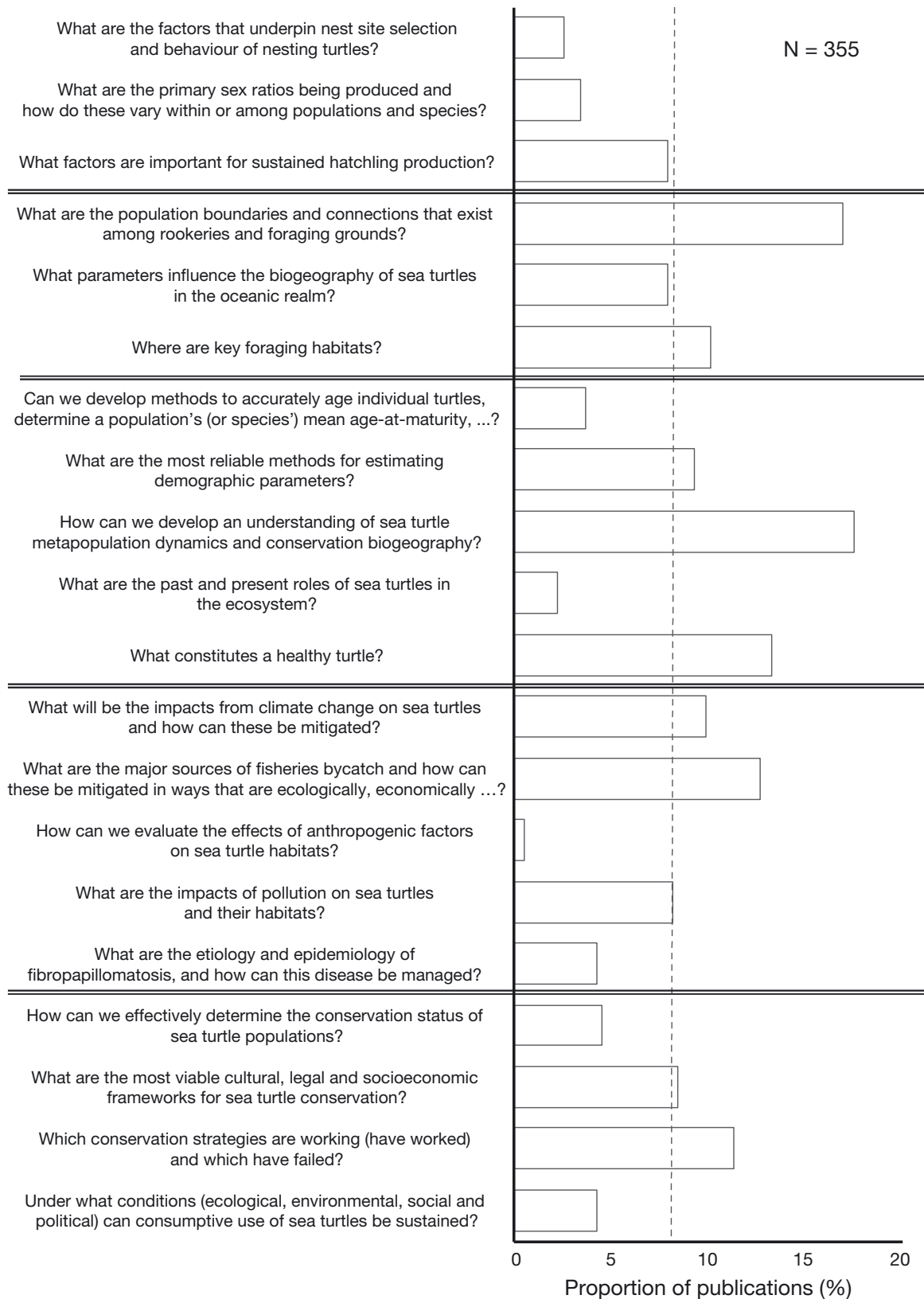


Fig. 1. Proportion of publications from 2014 and 2015 that address the 20 key questions of Hamann et al. (2010). Dashed line represents the mean value of the proportion of publications (8%). Percentages sum to greater than 100 as some publications covered more than one question

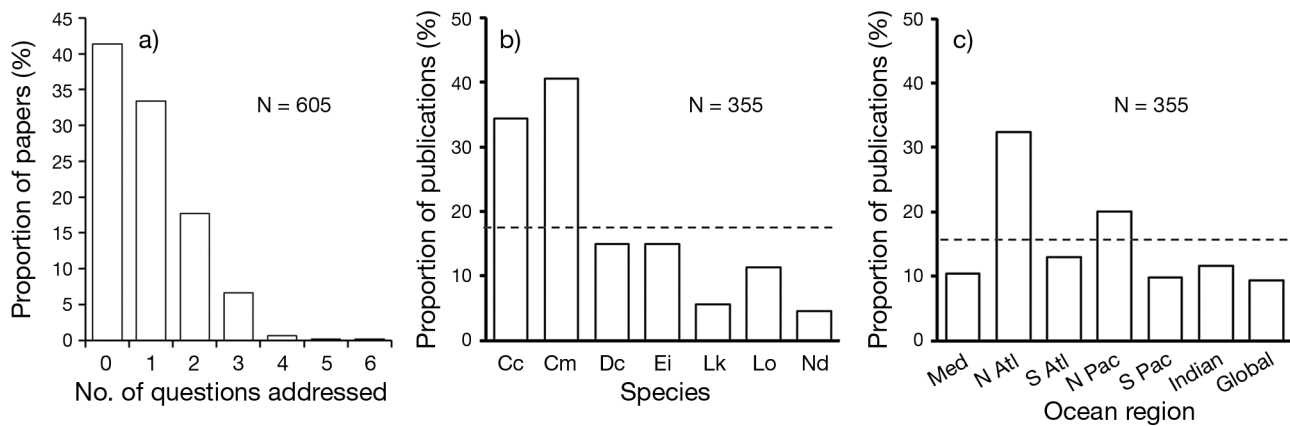


Fig. 2. (a) Proportion of papers addressing the key conservation questions highlighted by Hamann et al. (2010). Prevalence and biases in publications from 2014 and 2015 per (b) species and (c) ocean area. Dashed lines represent mean values. Percentages sum to greater than 100 as some publications covered more than one species. Cc = *Caretta caretta*, Cm = *Chelonia mydas*, Dc = *Dermochelys coriacea*, Ei = *Eretmochelys imbricata*, Lk = *Lepidochelys kempii*, Lo = *Lepidochelys olivacea*, Nd = *Natator depressus*

nesting monitoring reports that did not include extensive time series ($n = 20$; 3%), or reports of simple trophic interactions ($n = 16$; 3%), were further examples of articles that were not included in the final list, although we acknowledge that such data underpin studies of ecology, efficacy of conservation or assessments regarding the severity of threats. A total of 202 papers (33%) were considered to cover single key questions but 153 (25%) were more broadly scoped papers addressing up to 6 of the questions (Fig. 2a).

Outputs by species, ocean basin and publication venue

Species bias in published articles was prevalent (Fig. 2b). By far the most common species reported upon were green turtles (41% of articles) and loggerhead turtles (34% of articles). As might be expected, sea turtle species with more restricted ranges (Kemp's ridley and flatback turtles) featured least, appearing in less than 6% of the articles (see also Jeffers & Godley 2016). Geographically, work was biased towards the North Atlantic and, to a lesser extent, the North Pacific (Fig. 2c), possibly demonstrating the great interest and relatively enhanced funding in nations bordering these regions. Sea turtle literature contributing to the key questions was published in over 130 outlets, with the top 6 journals accounting for 32% ($n = 114$) of all articles (Fig. 3). Three of these are Open Access venues, with the other 3 being leading marine ecology journals.

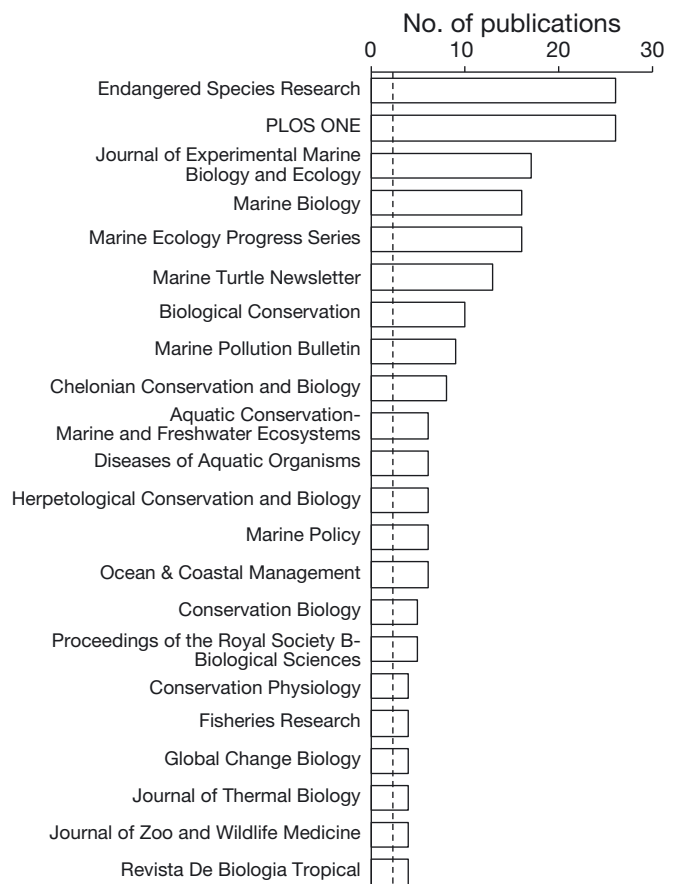


Fig. 3. Frequency of publishing outlet of all sources with 4 or more publications for the 355 articles that were adjudged as describing work that substantively informs sea turtle conservation or management that may be ascribed as contributing to answering the 20 key questions. Dashed line represents the mean value of publications per all publishing outlets, i.e. 2.6 publications

To what extent are the 20 questions being addressed?

Progress to answering the 20 questions in the 2 years of peer-reviewed literature was not uniform (Fig. 1). The related questions which extensively utilise modern technologies such as satellite tracking and molecular genetics: 'What are the population boundaries and connections that exist among rookeries and foraging grounds?' and 'How can we develop an understanding of sea turtle metapopulation dynamics and conservation biogeography?' featured most highly (both at 17% of publications numerically). Eight questions were each addressed in less than 5% of the literature with those relating to reproductive biology (Q1–3), threats (Q12–16) and conservation strategies (Q17–20) generally the least addressed. The question 'How can we evaluate the effects of anthropogenic factors on sea turtle habitats?' was singly the least represented (<1% of articles).

Quantifying peer-reviewed literature output is not the only metric for understanding research progress towards informing key conservation and management goals. Nevertheless, it is a useful tool with which to determine research output as an indicator of the focus and extent of work valuable to the management and conservation of sea turtles. The following 20 sections present synthesized expert opinion on the actual progress towards answering each of the original key questions set out by Hamann et al. (2010). They reference up-to-date findings together with foundation research carried out prior to publication of the 20 questions.

Q1. What are the factors that underpin nest site selection and behaviour of nesting turtles?

How do turtles decide where and when to lay their eggs? We know the necessary conditions for oviposition and incubation (Mortimer 1990, Ackerman 1997), we recognize that some anthropogenic activities can disrupt nesting (Miller et al. 2003) and have identified that delays to nesting can increase embryonic death (Rafferty et al. 2011, 2013). However, we still lack a deeper understanding of how sea turtles select nest sites at intra- and inter-beach levels. Natal homing has been the predominant explanation for maintenance of populations of turtles at specific nesting beaches (Bowen et al. 2016; see Q4 and Q9), and recent region-level analyses suggest that the interplay of abiotic patterns with natal homing, may also play a role in beach selection, including destructive

weather patterns (Fuentes et al. 2011a), access of hatchlings to major oceanic currents for dispersal (Putman et al. 2010a), and variation in the Earth's magnetic field used for geolocation (Brothers & Lohmann 2015). There may also be local adaptation to specific incubation conditions at the beach level that constrains where a turtle may choose to nest (Weber et al. 2012).

Once a beach is selected by a reproductive female, it remains unclear where along the beach she may emerge to lay her eggs, and whether lateral, spatial proximity to previous nests is the product of a randomized process (Nordmoe et al. 2004, Tiwari et al. 2005). Others have reported that nearshore factors such as wave height and steepness of approach (Yamamoto et al. 2012, Lamont & Houser 2014) or major beach-strand structures such as vegetation (Reising et al. 2015), buildings and other types of construction (Witherington et al. 2011), and natural or artificial debris (Fujisaki & Lamont 2016) influence where along the beach females lay their eggs.

Once a female has emerged from the ocean onto a nesting beach, she chooses where to place her eggs relative to the high tide line, dune line, and/or vegetation line. There has been some debate about the repeatability of nest site selection by individual females (e.g. Kamel & Mrosovsky 2005 vs. Pfaller et al. 2009 and Nordmoe et al. 2004). Recent studies have focused on quantifying nests laid in different beach zones such as open sand, intermediate and vegetation, and/or repeatability of location. Contrasting with lateral placement, most report that the nest locations are not randomly dispersed, and that individual females generally prefer to use the same zone for placing sequential nests in the same season (Neeman et al. 2015a). Interestingly, a multi-season study suggests that while females tended to lay clutches in similar zones in the same season, in other seasons the same females would change zones to lay their nests (Santos et al. 2016). The pattern of non-random nesting at a fine scale (on a given beach) while retaining the capacity to widely vary nest position at a larger scale (between beaches) would seem to be a prerequisite for populations of turtles to maximise hatching success while still being able to respond to environmentally caused changes in the suitability of beaches over time. Individuals with a lower nest site fidelity are needed for the establishment or drift of nesting along a coastline as conditions change. Overall, progress in understanding nest site selection and nesting behaviour has primarily been focused on observational research. While this is valuable for identifying the factors involved in these behaviours,

a deeper understanding will likely require an experimental approach, by manipulating either the habitat, nesting opportunity or sensory inputs of nesting females. Greater knowledge of these processes, particularly including inter-specific variability, may be critical to informing management decisions related to beach manipulation or beach construction following coastline changes from climate change and sea level rise (see Q3 and Q12).

Q2. What are the primary sex ratios being produced and how do these vary within or among populations and species?

The prevalence of temperature-determined sex determination (TSD) in reptiles (Charnier 1966), including turtles, is still puzzling from a molecular, ecological and evolutionary point of view. Progress has, however, been made. It has been suggested that TSD is a form of condition-dependent sex allocation favoured over genotypic sex determination when incubation temperature influences fitness in a manner that differs between the sexes (Charnov & Bull 1977). A new hypothesis linking the evolution of TSD with difference in age at maturity in males and females is very promising (Schwanz et al. 2016). Currently, however, we lack information on the age at maturity in sea turtles, although new data are becoming available (see Q7). Although the molecular and cellular mechanisms of temperature on sex determination still remain elusive, it seems clear that activity of the Sox9 gene is implicated at early stages (Sifuentes-Romero et al. 2013), and that gene methylation is used to lock gene expression after sex determination is complete (Venegas et al. 2016). The Cold-Inducible RNA-Binding Protein (CIRBP) gene could play an essential role as being the sensor of temperature for TSD in *Chelydra serpentina* (Schroeder et al. 2016).

Few recent studies have produced primary sex ratio estimates using histology (a lethal method) and most have used a small sample size, during a limited time in the nesting season or only for 1 season, which precludes a correct understanding of primary sex ratio for sea turtles (see Wyneken & Lolavar 2015 for discussion). A new promising method to estimate the sex of hatchlings based on steroids extracted from eggshell is a non-lethal sexing method (Xia et al. 2011, Kobayashi et al. 2015), but the approach remains to be validated. Many primary sex ratio studies use indirect proxies such as average temperatures during incubation (entire or middle-third) to cover all the nesting season or several seasons. These esti-

mates have been rendered possible by the development of new statistical methods to reconstruct the sand temperature from various proxies (Fuentes et al. 2013, Laloë et al. 2014, 2016, Girondot & Kaska 2015). However, the use of indirect proxies to establish primary sex ratio can generate significant error (e.g. Georges et al. 1994, Wyneken & Lolavar 2015). Additionally, many studies ignore the difference of thermal reaction norm for sex ratio (Hulin et al. 2009) or embryo growth (Morales Mérida et al. 2015) between populations (Girondot & Kaska 2014) and more research must be undertaken to produce validated proxies.

Primary, subadult and adult sex ratio have been established for loggerheads in the Mediterranean Sea, and it appears that a gradient in the sex ratio is observed, with a strong female bias for the primary sex ratio (Uçar et al. 2012, Sarı & Kaska 2015), a moderate female bias for the sex ratio in subadults (Casale et al. 2006), and no bias (White et al. 2013, Casale et al. 2014, Cocci et al. 2014, Stewart & Dutton 2014) or a male bias (Rees et al. 2013) observed in adults. These findings suggest that demographic or behavioural factors that do not generally reflect primary sex ratio can greatly affect subadult or adult sex ratios, but proximity to nesting areas may contribute to local sex ratio variation (see Q8). Finally, few studies take into account the multifactorial nature of the ecology of TSD. When it has been studied, data suggest that TSD may be more resilient in the face of climate change (see Q12) than originally thought (Fuentes et al. 2011b, 2013, Abella Perez et al. 2016).

Q3. What factors are important for sustained hatchling production?

Improving the knowledge of factors that influence hatchling production will aid the long-term maintenance of sea turtle populations, especially under changing climate or human-dominated landscapes. In 2010, the theme areas believed to be important were related to embryology and physiology, population-scale data on hatchling production, and developing and evaluating reliable techniques in order to assess hatchling fitness. Each of these areas remain relevant, but only some are well reflected as foci of recent research: (1) abiotic factors influencing embryonic development, emergence success, hatching success, and/or hatchling condition, including temperature (e.g. Horne et al. 2014, Rafferty & Reina 2014, Lolavar & Wyneken 2015) and oxygen availability (Cheng et al. 2015); (2) biotic factors that affect

embryonic development, emergence success, hatch success, and/or hatchling condition, including paternity (Phillips et al. 2013, Alfaro-Núñez et al. 2015) and maternal health (Perrault et al. 2012), microbes (e.g. Sarmiento-Ramírez et al. 2014b, Bézy et al. 2015), insect (Baena et al. 2015) and avian (Burger & Gochfeld 2014) predators; (3) population or rookery viability and hatchling production in a changing climate (e.g. Laloë et al. 2014, Santidrián Tomillo et al. 2014, 2015; see Q12) and (4) examinations of long-term programmes, policy or management instruments related to improving management of, or maintaining, high hatchling production (e.g. Brost et al. 2015, Fuentes et al. 2015b, Liles et al. 2015, Muñoz & Arauz 2015, Revuelta et al. 2015b; see Q19). Additionally, more research is required to investigate potential health effects (i.e. abnormalities) caused by contaminants on sea turtle development (Alava et al. 2011; see Q15).

Most research on hatchling production has focused on loggerhead, green and leatherback turtles, and the majority of studies have been conducted on North Atlantic and Pacific turtle populations. In general, the key species gaps are for hawksbill, flatback and ridley turtles, and studies on populations of any species from the Mediterranean, Indian Ocean and South Atlantic regions. These are important species and location gaps; 6 sea turtle Regional Management Units (RMUs) determined to be at highest risk and 8 of the 12 RMUs with critical data needs are in the Indian Ocean, and 8 of the 12 hawksbill turtle RMUs have critical data needs (Wallace et al. 2011). Although there are numerous turtle research and conservation initiatives throughout these regions, much of the data and publications from these regions exist as grey literature (project or governmental reports, etc.) and are not available to a wider audience.

In addition to filling knowledge gaps on population-scale hatchling production for species in these locations, further research is also required to develop and evaluate techniques to assess hatchling fitness, analyse long-term data sets on hatchling production, understand the abiotic factors that link hatchling production to nest site selection (see Q1) and determine critical thresholds for hatchling production for all sea turtle populations or management units. Our predictions of rookery and population viability and the ability of sea turtles to shift nesting locations in relation to human-impacted changes to the environment will be informed not only by measuring hatchling production, but also by understanding the effects of abiotic and biotic factors during incubation on hatchling survivorship and dispersal.

Q4. What are the population boundaries and connections that exist among rookeries and foraging grounds?

Defining the geographical boundaries of cryptic organisms including sea turtles is a fundamental but complex process. Major advances in defining breeding populations have led to a comprehensive understanding of stock structure for most species globally. Perhaps the biggest recent genetic advances have been made in the Indian and Pacific Oceans, for green (e.g. Dutton et al. 2014a,b, Nishizawa et al. 2014b, Bourjea et al. 2015a, Jensen et al. 2016), hawksbill (e.g. Gaos et al. 2016, Vargas et al. 2016) loggerhead (e.g. Nishizawa et al. 2014a, Shamblin et al. 2014, Matsuzawa et al. 2016), and olive ridley turtles (Jensen et al. 2013). Globally, significant advances have been made integrating male- and female-mediated gene flow by incorporating both mitochondrial and nuclear DNA (Dutton et al. 2013) for delineating demographically independent populations. Progress towards increasingly multidisciplinary approaches, where data such as genetics and ocean particle modelling (e.g. Gaspar et al. 2012, Monzón-Argüello et al. 2012, Putman & Naro-Maciel 2013, Putman et al. 2013), stable isotopes and satellite telemetry (e.g. Zbinden et al. 2011, Seminoff et al. 2012, Shimada et al. 2014, Vander Zanden et al. 2014, 2016), or tracking and modelling (Putman & Mansfield 2015), have been combined to reveal new information, including about the cryptic 'lost years'.

Nonetheless, researchers continue to identify and fill significant gaps in sampling and to address methodological limitations. There is insufficient information regarding connectivity in flatback turtles, which are still listed as 'Data Deficient' (Red List Standards & Petitions Subcommittee 1996). Some regions remain less studied than others in light of accessibility, permitting, funding, safety, or other obstacles. Despite recent pioneering work, to more fully understand the boundaries and constraints of sea turtle movements, connections among Management Units (MUs; rookeries) and less accessible juvenile/adult foraging grounds, and 'lost years' habitats, must be further investigated (see Q5).

New technological advances are increasingly being applied to address these gaps through tracking, modelling, and genomic analyses. Satellite tags are being developed for use on cryptic stages such as small pelagic turtles (Putman & Mansfield 2015), and high resolution particle models are challenging ideas of boundaries defined solely by passive pelagic drift (Wolanski in press). New DNA sequencing technolo-

gies are resolving stock structure through whole mitogenome approaches (Shamblin et al. 2012a,b) and short tandem repeats (STRs, Tikochinski et al. 2012). Indeed, the small segment traditionally sequenced stands to be dwarfed by next-generation data. One of the advantages of these genome-wide data, compared to traditional markers, possibly relies on the chance to identify traces of selection shaping population genetic differentiation (Funk et al. 2012). Furthermore, not only will more of the genome be covered, but sea turtle connectivity may soon be approached more comprehensively through environmental DNA (eDNA) sequencing of entire communities from water or soil samples. Although the significant obstacle of international comparisons has been overcome through the widespread adoption of a standardised sequence nomenclature for now, this will continue to be an important consideration in the genomics era. As we reveal the boundaries and constraints of sea turtles, we will better understand the processes leading to these biogeographic patterns. However, we should always keep in mind that boundaries must be viewed as being flexible, particularly in a changing world (see Q12).

Q5. What parameters influence the biogeography of sea turtles in the oceanic realm?

Satellite tracking has continued to expand our knowledge of adult oceanic movements with noteworthy advances in data-sharing and collaborative partnerships that have allowed assessment of the spatial distribution of populations over entire ocean basins, such as for leatherback turtles in the Atlantic, where it has been revealed how individuals target productive areas for foraging (Fossette et al. 2010, 2014, Benson et al. 2011). For oceanic juvenile stages, the last few years have seen a profusion of work using 3 distinct approaches: (1) assessing likely drift patterns for post-hatchlings based on ocean currents, (2) direct tracking of individuals that are large enough (generally >20 cm carapace length) to carry satellite tags, and (3) using chemical markers (trace elements and stable isotopes) in the tissues to indicate the likely oceanic foraging areas of individuals.

It is generally assumed that once their swimming frenzy finishes a few hours or days after they enter the water, hatchlings then drift passively, at least in their first months, so that their patterns of movement can be approximated by ocean circulation models or the movement of Lagrangian drifters (e.g. Hays & Marsh 1997, Hays et al. 2010a, Hamann et al. 2011,

Putman et al. 2012a), although in some cases the limited swimming ability of hatchlings has also been parameterized within these models (Hamann et al. 2011, Putman et al. 2012a, Scott et al. 2012a). Emerging from these studies is a view that the movements of post-hatchlings may shape the oceanic breeding migrations subsequently seen in adults, with adults travelling to foraging sites that they experienced in their earlier oceanic juvenile stage, i.e. adult migration patterns may not be innate but are rather a learned response to an individual's earlier experience (Scott et al. 2014b). Simulated drift of young turtles has also shed light on potential interactions of young turtles with pollutants (Putman et al. 2015a), helped to inform on growth rates (Scott et al. 2012b) and started to reveal how inter-annual variability in ocean currents may impact survival of oceanic juvenile stages and hence subsequent recruitment rates to adult populations (Ascani et al. 2016).

As young turtles grow and their swimming ability improves, these assumptions of largely passive drift become less realistic. There have been a number of landmark studies to directly track juvenile individuals, from 14 cm carapace length (Putman & Mansfield 2015) and bigger (Briscoe et al. 2016), as well as ongoing efforts to track larger (>50 cm) juveniles caught at sea (Dalleau et al. 2014). These studies suggest that even small oceanic turtles may sometimes show movements that are independent of the prevailing currents, presumably in cases where passive drift is not enough to ensure movements to favourable oceanic resources such as temperature and food. A challenge for our understanding of sea turtles and other marine megafauna remains the synoptic assessment of the ocean currents where turtles are located, to better resolve the roles of active directional swimming versus passive drift (Hays et al. 2016).

Chemical signatures in the tissues of individuals sampled once they have settled in neritic sites have started to reveal their previous oceanic habitats. Work on this topic suggests that from a single rookery each juvenile may occupy one of several distinct oceanic foraging areas, and that these areas are shared by multiple rookeries (López-Castro et al. 2013, 2014b, Fujioka et al. 2014a). A goal of future studies will be to see a convergence of the conclusions drawn from these different approaches (current models, direct tracking, chemical signatures), combined with niche modelling approaches (Varo-Cruz et al. 2016) to provide a more complete picture of oceanic foraging areas for juvenile turtles and how they connect to neritic developmental areas (see Q6).

Q6. Where are key foraging habitats?

Multi-disciplinary approaches have advanced our knowledge on the distribution and use of sea turtle foraging habitats. These approaches include telemetry (satellite, radio, acoustic), intrinsic markers (genetics, stable isotopes, trace elements), bycatch, mark-recapture (including photo-ID), strandings, aerial and underwater surveys, particle tracking, modelling and behaviour simulation (e.g. Foley et al. 2007, Putman et al. 2012b, Stewart et al. 2013, Dunbar et al. 2014, López-Castro et al. 2014b, Luschi & Casale 2014, Seminoff et al. 2014, Walcott et al. 2014, Ceriani et al. 2015, Fuentes et al. 2015a, Narazaki et al. 2015, Pikesley et al. 2015, Putman et al. 2015a,b).

While strong focus remains on post-nesting females (logistically more accessible; e.g. Griffin et al. 2013), more studies are investigating males and juveniles (Meylan et al. 2011, Arendt et al. 2012a,b, Casale et al. 2013, Mansfield et al. 2014; see also review by Jeffers & Godley 2016). Consequently, our understanding of migratory connectivity among breeding, foraging and developmental habitats has improved. This information facilitates the delineation of migratory corridors (Pendoley et al. 2014b, Baudouin et al. 2015, Shaver et al. 2016) and the identification of foraging habitats supporting high genetic diversity for protection (Hart et al. 2012, Hardy et al. 2014, Joseph et al. 2014). While some foraging habitats overlap with protected areas (Scott et al. 2012c, Hart et al. 2013, Revuelta et al. 2015a), others are more susceptible to fisheries pressure (Fossette et al. 2014, Seminoff et al. 2014) or industry (Whitlock et al. 2014).

Some foraging habitats support large aggregations of turtles of different species and size/age classes from different populations (Bresette et al. 2010, Vander Zanden et al. 2013, Sampson et al. 2014, Gorham et al. 2014), whereas others support small numbers of individuals distributed across wide areas (Hawkes et al. 2006, Luschi & Casale 2014). Turtles tend to exhibit high fidelity to oceanic and/or coastal foraging habitats (Goodman Hall et al. 2015, Shimada et al. 2016, Vander Zanden et al. 2016), which, in some places, could be the result of adults and late-stage juveniles retaining high fidelity to known resources after drifting there as hatchlings (Hays et al. 2010a, Putman et al. 2015a,b). However, turtle behaviour is also more complex than previously hypothesized, with many exceptions to traditional life-history models.

Plasticity in the distances travelled to foraging habitats, home range size, and foraging strategy exists (Hatase et al. 2013, Schofield et al. 2013), possibly driven by competition, resource quality or resource

availability, predation risk or climatic variability (Stadler et al. 2015, Prior et al. 2016). Our knowledge about movement patterns and interactions within foraging habitats is constantly advancing through the use of high-resolution technologies, including acoustic tracking, Fastloc GPS, ROVs, and camera systems (e.g. Narazaki et al. 2013, Smolowitz et al. 2015, Thomson et al. 2015a,b, Crear et al. 2016). An emphasis, however, is required on understanding resource partitioning and the trophic structuring of turtles at the ecosystem level (Thomson et al. 2015a,b; see Q10).

Ultimately, sea turtles spend most of their lives in foraging habitats, which are fundamental for juveniles to recruit into adult populations (Velez-Zuazo et al. 2014, Colman et al. 2015) and for adults to have sufficient reserves to breed and produce offspring. Thus, future studies must focus on how to assess which are the key foraging areas, including how their distribution and productivity will alter with climate change and impact reproductive output (Pikesley et al. 2015, Willis-Norton et al. 2015; see Q12), in order to prioritise the protection of these key habitats.

Q7. Can we develop methods to accurately age individual turtles, determine a population's (or species') mean age-at-maturity, and define age-based demography?

Understanding the demography of sea turtle populations is fundamental for accurate population models and conservation (see Q8). Age structure of individuals and populations, as well as age-at-maturity are crucial for such models, yet are among the most elusive aspects of sea turtle biology. So far, aging sea turtles has largely relied on skeletochronology, a technique that analyses humerus bones of dead animals (Zug et al. 1997, Snover & Hohn 2004). Indeed, skeletochronology can determine individual age (IA), offer some inferences about population age distribution, and when combined with capture-mark-recapture (CMR) techniques, provide insights about age-at-maturity (AM) (Van Houtan et al. 2014a). However, progress in these areas has been slow and these tools have been applied sparingly, due to the limitation that dead carcasses are required.

During the past decade, there have been several advances in understanding IA and AM of sea turtles based on (1) study of captive turtle growth and maturation (Bjorndal et al. 2014), (2) application of the 'living tag' technique on hatchlings (Tucek et al. 2014), and (3) increased use of skeletochronology and growth analysis (e.g. Avens et al. 2009, 2015, Hawkes et al.

2014, Ramirez et al. 2015, Turner-Tomaszewicz et al. 2015). New non-destructive, epigenetic approaches have also emerged for studying IA; however, these have yielded mixed results. For example, reduced telomere length in sea turtle blood cells has been suggested to be a function of age. However, while telomere length analysis has been promising in some cases (Hatase et al. 2008), others have found no link with age (Girondot & Garcia 1999, Plot et al. 2012). Measuring DNA methylation within tissues is another epigenetic approach; this shows promise for the study of tissue-specific changes that occur as a result of aging (Richardson 2003, Varriale & Bernardi 2006). Reduced DNA methylation in crocodylians has been shown to be a function of age (Nilsen et al. 2016), but substantial research and development is necessary to establish the efficacy of this technique for sea turtles.

Genetic approaches to determining AM represent a new frontier. Until now, CMR studies have been constrained by the absence of a reliable way of tagging hatchlings and identifying them later in life. Two recent advances have occurred that now make large-scale and long-term CMR studies of hatchlings through adulthood feasible, using DNA as genetic 'tags'. Firstly, the development of rapid non-injurious methods for collecting small genetic samples from hatchlings in the field (Dutton & Stewart 2013), and secondly, advancement in laboratory technologies for high throughput processing and genotyping of DNA (Hancock-Hanser et al. 2013). The rapidly accelerating pace of progress in molecular biology will continue to offer new techniques over the next decade to rapidly and cheaply genotype these DNA samples (Giardina et al. 2011, Schneider & Dekker 2012).

Knowledge of sea turtle demography will continue to be paramount to aiding in population modelling and conservation planning. Whereas traditional approaches will continue to yield important insights in this realm, the advent of genetic and epigenetic approaches shows even greater promise for studying sea turtle age dynamics. As these technologies become widespread and cost-effective, there will be opportunity to develop long-term monitoring experiments with wild populations to validate age estimates (e.g. Dutton et al. 2005) and ultimately better understand population vital rates and heterogeneity among individuals.

Q8. What are the most reliable methods for estimating demographic parameters?

Important demographic parameters include abundance, fecundity, age at sexual maturity (see Q7),

survival rates, and sex ratios (see Q2). Chaloupka & Musick (1997), Heppell et al. (2003) and National Research Council (2010) presented in-depth summaries of sea turtle demography and the role that demographic parameters play in sea turtle population assessments. A wide variety of methods with long time-series of data are necessary to estimate these parameters for sea turtle populations.

On nesting beaches, total counting (census) of nests is generally unnecessary and often infeasible; sampling can be a cost-effective option for abundance estimates based on nest counts; there are different ways to sample nests on a beach and to statistically estimate the total number of nests from a sample (Jackson et al. 2008, Sims et al. 2008, Girondot 2010, Whiting et al. 2013, 2014a). A time-series of hatchling production is essential for determining the change in the productivity of a population (e.g. Brost et al. 2015). In recent years, genetics, satellite telemetry and ultrasonography have been used to generate improved estimates of clutch frequency, the number of nesting females, and effective population size (Tucker 2010, Blanco et al. 2012, Frey et al. 2014).

Somatic growth is determined through long-term capture-recapture studies (e.g. Hawkes et al. 2014, Colman et al. 2015). A combination of skeletochronological and stable isotope analyses can be used to estimate growth rates and age at maturity (e.g. Avens et al. 2013, 2015; see Q7). Data collection at foraging grounds is essential because multiple stage classes, both sexes and turtles originating from different rookeries can be sampled at the same time. To estimate demographic parameters at a foraging ground, distance sampling and CMR methods can be used. Distance sampling is useful for estimating density and abundance as a snapshot (e.g. Lauriano et al. 2011, Seminoff et al. 2014), whereas CMR methods are useful for estimating various demographic parameters with long-time series of data (e.g. Sasso et al. 2007, Patrício et al. 2014, Stewart et al. 2014). Although a CMR study using both nesting beaches and foraging grounds is needed to obtain rookery-specific estimates on survival and movement rates within a population, this kind of approach has not been implemented because of the logistical difficulty in collecting sufficient data at nesting beaches and foraging grounds simultaneously.

The sex ratio is a poorly understood demographic characteristic of sea turtle populations (see Q2). Primary sex ratios at a nesting beach have been estimated from histological examination of hatchlings, laparoscopy (after allowing some growth of the

hatchlings), incubation durations, or environmental temperatures (e.g. Maulany et al. 2012, Woolgar et al. 2013, Lolavar & Wyneken 2015, Marcovaldi et al. 2016; see Q2 for a discussion on methodological issues and new developments concerning primary sex ratio estimation). In foraging areas, hormone-based sex determination methods (Wibbels 2003, Braun-McNeill et al. 2007, Allen et al. 2015) require minimal invasive procedures and are promising; more validation studies of hormone-based methods should be conducted (e.g. Allen et al. 2015).

A fundamental issue in studies of sea turtle demography is the characterisation of the functional demographic units (Chaloupka & Musick 1997), which can be accomplished via multiple techniques, including genetics, tagging and telemetry (Wallace et al. 2010; see Q4 and Q5). There exists a need for assessing the intrinsic variability of demographic parameters (Bjornndal et al. 2014, Tucek et al. 2014) and for comparing and combining subpopulation data to capture variabilities of demographic parameters in the wider population (Patrício et al. 2014, Bjornndal et al. 2016).

Q9. How can we develop an understanding of sea turtle metapopulation dynamics and conservation biogeography?

The first step is to identify the metapopulations. Significant advancements have been made in recent years, with the identification of groups of populations occupying large areas at the ocean basin level, such as RMUs by IUCN (Wallace et al. 2010) or Distinct Population Segments by NOAA, USA (e.g. Seminoff et al. 2015). These units were identified mainly — although not exclusively — through a high degree of genetic differentiation among nesting sites caused by the homing behaviour of adults, particularly of females. Hence, these units are basically ‘anchored’ to groups of nesting sites and may still be subject to changes. The same genetic data indicate that these large units are also structured internally (e.g. Carreras et al. 2014b, Shamblin et al. 2014, Bourjea et al. 2015a, Gaos et al. 2016, Vargas et al. 2016) and can be regarded as the metapopulations targeted by the present question. These unit approaches were particularly valuable and needed for circumglobal species, as many are known to exhibit local adaptations (Seminoff & Shanker 2008, Wallace et al. 2011, Fukuoka et al. 2015, Liles et al. 2015, Vargas et al. 2016). For example, in the Indian Ocean and southeast Asia there are 9 RMUs identified by Wallace et al. (2010) but these 9 RMUs contain at least 30 genetically dis-

tinct genetic stocks (Dethmers et al. 2006, Fitz-Simmons & Limpus 2014).

A second step is to assess the structure within a metapopulation, with each population anchored to a nesting area (group of nesting sites with genetic similarity) and occurring at one or multiple foraging grounds. When compared to genetic data, the degree of geographic overlap among different populations can help in understanding metapopulation structure and dynamics. While a population is intrinsically linked to a nesting site, identifying foraging grounds is particularly challenging. First approaches to assess connectivity between nesting and foraging sites were represented by flipper tag returns (Mortimer & Carr 1987, Limpus et al. 1992), satellite tracking of adults from nesting sites (reviewed in Godley et al. 2008, Hart & Hyrenbach 2009, Jeffers & Godley 2016) and genetic analyses of individuals sampled at foraging grounds (See Q4). However, these approaches are limited by numbers of tracked individuals and numbers of sampled foraging areas, respectively. Significant advancements are derived from coupling satellite tracking and stable isotope analyses (Zbinden et al. 2011, Ceriani et al. 2012, Pajuelo et al. 2012, Jones & Seminoff 2013, Vander Zanden et al. 2015; see Q4 and Q6) and from understanding the role of currents in the dispersal of hatchlings into their future foraging grounds (e.g. Casale & Mariani 2014, Putman & Mansfield 2015, Naro-Maciel et al. 2016). Technological advances to track smaller turtles are improving the understanding of habitat use by sea turtles during their first and most cryptic life stage (Mansfield et al. 2014, Scott et al. 2014a; see Q5). All these aspects can also inform the degree of dispersal and exchanges within a metapopulation, which plays a key role in a context of extinction-recolonisation and, ultimately, in the vulnerability of the metapopulation. Understanding how specific features of different nesting sites affect metapopulation dynamics in terms of extinction-recolonisation cycles can inform where to prioritise conservation efforts. In this respect, attempts to consider factors like incubation temperature (Pike 2013a) and dispersal facilitation (Putman et al. 2010b) are promising.

A third step is to assess population-specific demographic parameters (see Q7 and Q8). While separate approaches at nesting sites and foraging grounds (e.g. for growth rate, fecundity) are consolidated, novel approaches can relate the 2 different habitats, for instance reproductive output as dependent on the foraging area (Zbinden et al. 2011, Vander Zanden et al. 2014, Ceriani et al. 2015, Patel et al. 2015b).

In conclusion, despite significant advances in tools to determine population-level connectivity as well as the level of heterogeneity and the geographical range of a sea turtle metapopulation, a true understanding of metapopulation dynamics and the application of spatially structured models (Akçakaya 2000) are probably still far in the future.

Q10. What are the past and present roles of sea turtles in the ecosystem?

When recovery goals are set at returning sea turtle populations to ‘fulfil ecological roles’ (Bjorndal & Bolten 2003), this definition extends beyond simple metrics of abundance or dietary intake, and precisely because of the complex nature of studying sea turtles in this context, research in this category remains underrepresented. Ecological models aimed at characterising the complexity of the relationships between organisms in a given ecosystem can allow an exploration of the consequences of different management scenarios, past and future impacts of fisheries and environmental disturbance, disease, or the carrying capacity for different species.

Ecopath trophic models that include sea turtles represent advances in understanding their ecological roles (Wabnitz et al. 2010, Viet Anh et al. 2014, Piroddi et al. 2015), but remain limited by the extensive data required for model parameterisation, as the analysis is highly dependent on the availability and quality of such data. Nevertheless, these models can provide insight into the structure and functioning of marine ecosystems. Additionally, other intrinsic markers such as stable isotopes and fatty acids can be important to understanding food web structure and the basal resources contributing to different food webs that include sea turtles (Cardona et al. 2015).

Some of the most pressing research needs identified in 2010 included studies to address roles of sea turtles as ecosystem engineers, nutrient transporters, consumers, and prey (Hamann et al. 2010). With respect to ecosystem engineers and consumers, research on green turtles—the only herbivorous sea turtle species—has composed the majority of research in these areas. The past and present roles of green turtle grazing in seagrass pastures and the regulation of green turtle populations by top-down vs. bottom-up processes are critical to understanding the ecosystem effects of green turtle recovery (Bjorndal & Jackson 2003, Burkholder et al. 2013, Heithaus et al. 2014). As densities of green turtles increase in seagrass pastures, reports of ‘destructive foraging’

that may prevent seagrass recovery after grazing have garnered much attention (Fourqurean et al. 2010, Lal et al. 2010, Christianen et al. 2014). Understanding green turtle foraging strategies, including rotational grazing and cues that trigger patch abandonment (Bresette et al. 2010, Lacey et al. 2014, Molina Hernández & van Tussenbroek 2014), as well as seagrass responses to grazing, are critical to evaluation of carrying capacities of seagrass pastures for green turtles. Whether high densities of green turtles represent historical conditions (Bjorndal & Jackson 2003) or a release from predation with the decline of shark populations (Heithaus et al. 2014) is an essential question to ask when determining recovery goals in restoring ecosystem structure and function. Additionally, sea turtle grazing may have implications for the resilience of coral reef habitats, as hawksbills and green turtles target the consumption of algal turfs and macroalgae (Goatley et al. 2012).

Sea turtles have important roles in the terrestrial environment as nutrient transporters and prey. Nutrients from productive marine ecosystems are transported to less productive beach ecosystems by nesting turtles. These nutrient subsidies are assimilated by beach vegetation, predators, and detritivores and may influence the productivity and community structure of coastal ecosystems (Bouchard & Bjorndal 2000, Hannan et al. 2007, Madden et al. 2008, Vander Zanden et al. 2012, Peterson et al. 2013). As prey, nesting sea turtles provide a supplemental food resource for terrestrial species such as jaguars, crocodiles, and alligators (Nifong et al. 2011, Whiting & Whiting 2011, Verissimo et al. 2012, Guilder et al. 2015), and as a possible last-resort resource for Mediterranean monk seals during the nesting season (Margaritoulis & Touliaou 2011, Tonay et al. 2016). Sharks remain an important predator of sea turtles, and tiger sharks appear to alter their surfacing behaviour to enhance predation opportunities in areas of high sea turtle activity (Hammerschlag et al. 2015). Future emphasis should be on quantitative studies of all sea turtle species in oceanic, neritic, and terrestrial habitats that address the complex functions of sea turtles in healthy, functioning ecosystems.

Q11. What constitutes a healthy turtle?

This overarching question is addressed as 5 sub-topics, as it was previously divided.

(1) *The need for normal baseline physiological (blood work) studies.* This has been amply addressed with numerous studies presenting basic haematology and

blood chemistry: juvenile and adult loggerhead turtles (Delgado et al. 2011, Ley-Quinónez et al. 2011, Flower et al. 2015, Kelly et al. 2015), juvenile and adult green turtles (Prieto-Torres et al. 2013, Lewbart et al. 2014, McFadden et al. 2014, Zwarg et al. 2014, Flint et al. 2015a, Li et al. 2015, Page-Karjian et al. 2015c), adult leatherback turtles (Harris et al. 2011, Perrault et al. 2012, Stewart et al. 2012, Innis et al. 2014), and hawksbill turtles (Montilla et al. 2014, Whiting et al. 2014b). Data for other species are still lacking and obtaining regional values for different sub-populations would contribute to better understanding spatial variation. Overall, these studies have enriched the archive of reference values that are needed to assess the health status of both free-ranging and rehabilitating turtles. Rehabilitation plays an important role in stabilising debilitated turtles (Baker et al. 2015) and reintroducing them into the wild, yet, a consensus on declaring a rehabilitated turtle suitably healthy for release has still to be achieved.

(2) *Impacts of disease on population viability.* This hinges on ways to assess or predict the survivorship of sea turtles carrying disease and prevalence of the disease within the population. Flint et al. (2015b) identified clear links between infectious and non-infectious diseases and poor body condition of green turtles. Similarly, Work et al. (2015a) identified infectious/inflammatory diseases as a significant contributor to turtle mortality (18% of known causes of death) in green turtles. Page-Karjian et al. (2014) found that ocular tumours increased the likelihood of mortality eight fold in turtles with fibropapillomatosis (FP). Finally, a number of sea turtle health and mortality indexes (based on blood chemistry) recently proposed for predicting sea turtle survival (e.g. Stacy et al. 2013, Li et al. 2015) could have important applications.

(3) *The role of environmental factors in disease.* This remains poorly understood, but there are some recent advances in understanding the links between climate change and sea turtle health. Extreme temperatures can lead to sea grass diebacks, reducing body condition of green sea turtles (Thomson et al. 2015a). Climate change has also been linked to increases in the geographic distribution, intensity, frequency and toxicity of harmful algal blooms (Wells et al. 2015). Cold stress continues to be an issue in eastern USA, and an index to predict events has been developed (Pirhalla et al. 2015).

(4) *Health impacts.* Helminth parasites continue to dominate the infectious disease literature for sea turtles (Werneck & Silva 2015), and a new coccidian parasite has been found in leatherback adrenals (Ferguson et al. 2016). Fungi are starting to become

more prominent, with recent descriptions of new fungal infections in green (Donnelly et al. 2015) and loggerhead (Schumacher et al. 2014) turtles, and documentation that the ovopathogenic fungus *Fusarium* has a broad global distribution (Sarmiento-Ramírez et al. 2014a). There is also increasing evidence that exposure of sea turtles to marine toxins can be widespread (Capper et al. 2013) and adversely affect turtle health (Fauquier et al. 2013) (see Q15).

(5) *Health status of pelagic turtles.* This remains poorly understood, primarily due to the lack of information on this life stage (see Q5).

Overall, there is a clear need for new and innovative laboratory tools to understand physiology and disease pathogenesis. Several new such tools have recently been developed: computer-aided tomography to diagnose decompression sickness (García-Párraga et al. 2014); COMET assay to look at DNA damage (Caliani et al. 2014); haemoglobin binding protein adds to the repertoire of acute phase proteins useful for monitoring turtle health (Dickey et al. 2014); and laser capture microdissection (Page-Karjian et al. 2012).

Q12. What will be the impacts from climate change on sea turtles and how can these be mitigated?

Given the potential impacts of climate change on sea turtles, there has been a substantial growth in the number of studies exploring this topic. Most of the earlier studies explored the relationship between temperature and the sex of sea turtles (Mrosovsky et al. 1984) and highlighted potential impacts from projected increases in temperature. Consequently, several studies have estimated primary sex ratio at nesting grounds (Fuller et al. 2013, Marcovaldi et al. 2016) and predicted sex ratios under several scenarios of climate change (Hawkes et al. 2007, Laloë et al. 2014), using a variety of proxies (Girondot & Kaska 2014, 2015, Wyneken & Lolavar 2015; see Q2).

Despite a more robust understanding of sex ratio baseline in advance of climate change, limited knowledge still exists in relation to the operational sex ratio of the sea turtle population, and this has been highlighted as an emerging theme, although some studies have made some advancements in this area (see Hays et al. 2010b, 2014a, Wright et al. 2012, Lasala et al. 2013, Laloë et al. 2014). A focus also exists on the implications of projected increases in temperature on hatching success and population sustainability (Santidrián Tomillo et al. 2014, 2015a,b; see Q3), with recent work suggesting that the embryos of some

species may be more resilient to higher temperatures than previously thought and that their thermal tolerance may change as they grow (Howard et al. 2014, 2015).

The development of new biomarkers to detect thermal stress on clutches is a promising tool to detect the negative effects on the nesting environment and the resilience of embryos to extreme heating events (Tedeschi et al. 2015). The direct effect of temperature on hatchling attributes has also been explored, including clutch success, hatch weight and hatchling performance (Dudley & Porter 2014, Fisher et al. 2014, Horne et al. 2014). Further, studies have focused on impacts of sea level rise on nesting grounds and future availability of nesting areas (Katselidis et al. 2014, Patino-Martinez et al. 2014, Calvillo Garcia et al. 2015) as well as the overlap between cyclonic activities and nesting activities (Fuentes et al. 2011a, Dewald & Pike 2014, Kumar et al. 2014) highlighting the fact that monitoring the morphological changes of nesting habitat is a key factor in assessing the impact of climate change on sea turtles (Yamamoto et al. 2015).

Advancements have been made in evaluating the impacts of climate change on the oceanic realm; predicted variations in wave regimes and currents (Osorio et al. 2014) may have a great impact on foraging areas for several sea turtle species (Robinson et al. 2014, Thomson et al. 2015a, Willis-Norton et al. 2015), highlighting the need to also monitor the vulnerability of the ecosystems used by sea turtles. Typically the impacts of climatic processes on sea turtles have been explored individually, but processes are likely to occur simultaneously with other anthropogenic threats and cause cumulative and synergetic effects, emphasizing the need to simultaneously analyse multiple threats (Fuentes et al. 2011b). This is important, since the resilience of sea turtles to climate change is likely affected by several factors including non-climate-related threats such as disease, pollution and fisheries interactions (Fuentes et al. 2013, Abella Perez et al. 2016). The adaptive capacity of sea turtles to climate change, among other factors, may be dependent on their dispersal potential (Boyle et al. 2014). This dependence is especially relevant as climate change has been suggested to affect dispersal by impacting key offspring attributes, such as fitness (Cavallo et al. 2015, Sim et al. 2015). Some changes in the timing of the nesting season, possibly as an adaptation, have been detected and related to sea surface temperature (Neeman et al. 2015b). Adaptive capacity will also be dependent on the future availability of habitat with optimal incubating environ-

ment (Pike 2013b). Thus, further knowledge of the factors contributing to population expansion and species range, such as nest site selection, fidelity and dispersal from nesting areas is important (Pike 2014, Mazaris et al. 2015, Neeman et al. 2015c, Pikesley et al. 2015, Maffucci et al. 2016). Although several strategies (e.g. shading of nests, sprinkling, assisted migration) have been suggested to mitigate potential impacts from climate change on sea turtles (Wood et al. 2014, Hill et al. 2015b, Jourdan & Fuentes 2015, Lopez et al. 2015), there is general consensus that robust knowledge of their risks and effectiveness is needed before implementation.

Q13. What are the major sources of fisheries bycatch and how can these be mitigated in ways that are ecologically, economically and socially practicable?

Drifting longlines have attracted most of the research attention during the past 5 years, partially because along with purse seiners, industrial longliners often carry on-board observers collecting bycatch data. As a result of this new information, researchers have developed risk assessment models (Fossette et al. 2014, Roe et al. 2014, Pikesley et al. 2015) and tools to help predict bycatch risk in near-real time (Howell et al. 2015). There is also growing evidence that hook removal has the potential to reduce post-release mortality (Swimmer et al. 2006, Álvarez de Quevedo et al. 2013, Swimmer et al. 2014, Gilman & Huang 2016).

Recent research on trawl fisheries has demonstrated that in some regions, only bottom trawls operating on shallow water are likely to catch significant numbers of turtles (Warden 2011, Domènech et al. 2015). Although turtle excluder devices (TEDs) and tow times have been enforced in some fleets operating in shallow water, recent evidence indicates that captured turtles may suffer decompression sickness, and hence there is a high risk of significant post-release mortality (García-Párraga et al. 2014). There remains an urgent need to assess post-release mortality of turtles caught in bottom trawls.

There is increasing evidence that passive net fisheries, drift nets in particular, are a major threat for sea turtles in many ocean regions around the world (e.g. Gilman et al. 2010, Casale 2011, Wang et al. 2013a, Wilcox et al. 2013, Girard et al. 2014, Ayissi et al. 2015, Ortiz et al. 2016). Many of these are small-scale fisheries that are poorly monitored and studied. The use of LED lights or chemical light sticks has proven promising in reducing bycatch (Wang et al.

2010, 2013a, Ortiz et al. 2016), as well as the use of buoyless nets (Peckham et al. 2016). However, the use of shark models, as visual deterrents near fishing gear may also reduce the value of the commercial catch to unacceptable levels (Wang et al. 2010, Bostwick et al. 2014). These mitigation measures require additional testing in other fisheries before their use can be recommended.

Recent studies indicate very low levels of bycatch associated with purse seiners (Hall & Roman 2013, Bourjea et al. 2014). Drifting fish aggregating devices (DFADs), however, might result in some ghost fishing (Balderson & Martin 2015, Maufroy et al. 2015). It is therefore essential to assess the magnitude of overall mortality of turtles through entangling in DFADs at sea or beached.

Efforts to develop risk assessment models, predict the demographic consequences of bycatch and set limit reference points (Curtis et al. 2015a,b, Murray 2015, Warden et al. 2015, Casale & Heppell 2016) are complicated by: variation over time in fishing gear and fishing area resulting in fluctuations in turtle bycatch (e.g. Álvarez de Quevedo et al. 2013, 2014, Báez et al. 2014a,b); poor coverage of species' entire foraging grounds affected or the suite of fisheries operating in a region (with small-scale fisheries particularly under-represented; Alfaro-Shigueto et al. 2010); and large uncertainties about reproductive parameters (Warden et al. 2015) and post-release mortality (Murray 2015).

Further research should encompass all major fisheries of concern, assess both direct and post-release mortality, determine the species and natal populations of captured turtles (Dutton et al. 2014b), contextualize bycatch figures according to life stage and population size, and periodically update bycatch numbers (Casale & Heppell 2016). Additional effort is required in regions other than the North Pacific, North Atlantic and Mediterranean, because large portions of the oceans and their resident turtle populations are under-studied and vulnerable to massive levels of fishing effort, especially from net gears. Artisanal fisheries deserve particular attention and on-board observers may play a critical role in the monitoring of industrial fleets.

Q14. How can we evaluate the effects of anthropogenic factors on sea turtle habitats?

Recent advancements in remotely sensed data and spatial analysis tools have greatly improved our ability to map sea turtle habitats, detect changes over

time and model habitat suitability. For example, Hedley et al. (2016) mapped persistence of seagrass habitat in Moreton Bay from 1998 to 2010, Yamamoto et al. (2015) mapped morphological changes of nesting beaches in southeastern Florida from 1999 to 2005, and Dunkin et al. (2016) mapped loggerhead nesting habitat suitability along part of Florida's Atlantic coast. In addition, cumulative human impacts in marine environments (e.g. climate change, pollution, commercial shipping) have been mapped on a global scale (Halpern et al. 2015). These types of studies generally have a global overview and focus on a particular habitat type (e.g. seagrass, mangroves, coral reefs). However, it could be argued that understanding the anthropogenic effects on marine habitats at a coarse, global scale is, in fact, providing important information on the human impacts in local sea turtle habitats. Certainly, there is great potential within the current literature to overlap global anthropogenic-induced changes to marine habitats with known sea turtle habitat locations. However, there is still some question as to whether the scale of these global assessments is fine enough to provide meaningful information about the anthropogenic impacts within specific sea turtle habitats.

The effects of sea turtle habitat degradation on sea turtle populations have been relatively well researched in recent years (Mathenge et al. 2012, Schuyler et al. 2014a, Vander Zanden et al. 2016), as have acute, large-scale impacts such as the BP *Deepwater Horizon* discharge (Bjorndal et al. 2011, Putman et al. 2015a, Vander Zanden et al. 2016). Research has continued to assess the impact of nesting beach development on nesting turtles (Flores-Monter et al. 2015), and the effects of artificial lighting on hatchling dispersal and nesting (Kamrowski et al. 2012, 2014a, Berry et al. 2013). Assessments of specific anthropogenic impacts on sea turtles on nesting beaches continue (e.g. van de Merwe et al. 2012). In addition, it could be argued that impacts such as climate change (see Q12; although impacts may not always be negative, Hawkes et al. 2007) and pollution (see Q15) are affecting sea turtle populations via habitat degradation. For example, increases in nesting beach temperature affect hatchling survival and sex ratios (Santidrián Tomillo et al. 2015a), and accumulation of plastic in core foraging areas results in plastic ingestion in young green turtles (González Carman et al. 2014a). A threat of emerging concern is that of anthropogenic noise (Estabrook et al. 2016, Nelms et al. 2016a)

However, due to the often cumulative nature of human-induced impacts on sea turtle habitats, deci-

sion and risk-based frameworks (e.g. Whittock et al. 2014, Fuentes et al. 2015b, Riskas et al. 2016) are required to better identify the most important impacts of anthropogenic activities on sea turtle populations. Likewise, more studies establishing attributes of good quality habitat (e.g. beach characteristics and environmental conditions that support mass nesting events, Barik et al. 2014; see Q1) are needed for a systematic evaluation of sea turtle habitats. This will promote more efficient and effective allocation of conservation and management resources.

Q15. What are the impacts of pollution on sea turtles and their habitats?

The primary pollutants influencing sea turtles and their ecosystems may be grouped into plastic and other debris (including microplastics), toxins, and nutrient runoff. Although not discussed here, artificial lighting and anthropogenic noise are discussed elsewhere (see Q14).

The understanding of the impacts of plastic debris, broadly to marine life (Vegter et al. 2014, Ryan 2016) and specifically to sea turtles, has gained significant attention since the previous review (Barreiros & Raykov 2014, Schuyler et al. 2014a, 2016, de Carvalho et al. 2015, Nelms et al. 2016b). Acute threats posed by plastic debris include physical entanglements in derelict fishing gear (discarded monofilament lines, 'ghost' nets etc.) and other plastic debris (Poli et al. 2014, Wilcox et al. 2015). Mortality associated with gastrointestinal tract blockage from ingested plastic is another known acute impact. Ingestion of debris can also cause sub-lethal effects such as internal injuries, dietary dilution, malnutrition, and increased buoyancy (Nelms et al. 2016b). These effects may result in poor health, reduced growth rates and reproductive output but are not well quantified. Additional indirect impacts may include harm from persistent organic pollutants that adsorb to ingested plastic, and endocrine disruption resulting from chemicals leached from plastic (Santos et al. 2015), but these are also poorly understood and challenging to obtain (Casale et al. 2016).

Juveniles may be particularly susceptible to ingestion of plastics, as the offshore convergence zone ecosystems where they reside also concentrate ocean debris (González Carman et al. 2014a, Van Houtan et al. 2016). Further research to locate these areas (see Q5) and understand the trophic structure of these ecosystems (Choy et al. 2015) and the resulting bioaccumulation of contaminants is needed. There is

increasing research on the detection of microplastics in the marine environment and marine fauna, both resulting from macroplastic degradation or from sewage. However, very little is published on the presence or impact of microplastics on sea turtles, and this deserves future attention.

Literature on the accumulation of heavy metals (e.g. García-Fernández et al. 2009, Bucchia et al. 2015) and organic contaminants (e.g. Orós et al. 2009, Lazar et al. 2011, Camacho et al. 2013b) in sea turtles continues to grow. However, only 3 studies have further assessed the risks associated with chemical accumulation in sea turtles (Lam et al. 2006, van de Merwe et al. 2009, Dyc et al. 2015). Toxicity of heavy metals varies with species, developmental stage, environmental conditions, and the anthropogenic source (Godley et al. 1999, references in Bucchia et al. 2015). Maternal transfer of pollutants to eggs has also recently been described (Guirlet et al. 2008, 2010, van de Merwe et al. 2010, Ikonopoulou et al. 2011), indicating potential risk to developing embryos. However, very little is known about the toxic effects of chemical contaminants on sea turtles (Finlayson et al. 2016). Most recent studies in this area focus on correlations between contaminant concentrations (mostly PCBs, PAHs and DDT) and effects, such as clinical blood parameters (e.g. Swarthout et al. 2010, Komoroske et al. 2011, Camacho et al. 2013a,c), FP (e.g. Keller et al. 2014, da Silva et al. 2016; see Q16), diseases (e.g. Orós et al. 2013) and hatchling body condition (e.g. Perrault et al. 2011). Not surprisingly, considering the conservation status of sea turtles, direct *in vivo* exposure of contaminants to measure toxicity has decreased in recent years. More recently, *in vitro*, or cell-based, approaches have been used as an ethical alternative for assessing the effects of contaminants in sea turtles (e.g. Wang et al. 2013b, Webb et al. 2014, Wise et al. 2014, Young et al. 2015). Investigating toxicity thresholds for pollutants and the effects of complex chemical mixtures are important areas for future research.

Oil spills can lead to varied threats, including injuries, oil-derived toxic effects and habitat degradation (Putman et al. 2015a). However, immunotoxicity is not typically assessed during oil spills (Barron 2012). On the other hand, due to the migratory behaviour and sharing of feeding grounds, oil spills may impact turtles from different, distant populations (Putman et al. 2015a).

Exploratory analyses must also be carried out to reveal the presence of currently undetected pollutants from land-based activities. Land-based nutrients originating from human wastewater and agri-

culture cause eutrophication, harmful algal blooms, hypoxia, and alter coastal ecosystems dramatically (Carpenter et al. 1998). Cyanobacteria blooms favoured by such wastes, e.g. *Lyngbya majuscula* blooms in East Australia, are noted to impact sea turtle habitats and turtle health, but to varying degrees over large spatial scales (Arthur et al. 2006, 2008). Impaired waterways are often hotspots for FP (Aguirre & Lutz 2004), and eutrophication has recently been linked as a potential key factor (Van Houtan et al. 2010; see Q16).

Q16. What are the etiology and epidemiology of fibropapillomatosis (FP), and how can this disease be managed?

Since the previous update, there have been 2 published reviews (Kane et al. 2012, Jones et al. 2016) and one international symposium (Hargrove et al. 2016) on FP, all identifying needs for research that may lead to better understanding of the manifestation, occurrence, cause, and population impacts of FP. Though yet to be conclusively proven, FP is still considered to be caused by a herpesvirus. Description of the genetic sequence of the ChHV5 virus (Ackermann et al. 2012) was a big step forward. Further, a global phylogeography of FP-associated herpesviruses (Patricio et al. 2012) revealed no recent viral mutations, suggesting the recent epizootic may be driven by other factors. Nested and quantitative PCR documented high levels of ChHV5 in normal tissues of several species (Page-Karjian et al. 2012, Alfaro-Núñez & Gilbert 2014, Alfaro-Núñez et al. 2014, 2016, Page-Karjian et al. 2015b).

Aside from the well-known occurrence of FP in green turtles from Hawaii, Florida, and Australia, more information is emerging in other regions. New descriptions of FP for olive ridleys in Costa Rica (Chaves et al. 2013), green turtles in Principe (Duarte et al. 2012) and Brazil (Rodenbusch et al. 2012, Rodenbusch et al. 2014, Zwarg et al. 2014, Monezi et al. 2016), and loggerheads in Brazil (Rossi et al. 2015) are available. In green turtles, the population-level prevalence varies among sites (e.g. Sterling et al. 2013, López-Mendilaharsu et al. 2016). Turtle fishers in the Caribbean may elevate FP prevalence by selecting against tumoured turtles (Stringell et al. 2015b).

Previously documented in Hawaii, tumour regression was also described in Brazil (Machado Guimarães et al. 2013) and Puerto Rico (Patricio et al. 2016). For Puerto Rico green turtles, FP does not appear to be

influenced by demographics (Patricio et al. 2011, 2016) and may not always alter growth rates (Patricio et al. 2014). In Hawaii, disease transmission may depend in part on disproportional viral shedding from a few individuals (Work et al. 2015c). Electrotherapy (Brunner et al. 2014) and phototherapy (Sellera et al. 2014) may be promising tools for treatment of affected turtles. Additional studies retrospectively examined FP rehabilitation cases in green (Page-Karjian et al. 2014) and loggerhead (Page-Karjian et al. 2015a) turtles from Florida.

FP has long been associated with impaired coastal ecosystems but the exact mechanisms are unknown (see Q15). Heavy metal burdens are associated with FP in green turtles from Brazil (da Silva et al. 2016). However, persistent organic pollutants do not appear to be associated with FP in green turtles from Hawaii (Keller et al. 2014) or Brazil (Sánchez-Sarmiento et al. 2016). In Hawaii, FP is prevalent in watersheds where invasive algae and land-based nutrients are chronic management concerns (Van Houtan et al. 2010). Elevated nitrogen is sequestered by macroalgae in arginine, which when consumed, may contribute to FP by promoting herpes (Van Houtan et al. 2014b), but this is subject to debate (T. M. Work et al. unpubl. data).

Q17. How can we effectively determine the conservation status of sea turtle populations?

This can be divided into 2 sub-questions: (1) What is the appropriate conservation unit and (2) What are the appropriate methodological approaches to assess the extinction risk and type of data required?

(1) The IUCN Red List assessments are the most cited. Significant advancement has been made from the original global scale at species level to a new scale: the RMU (Wallace et al. 2010). Thus far, the RMU approach has been applied to leatherback and loggerhead sea turtles (www.iucnredlist.org), while others are underway. Although an improvement, an RMU may include several biological units whose individual fate is not reflected by the overall risk assessment. As genetic markers improve, smaller biological units are recognised (Shamblin et al. 2015a,b, Gaos et al. 2016).

(2) Trends or indices of abundance are often used to determine population status, but require precise annual abundance estimates, which can be difficult to ascertain (see Q8). Thus, models have been developed to obtain reliable abundance estimates from partial nest counts (e.g. Girondot 2010, Delcroix et al. 2014, Whiting et al. 2014a). Trend analysis can be

improved by additional demographic parameters obtained through physical tagging (flipper and PIT) of nesting females (e.g. survival, movements, detection, recruitment of nesting females; Pfaller et al. 2013, Stokes et al. 2014, García-Cruz et al. 2015). However, these analyses require consistent, thorough data collection, which may be implausible at remote nesting beaches. To include more than adult females in trend analysis, in-water indices (e.g. Brette et al. 2010, Pons et al. 2010, Casale et al. 2012, Redfoot & Ehrhart 2013, Lagueux et al. 2014, Patrício et al. 2014, 2016, Williams et al. 2015), especially for the juvenile life-stages, are necessary to complement nesting indices and detect population changes before they are observed at nesting beaches (see Q7 and Q8). Unfortunately, abundance estimates at foraging areas are challenging to obtain and unavailable for many populations (Fuentes et al. 2015a). Possible future technological development may include the use of drones or improvements to sampling techniques such as photo identification coupled with citizen science. These would reduce or eliminate the cost and risk of conducting aerial surveys at near-shore foraging grounds and nesting beaches. With these demographic data, the status of a marine turtle population can be determined via population modelling, which can be used to estimate the probability of persistence (e.g. Dethmers & Baxter 2011).

Additionally, incorporating the human dimensions, via traditional ecological knowledge, can strengthen species assessments and provide unique insight into a population's conservation status, especially for data-limited populations and locations where baselines are lacking (Sáenz-Arroyo et al. 2005, Drew & Henne 2006, Fraser et al. 2006, Gaos & Yañez 2012). To include human dimensions, combining the social (e.g. interviews, workshops) and natural sciences can provide unique insight via traditional ecological knowledge. Studies have used this inter-disciplinary approach to assess local perceptions of species (Gaos et al. 2010, Butler et al. 2012, Braga & Schiavetti 2013, Liles et al. 2014), sea turtle bycatch in artisanal fisheries (Moore et al. 2010, Braga & Schiavetti 2013), and to inform species assessments of endangered whales (Frans & Augé 2016).

Q18. What are the most viable cultural, legal and socioeconomic frameworks for sea turtle conservation?

Generally, the same 4 categories identified by Hamann et al. (2010) addressed topics related to cultural, legal, and socioeconomic frameworks of con-

servation. From the literature reviewed, we found the emphasis remained on description and assessment, rather than quantifying relative costs and benefits and how they are distributed among impacted human populations. Slow progress has been made, although there have been some novel approaches. These include several methods for ecological assessments and further identification of conservation priorities — such as the use of fuzzy logic mathematical systems (Aguilar-González et al. 2014), habitat modelling (Fujioka et al. 2014a), modelling food webs (Viet Anh et al. 2014), modelling of threat risk and mitigation measures (Kvamsdal & Stohs 2014, Watson & Bigelow 2014), and including budget constraints together with local and expert opinions (Fuentes et al. 2015b) — in order to model cost effective management options (Gjertsen et al. 2014). A further novel approach was the use of religious education addressing turtle conservation (Macrae & Whiting 2014).

Several studies have shown the importance of applying inter-disciplinary frameworks which consider social, cultural, ecological and governance factors to bring about management changes (Jackson et al. 2015, Stringell et al. 2015a, Teh et al. 2015). However, the limitations on the extent to which research can effectively support legislation, management and overall conservation seem to be a general concern (Lagueux et al. 2014, Kvamsdal & Stohs 2014, Harris et al. 2015, Humber et al. 2015, Lewison et al. 2015, Lopez 2015, Lopez et al. 2015, Stringell et al. 2015a). For instance, sea turtle conservation within the context of other long-distance marine migratory species (Gredzens et al. 2014, Lascelles et al. 2014), assessments of critical habitat and environmental sensitivity (Lopez et al. 2015, Martin et al. 2015b), management of wider ocean ecosystems (Maxwell et al. 2014, 2015) and understanding the connections between diverse stakeholders (e.g. Weiss et al. 2012, 2013) all call into play broad international and cross-sector governance and legal issues which are as yet unresolved. Insufficient integration and application of social and natural science in institutions, agencies, universities, and organisations remains an impediment, along with the limits to collaboration created by thematic siloes.

Although on the increase, psychological and behavioural research is still limited (Kamrowski et al. 2014b, McDonald et al. 2014, Hill et al. 2015a). Neuropsychology, neuroeconomics and neuroconservation are areas to watch for emerging themes and breakthrough insights within this category, as applications of neuroimaging technology become more viable. Studies of the cognitive, emotional, psycho-

logical, social, and spiritual value of access to 'blue space', wildlife, and biodiversity will begin to include sea turtles, their habitat, and conservation projects (Kuo 2015, Cracknell et al. 2016, White et al. 2016).

Despite some historical knowledge of sea turtle fisheries around the world (Halkyard 2014, Lagueux et al. 2014, Van Houtan & Kittinger 2014), we still have a lot to learn about the long-term impact of harvests. On the other hand, with successful conservation efforts, some sea turtle populations have been downlisted. In many places the conversation about legal consumption (see Q20) is increasing and will have to be addressed within cultural, legal, and socio-economic frameworks to avoid conflict. Thus, studies of conflict resolution will be useful in addressing these issues.

As technologies to monitor both human and animal behaviour expand in use, concerns about privacy, rights, and access to data will enter this discussion with increased frequency, and could be considered an emergent area for further study. Conservation efforts must adapt to this digital age through a better appreciation of the drivers of human behaviour, social structure and effective communication. Advancements on these emerging themes may help resolve some of the longstanding challenges, limitations, and conflicts by offering a wider, deeper, and more inclusive and robust framework for understanding the human-sea turtle relationship.

Q19. Which conservation strategies are working (have worked) and which have failed?

Complex population dynamics and life cycles, long lifespans and extended generation times, and multiple natural and anthropogenic stressors across wide distributions present significant challenges to comprehensive, effective conservation approaches for sea turtles. There is clearly room to improve the critical appraisal of our interventions and to incorporate lessons learned from holistic approaches to sea turtle conservation that explicitly integrate human communities at relevant geographic scales to maximise their effectiveness. See discussion of evidence-based conservation (Flaspohler et al. 2000, Pullin & Knight 2001, 2009, Pullin et al. 2004, Sutherland et al. 2004, Fazey et al. 2005) and scale-dependent engagement of human actors in holistic sea turtle conservation (Campbell 2007, Dutton & Squires 2011). A comprehensive, integrated analysis of current conservation practices that includes political and human dimensions at different geographic scales (*sensu* Frazier

1999, Marcovaldi & Thomé 1999, Campbell 2007, Dutton & Squires 2011) is beyond the scope of this section; below we focus discussion on the progress (or lack thereof) of some sea turtle conservation approaches in recent years.

Decades of protection of females at nesting beaches and the advent of CITES and locally enabling legislation have likely contributed to successful population recovery at nesting sites around the world (Dutton et al. 2005, Marcovaldi & Chaloupka 2007, Abreu-Grobois & Plotkin 2008, Chaloupka et al. 2008, Allen et al. 2010, Mortimer et al. 2011, Ehrhart et al. 2014, Weber et al. 2014, Balazs et al. 2015b, Bourjea et al. 2015b). Preserving nesting females (and their breeding, migratory and foraging habitats) remains an essential element of any conservation programme because their delayed sexual maturity and lifetime fecundity makes each mature female disproportionately valuable to the population. In contrast, conservation efforts focused only on the youngest sea turtle life stages have not shown clear benefits—e.g. 19th/20th century fisheries legislation protecting small turtles preferentially to adults (Mortimer 1984), and head-starting of hatchlings in captivity (Mortimer 1995, but see Bell et al. 2005). Nevertheless, it is essential to develop conservation strategies that also target the often overlooked in-water life stages (Crouse et al. 1987). Efforts must be expanded to address threats to, and monitor status of, all life stages of individual population segments to effect durable sea turtle population recoveries. In some cases, this can be challenging: for example, green turtle recovery in various geographies is leading to concerns regarding ecosystem collapse and human-wildlife conflict (Lal et al. 2010, Christianen et al. 2014) in some instances, while in others it has been posited that increases in abundance may be a result of predator release due to shark overfishing (Heithaus et al. 2014).

A major threat is fisheries bycatch (see Q13), and there have been significant advances evaluating and addressing this threat, particularly in small-scale fisheries in developing nations (Wallace et al. 2013, Lewison et al. 2015). Rapid, port-based interviews and radio communication with fishers from large numbers of ports provide baseline information about sea turtle bycatch in fisheries that are typically poorly monitored, if at all, by conventional techniques (e.g. on-board observers) (Alfaro-Shigueto et al. 2011, 2012). The ability to identify areas of bycatch risk improves predictions and informs management through analyses that overlay sea turtle distribution and abundance, fishing effort, and environmental correlates of both (Howell et al. 2008, Fossette et al. 2014, Roe et al.

2014). Although effectiveness of bycatch mitigation—typically through changes in fishing gear—has been the focus of more critical research effort than any other interventions (Gilman et al. 2006, 2007, 2010, Read 2007, Alessandro & Antonello 2010, Bostwick et al. 2014, Senko et al. 2014b, Ortiz et al. 2016, Peckham et al. 2016), there is a paucity of published papers evaluating the success of other conservation interventions in reducing effects of bycatch on sea turtles, especially in recent years. Exceptions include efficacy of marine protected areas (Revuelta et al. 2015a) and rehabilitation success (Baker et al. 2015).

Restoring sea turtle populations to their historic abundance may be infeasible in most cases, given the current state of available habitats and anthropogenic threats. Nonetheless, tangible, measurable recovery goals are needed to orient management efforts, especially at regional and global scales. Indeed, several sea turtle populations have increased significantly in abundance, thrusting a challenging, but positive, question before the conservation community: What protections should remain in place, if any, when a population reaches levels by status assessment frameworks (e.g. IUCN Red List, USA Endangered Species Act, Australia's Environmental Protection and Biodiversity Conservation Act) that merit 'downlisting' to less- or non-threatened categories? There is a valid concern that downlisting will encourage excessive resource use by communities whose activities are currently constrained by protective regulations (see Q20). However, conservation approaches should engage human actors appropriately at different geographic scales, paying special attention to how communities use, value, and manage sea turtles at local scales (Campbell 2007). Nevertheless, as this challenge continues to emerge, the sea turtle conservation community must embrace a holistic perspective that recognises the need to both celebrate and ensure conservation gains.

Q20. Under what conditions (ecological, environmental, social and political) can consumptive use of sea turtles be sustained?

The issue of sustainable use of sea turtles continues to be contentious (Campbell 2012). Since 2010, 3 categories of research have featured in the literature: (1) biological sustainability, (2) social, economic, or cultural sustainability, or (3) both of the above. Although there are studies of illegal take of sea turtles and eggs, we focus on legalized take regimes where sustainability is an explicit or implicit goal.

In the first category, studies focus on documenting and describing levels of legal take of sea turtles, either for a specific project or area over time (Humber et al. 2011, Valverde et al. 2012, Lagueux et al. 2014), or globally (Humber et al. 2014). These datasets provide necessary information for improved understanding of what kind of directed take exists, and help establish a baseline against which to evaluate future trends. Beyond this, focused research on what level of harvest is sustainable to the target population is relatively rare. Nearly all recent research on harvest has focused on stage class survivorship and population trends of turtle rookeries exposed to directed take of either eggs or later life stages, and these studies tend to suggest that any harvest will cause population decline (e.g. Campbell & Lagueux 2005, Santidrián Tomillo et al. 2008, Macrae & Whiting 2014, Senko et al. 2014a, Bourjea et al. 2015b), even if there has been no documented decline in all the study populations.

In the second category, 2 relevant papers were published in the same year as the Hamann et al. 20 questions, in a special issue of the journal *Conservation and Society* dedicated to social science research on sea turtle conservation (Campbell 2010, Garland & Carthy 2010). Garland & Carthy (2010) describe shifts in consumption of turtle meat among the Miskito people of Nicaragua, and how this was influenced by changing taste preferences and economic context, among other things. They found pressures for both increased and decreased consumption in the future. Grayson et al. (2010) evaluate the potential for community-based versus regionally-based co-management of sea turtles by Hammond Islanders in the Torres Straits, with the aim of balancing the rights of Torres Strait Islanders with long-term sustainability of turtle harvesting. More recently, a long standing and well known case of use—the legal harvest and sale of olive ridley sea turtle eggs from Ostional, Costa Rica (Campbell 1998, Campbell et al. 2007)—was assessed through the lens of common property resource (CPR) theory. Madrigal-Ballesterro et al. (2013) analyse how rule-following behaviour among egg harvesters varies according to demographics, economic dependence, perceived legitimacy of rules, and social norms. Schlüter & Madrigal (2012) also use the Ostional case to further methodological thinking about social-ecological systems. All these studies recognise that questions of biological sustainability do not exist in isolation; they are tightly linked to, and arguably dependent on, social, economic, and cultural sustainability of institutions guiding management.

The third category both recognises, and empirically interrogates, these linkages. A multi-disciplinary study on the legal fishery of green and hawksbill turtles in the Turks and Caicos Islands (Richardson et al. 2009) assessed ecological, social, economic, and cultural aspects of the fishery, and led to national legislative changes. These changes were directed at maintaining the fishery while reducing negative impacts to population growth and on the more vulnerable hawksbill turtle (Stringell et al. 2015a). An innovative participatory research method (CommunityVoice Method.org) was used both to collect data and to engage fishers and community members in discussing and vetting the recommended legislative changes before they were submitted to government (see TCI case study in Christie et al. 2014). Continued monitoring will reveal whether this fishery is sustainable, and highlights the need for long-term monitoring for assessing sustainability.

Although legal harvest regimes for sea turtles are uncommon in contrast to other conservation approaches, the need to assess the possibilities for sustainable use remains. For example, green turtles make up more than 80% of turtles harvested legally world-wide (Humber et al. 2014), and with the recovery of many green turtle rookeries globally (Weber et al. 2014, García-Cruz et al. 2015), we need further research into how to manage turtle fisheries to minimize negative impacts, as it is unlikely that they will become a thing of the past. Research must include socio-economic studies into the drivers of both legal and illegal fisheries in order to better manage and protect populations (Hancock et al. in press).

GENERAL DISCUSSION

This review finds that significant effort is being expended towards global research priorities for management and conservation of sea turtles. Sea turtles are now a very well researched taxon, and are subject to a wide variety of conservation actions which appear, in some cases, to be leading to recovering turtle populations.

Although variable, there has been clear advancement towards the key research questions identified by Hamann et al. (2010), whether we look at the systematic review of 2 recent years of publications or the integrated expert opinion of contributing authors. As yet under-researched are those relating to reproductive biology (Q1–3), threats (Q12–16) and conservation strategies (see Q17–20). Some of these biases may have been less marked if we had incorporated

non-peer-reviewed literature and/or non-English literature sources. Additionally, no proactive effort was made to promote the 20 key questions, other than Open Access publication which may have lessened the impact of the exercise.

Compiling this critical review has highlighted that it may be timely to undertake one or more new prioritizing exercises. For this work to have maximal benefit we make the following recommendations that echo those of the original exercise.

A need for a far greater engagement with social sciences

Although the field of conservation has traditionally been dominated by natural scientists—primarily conservation biologists and ecologists—calls for increased engagement with social sciences from those within and external to the field are now ‘routine’ (Bennett et al. 2016) and have been directed to sea turtle conservation specifically (Frazier 2005, Campbell 2010). Yet, as this paper reveals, the tendency to prioritize biological questions remains. Although this prioritization reflects both ‘who’ participated in the original question setting and in this review of progress, and ‘how’ the review of progress was conceptualized, it also likely reflects 2 related realities: (1) sea turtle conservation remains dominated by natural scientists, (2) integration of natural and social sciences is difficult, both generally (Sandbrook et al. 2013, Bennett et al. 2016) and for sea turtle conservation, specifically (Campbell 2007).

However, if we accept that natural science alone is ‘insufficient to find solutions to complex conservation problems that have social dimensions’ (Sandbrook et al. 2013, p. 1488), then we need to tackle, rather than shy away from, these difficulties. Social science research ‘for’ sea turtle conservation—defined as research that strives to enhance conservation by studying, for example, how humans interact with and impact on biodiversity, and how individuals or communities can be motivated or incentivised to reduce negative impacts or contribute directly to conservation (cf. Sandbrook et al. 2013)—is evident in this review, but we need more of it. Furthermore, most of the existing research ‘for’ conservation is directed at specific field sites or conservation projects. Although it is essential to understand the history, culture, politics and economics of people and communities who interact with sea turtles in particular places, there is also a need for work at broader scales or on general policies that influence these place-specific outcomes,

i.e. to understand how decisions are made, policies formulated and finally translated into practice. For example, how do new national or regional policies in support of other sectors or goals—e.g. tourism, poverty reduction, fisheries reform, port development, coastal resilience—interact with or impact existing formal and informal institutions for sea turtle conservation and management? Current quantitative frameworks such as network analyses and graphical models provide both an approach to understand these processes as well as tools for effective decision and practice.

Social science research 'on' conservation 'studies the conservation movement itself as a social phenomenon' (Sandbrook et al. 2013, p. 1488) and is less evident in this review (e.g. Campbell 2012, Liles et al. 2014). Research 'on' conservation is often met with hostility by conservationists, seen as counter-productive to their interests. However, Sandbrook et al. (2013, p. 1489) argue that conservation professionals need to 'understand themselves as a community with particular interests, habits, and characteristics', and understand 'the political and economic processes that not only affect the state of the natural world, but also frame and constitute the work of conservation organizations themselves' (p. 1489). This kind of research may prove particularly important if and when conservation biologists and practitioners have to reorient their activities and priorities in the face of recovering sea turtle populations, as referenced in several sections above.

After over 50 years of orienting activities around the perceived threat of extinction, how will existing institutions for sea turtle conservation be transformed and remain relevant in the face of recovered populations? The response of scientists, volunteers, local residents, and conservation professionals and governments (local, state, and federal) invested in a particular vision of sea turtle conservation will have important impacts for the sustainability of existing institutions and/or the emergence of new ones.

Widening the pool of contributors

As pointed out in Hamann et al. (2010) future exercises would benefit from a wider range of stakeholders consulted and involved in generating questions, and weighting their importance. This would include more management and policy professionals, governmental environmental resource managers and practitioners from industrial sectors that interface with turtle conservation, e.g. fisheries, port development, tourism,

petrochemicals, government agencies and legal experts. Such engagement would help identify research needs for specific conservation problems, such as testing gear modifications to reduce bycatch of sea turtles (e.g. Murray 2015) or policy innovation. Including stakeholders from a wider array of countries will help ensure that a diversity of issues and approaches to research and sea turtle conservation is included in this type of assessment. It should also help avoid a biased emphasis on sea turtle issues that are experienced by certain regions or research groups that tend to be over-represented in the published literature (Fig. 2).

Focussing the questions

In undertaking this appraisal, it became clear that the focus of the questions generated in the first exercise was not precise enough. Any subsequent prioritizing exercise would need to develop more specific and discrete questions, even if it means they are not so easily prioritized into a 'top 20'. The considerable overlap among the questions became obvious as they were reviewed, and there are clearly emerging themes which could be more effectively highlighted in any new exercise. Given the biases outlined above it is likely that we should disentangle ecology from conservation (see Sutherland et al. 2006, 2009). A further step forward could be improving the connection between the priority research questions and priority conservation actions; moving from a qualitative to a quantitative assessment of how the field is heading. Finally, a concerted effort should be made to publicize resultant priority questions and enhance their impact.

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Appendix 1. Scientific literature (details below table) published in 2014 and 2015 that address the 20 questions highlighted by Hamann et al. (2010)

Question	References
1 What are the factors that underpin nest site selection and behaviour of nesting turtles?	1–9
2 What are the primary sex ratios being produced and how do these vary within or among populations and species?	10–21
3 What factors are important for sustained hatchling production?	8, 14, 15, 18, 19, 21–41, [42], [43]
4 What are the population boundaries and connections that exist among rookeries and foraging grounds?	44–101
5 What parameters influence the biogeography of sea turtles in the oceanic realm?	48, 51–53, 70, 71, 79, 82, 85, 87, 88, 91, 102–117
6 Where are key foraging habitats?	45, 46, 49, 58, 60–62, 70, 71, 73, 80–84, 96, 99, 103, 104, 108, 117–133
7 Can we develop methods to accurately age individual turtles, determine a population's (or species') mean age-at-maturity, and define age-based demography?	111, 134–145
8 What are the most reliable methods for estimating demographic parameters?	25, 42, 59, 98, 112, 121, 131, 134–138, 140, 146–165
9 How can we develop an understanding of sea turtle metapopulation dynamics and conservation biogeography?	44, 48–50, 52–57, 59–63, 65–69, 72–78, 80, 81, 83–90, 92–95, 97, 98, 100, 101, 116, 137, 142, 145, 151, 159, 160, 166–174
10 What are the past and present roles of sea turtles in the ecosystem?	175–182
11 What constitutes a healthy turtle?	183–229
12 What will be the impacts from climate change on sea turtles and how can these be mitigated?	5, 10, 11, 14, 18, 19, 21, 28–30, 35, 39, 82, 110, 117, 166, 230–248
13 What are the major sources of fisheries bycatch and how can these be mitigated in ways that are ecologically, economically and socially practicable?	58, 64, 82, 96, 102, 106, 181, 249–285
14 How can we evaluate the effects of anthropogenic factors on sea turtle habitats?	246, 286
15 What are the impacts of pollution on sea turtles and their habitats?	196, 197, 217, 287–311
16 What are the etiology and epidemiology of fibropapillomatosis (FP), and how can this disease be managed?	183–185, 193, 197, 207–209, 212, 227, 229, 297, 312–314
17 How can we effectively determine the conservation status of sea turtle populations?	47, 62, 81, 97, 112, 147, 149, 150, 164, 165, 315–320
18 What are the most viable cultural, legal and socioeconomic frameworks for sea turtle conservation?	97, 175, 250, 259, 264, 266, 269, 279, 283, 285, 317, 319, 321–337
19 Which conservation strategies are working (have worked) and which have failed?	22, 26, 32, 47, 67, 97, 149, 164, 236, 239, 266, 277, 278, 316, 317, 319, 321, 323, 324, 326, 329, 331, 335, 336, 338–353
20 Under what conditions (ecological, environmental, social and political) can consumptive use of sea turtles be sustained?	69, 97, 250, 266, 277, 316, 319, 322, 324, 327, 331, 336, 341, 354, 355

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