



REVIEW

Climate change and marine turtles: recent advances and future directions

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ABSTRACT: Climate change is a threat to marine turtles that is expected to affect all of their life stages. To guide future research, we conducted a review of the most recent literature on this topic, highlighting knowledge gains and research gaps since a similar previous review in 2009. Most research has been focussed on the terrestrial life history phase, where expected impacts will range from habitat loss and decreased reproductive success to feminization of populations, but changes in reproductive periodicity, shifts in latitudinal ranges, and changes in foraging success are all expected in the marine life history phase. Models have been proposed to improve estimates of primary sex ratios, while technological advances promise a better understanding of how climate can influence different life stages and habitats. We suggest a number of research priorities for an improved understanding of how climate change may impact marine turtles, including: improved estimates of primary sex ratios, assessments of the implications of female-biased sex ratios and reduced male production, assessments of the variability in upper thermal limits of clutches, models of beach sediment movement under sea level rise, and assessments of impacts on foraging grounds. Lastly, we suggest that it is not yet possible to recommend manipulating aspects of turtle nesting ecology, as the evidence base with which to understand the results of such interventions is not robust enough, but that strategies for mitigation of stressors should be helpful, providing they consider the synergistic effects of climate change and other anthropogenic-induced threats to marine turtles, and focus on increasing resilience.

KEY WORDS: Climate change · Marine turtles · Sea turtles · Sex ratio · Phenology · Sea level rise · Impact mitigation · Resilience

1. INTRODUCTION

Human-induced climate change is one of the main threats to nature and human civilization (Pecl et al. 2017, Lenton et al. 2019). Each decade since the 1980s has been warmer than any before on record, 9 of the 10 warmest years have occurred since 2005, Arctic

temperatures have likely been the warmest in the last 2000 years, and atmospheric carbon dioxide is now at 414 ppm, higher than any time in more than 100 000 yr (<https://climate.nasa.gov>). This planetary-scale modification of the climate is having strong effects on biodiversity and ecosystems, with major impacts forecast (Newson et al. 2009, Walther 2010). Numerous

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species are already responding by changing their phenology and distribution, among other adaptations (Walther 2010, Feeley et al. 2017, Piao et al. 2019), while others are declining (Pecl et al. 2017) or have become extinct (Urban 2015, Waller et al. 2017). Notably, species responses to current rapid changes are not necessarily effective and can lead to mismatches between periodic events (e.g. breeding, wintering) and resource availability (Edwards & Richardson 2004, Post & Forchhammer 2008).

Research on the effects of climate change on biodiversity has been disproportionately centred on terrestrial organisms (Feeley et al. 2017), likely due to easier accessibility and accordingly better baseline data on both species and climate, yet numerous impacts on marine biodiversity have now been documented, from local to global scales (Poloczanska et al. 2016, Worm & Lotze 2016, Crespo et al. 2019). Most long-term studies have focussed on fish and plankton (Worm & Lotze 2016), with recent research assessing impacts on large marine megafauna (Erauskin-Extramiana et al. 2019, Albouy et al. 2020), corals (Hughes et al. 2018), seagrasses (Chefaoui et al. 2018), and seaweeds (Martins et al. 2019).

Marine turtles are a particularly interesting case study, as they have a marine and a terrestrial phase and depend on productive neritic or oceanic ecosystems for foraging, and on low-lying sandy beaches for nesting (Bolten 2003). Thus, all 7 extant species of marine turtles, which as a group are globally distributed across the Earth's tropical, subtropical and temperate marine habitats (Wallace et al. 2010), will likely be directly and indirectly affected by climate change, with impacts varying geographically, temporally, and between species and populations (Hawkes et al. 2009, Poloczanska et al. 2009, Hamann et al. 2013, Fuentes & Saba 2016). Here, we present a review of the most recent literature on climate change impacts on marine turtles, providing an update since a previous similar review by Hawkes et al. (2009), to help guide future work on the topic.

2. METHODS

To identify the relevant literature, we applied the search terms 'marine turtle climate change' and 'sea turtle climate change' in Web of Science and Google Scholar, and then used the 'snowball' approach, by thoroughly searching both the literature cited in these articles and the articles in which they were cited. We then screened the abstracts of each article and rejected papers that were not related to climate

change and marine turtles. The papers that were kept were categorized by habitat, climate change threat, expected climate change impact, species, and geographic location. Papers previously reviewed by Hawkes et al. (2009), which were published between 1988 and April 2009 ($n = 54$), were also categorized in the same manner and referred to as the 'original database'. Throughout this review, we summarize where most research on this topic has focussed (Section 3), review the most recent studies assessing climate change impacts on different marine turtle life stages/parameters (Section 4), outline management strategies to reduce predicted impacts (Section 5), and set research priorities to improve our knowledge on how climate change may impact marine turtles (Section 6).

3. SUMMARY OF MAIN RESEARCH TOPICS

Interest in the impacts of climate change on marine turtles has increased (Fig. 1), and we found 202 peer reviewed papers on this subject, published from May 2009 to October 2020, representing 76% of all the peer-reviewed papers on this topic since 1988. Overall, the main areas of research were consistent between the new and the original database, for all categories, and are summarized in Fig. 2. Considering both the 'original database' (1988–2009) and the new database (2009–2020), by far, most research was focussed on the terrestrial phase only (Fig. 2). Considering climate-change-induced threats to marine turtles or their habitats, during both periods, the

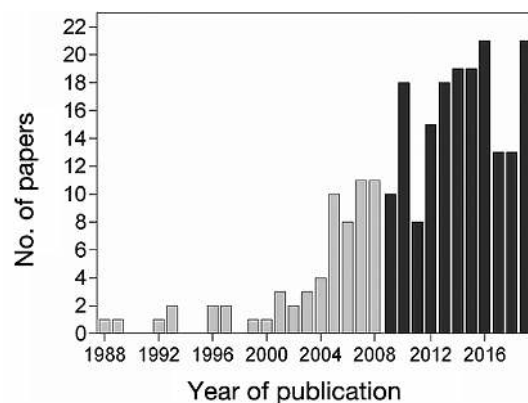


Fig. 1. Number of peer-reviewed studies per year on climate change impacts on marine turtles; grey bars: studies published between 1988 and April 2009 and reviewed by Hawkes et al. (2009), black bars: studies published from May 2009 to December 2019. Publications from 2020 are not included in the figure (although they have been reviewed in the article), as the numbers would not be representative of the whole year

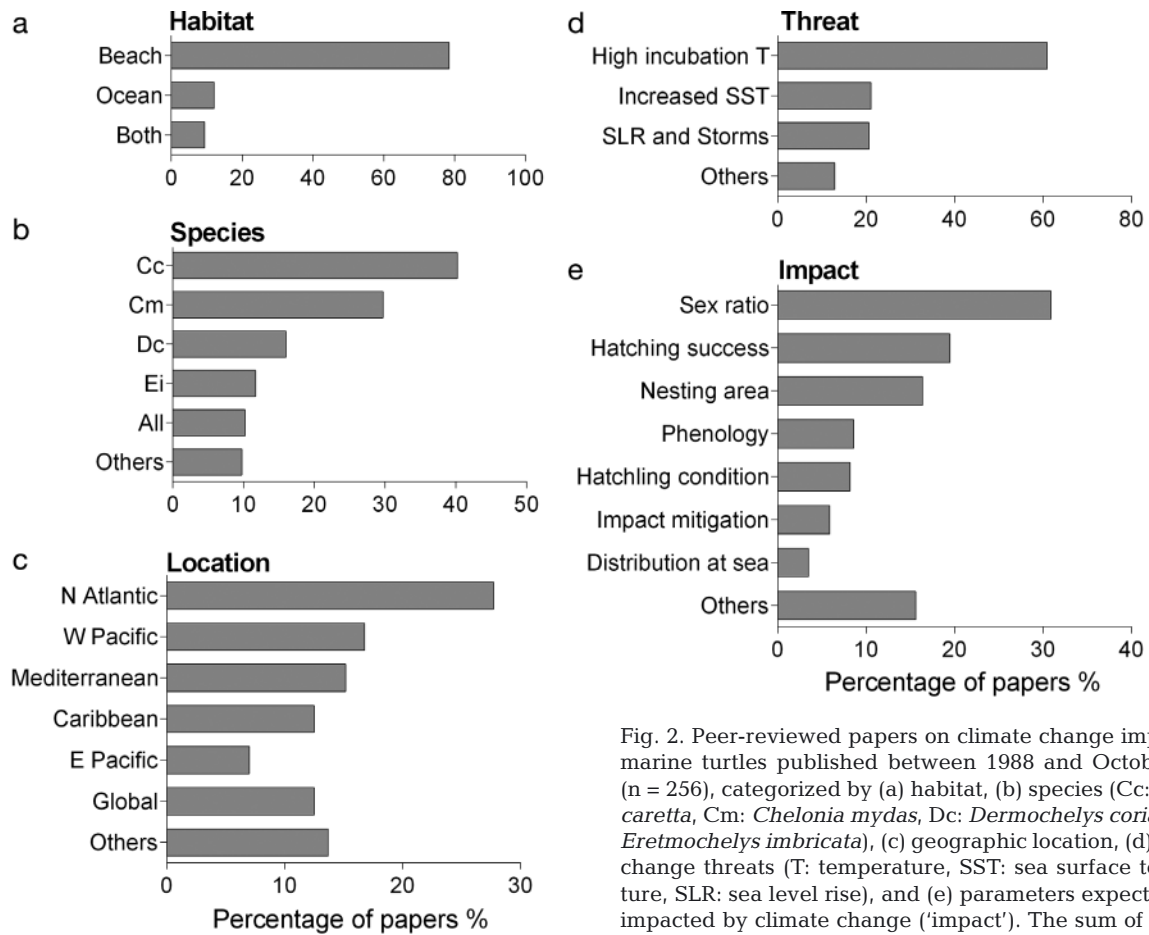


Fig. 2. Peer-reviewed papers on climate change impacts on marine turtles published between 1988 and October 2020 (n = 256), categorized by (a) habitat, (b) species (Cc: *Caretta caretta*, Cm: *Chelonia mydas*, Dc: *Dermochelys coriacea*, Ei: *Eretmochelys imbricata*), (c) geographic location, (d) climate change threats (T: temperature, SST: sea surface temperature, SLR: sea level rise), and (e) parameters expected to be impacted by climate change ('impact'). The sum of the percentages can be above 100%, as some papers assess more than 1 species, location, threat, or impact

future increase in incubation temperatures received the most attention, followed by sea level rise and storms and by increases in sea surface temperature (SST). As for the potential impacts from climate change, biased sex ratios were the most addressed during the both periods, followed, in the new database, by reduced hatching success, loss of nesting area, hatchling morphology, survival and performance ('hatchling condition' in Fig. 2), changes in breeding phenology, and strategies for impact mitigation. In the original database, the most researched impacts after biased sex ratios were changes in movements and distribution at sea, reduced hatching success, and changes in breeding phenology. Loggerhead turtles *Caretta caretta* and green turtles *Chelonia mydas* were the most researched species during both periods. Lastly, when considering the geographic distribution of studies, most focussed on the North Atlantic, the West Pacific, the Mediterranean, and the Caribbean, with a small number of global assessments.

4. CURRENT KNOWLEDGE, RESEARCH ADVANCES, AND KNOWLEDGE GAPS

Throughout this section, we recap the base knowledge on how climate change can impact different life-stages/parameters (Fig. 3), we review the most recent literature, highlight research advances made in the last 11 yr, assess knowledge gaps, and briefly suggest ways forward to improve our knowledge on the impacts of climate change on marine turtles.

4.1. Sex ratios

The effects of climate change on the primary sex ratio of marine turtles, i.e. the sex ratio of offspring, was the first parameter that researchers warned would be affected by climate change (Davenport 1989, 1997, Janzen 1994, Mrosovsky 1994). Since marine turtles have temperature-dependent sex determination (TSD; Yntema & Mrosovsky 1980,

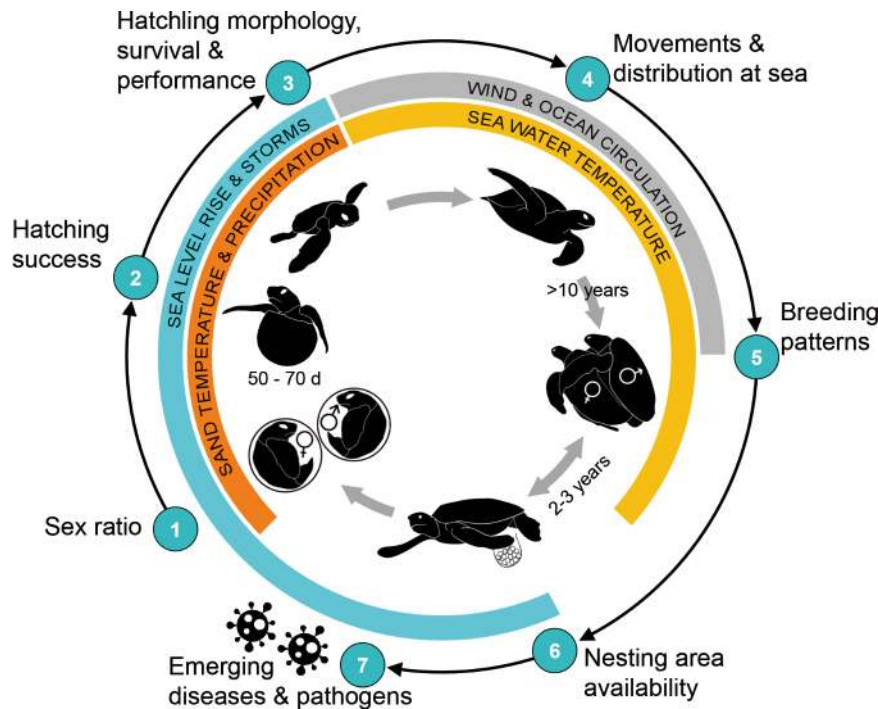


Fig. 3. Generic life cycle of marine turtles with parameters expected to be impacted by climate change as reviewed in Section 4. Predominant associated climate threats are noted. Parameter numbers link to subsection numbers in Section 4

Ackerman 1997), it is predicted that increases in incubation temperatures will eventually lead to feminization of some marine turtle populations (Janzen 1994, Santidrián Tomillo et al. 2015a). The majority of studies estimating current primary sex ratios reported female biases, for all species of marine turtles in all ocean basins in which they occur (e.g. Mrosovsky & Provancha 1992, Godfrey et al. 1996, Binckley et al. 1998, Hanson et al. 1998, Broderick et al. 2000, Sieg et al. 2011, King et al. 2013, Binhammer et al. 2019, Monsinjon et al. 2019a, Tanner et al. 2019), with few reports of balanced to slightly male-biased primary sex ratios (Stubbs et al. 2014, Esteban et al. 2016, Patrício et al. 2017, Laloë et al. 2020). Thus, when modelling primary sex ratios of marine turtles under future climate change scenarios, several studies projected that male production may cease in the near future (2100; e.g. Janzen 1994, Hawkes et al. 2007a, Witt et al. 2010, Monsinjon et al. 2019a), particularly in populations that are already producing extremely female-skewed primary sex ratios (Hays et al. 2017, Monsinjon et al. 2019a, Tanner et al. 2019). For example, in one of the world's largest green turtle populations (northern Great Barrier Reef, Australia; Limpus 2008), 99.1% of the juveniles, 99.8% of the subadults, and 86.8% of the adults were estimated to be female (Jensen et al.

2018), suggesting that the primary sex ratio has been increasingly female skewed for around 20 to 30 yr (Chaloupka et al. 2004), with projections indicating the future feminization of this population (Fuentes et al. 2010a).

4.1.1. Direct methods to identify the sex of hatchlings: from the examination of gonads to molecular clues

Determining primary sex ratios currently requires sacrificing hatchlings for histological examination of gonads. This is ethically challenging given that most marine turtle species are protected in many countries. Laparoscopy is a non-lethal alternative (Wyneken et al. 2007), but is a highly skilled procedure, and is labour and resource intensive, as sexing cannot be carried out until hatchlings are several months old (Wyneken & Lolavar 2015). Consequently, several studies have explored the potential of molecular markers, such as the accumulation of sex steroid hormones in the plasma of neonates (Gross et al. 1995), in the amniotic fluid from the egg (Xia et al. 2011), and in eggshells (Kobayashi et al. 2015), to identify the sex of marine turtle hatchlings, with reports of high levels of agreement in sex identification between hormone ratios and gonad histology observa-

tions. Other studies have looked at temperature-dependent expression of an RNA-binding protein in gonads (Tezak et al. 2017), and at compounds expressed at either male- or female-promoting temperatures (e.g. Anti-Müllerian hormone and CYP19A1 aromatase, respectively, Tezak et al. 2020a). These methods are promising and could facilitate the identification of sex ratios in the field, but will be limited to researchers who have access to the analytical skills and facilities required to run such samples at large scales, and their application at ecologically relevant spatial (beaches) and temporal (nesting seasons) scales may remain unrealistic in the near future. Further, testing and modelling tools and the potential for low-cost field assays are required to properly extrapolate this critical population parameter under climate change scenarios.

4.1.2. Indirect methods to predict primary sex ratios: scaling up from a clutch to the entire beach

Given the challenges in directly assessing the sex of hatchlings, the majority of studies to date have relied on estimating primary sex ratios from either local air, sea surface, and/or sand temperature, or temperature measured inside egg clutches, often also estimating metabolic heating and the extent of thermal heterogeneity within the nest (Girondot & Kaska 2015, Monsinjon et al. 2017a,b, 2019a, Laloë et al. 2020). At the scale of an embryo, sex is determined by temperature during a thermosensitive period of development (TSP, Mrosovsky & Pieau 1991), which falls during the middle third of incubation under constant incubation temperatures. This has often led to the use of the mean nest temperature during the middle third of incubation to predict sex ratios (e.g. Sieg et al. 2011, Fuller et al. 2013, Laloë et al. 2014, 2016, Sari & Kaska 2015, Esteban et al. 2016, Yalçın Özdilek et al. 2016). More recent work shows that (1) the TSP shifts away from the middle third of incubation in field conditions (i.e. under variable thermal conditions, Girondot & Kaska 2014) and that (2) the mean temperature does not account for the role of embryonic growth during sex determination (Fuentes et al. 2017, Girondot et al. 2018), so previous models have now been improved by incorporating these adjustments. Additionally, sex ratio estimates have been found to vary depending on the metric used (i.e. temperature-based or duration-based) and the period over which it is calculated (whole incubation, middle third of incubation or actual TSP, Fuentes et al. 2017). It has been suggested that the constant

temperature equivalent (CTE, Georges 1989, Georges et al. 1994), defined as the temperature above (or below) which 50% of development occurs, is a better metric (Fuentes et al. 2017). This method has benefited from considerable improvements in recent years, specifically: an understanding of reaction norms that describe the progression of embryonic growth during incubation (Georges et al. 2005, Mitchell et al. 2008, Woolgar et al. 2013, Stubbs et al. 2014), a non-linear embryonic growth function (Girondot & Kaska 2014), a TSP based on embryonic stages (Fuentes et al. 2017, Girondot et al. 2018), and a new formulation of the CTE (CTE_{GROWTH}) that accounts for changes in the rate of embryonic growth (Fuentes et al. 2017). The CTE_{GROWTH} model (e.g. using the R package 'embryogrowth', Girondot 2020a) can be used to predict the sex ratio of a clutch based on the TSD reaction norm (also called sex ratio thermal reaction norm) if it has been derived from constant-temperature incubation experiments for the same population (see Abreu-Grobois et al. 2020 for a review of existing models).

Notably, to extend primary sex ratio estimates at the scale of an entire rookery, additional scaling parameters must be taken in consideration, because nests can experience different incubation conditions on the same beach depending on thermal microhabitats (Fuentes et al. 2010a, Patricio et al. 2017, Flores-Aguirre et al. 2020). Microclimate models (e.g. NicheMapR; Kearney & Porter 2017) are promising and can be used to explicitly characterize the heterogeneity of sand temperatures due to beach topography, shade, moisture, presence of vegetation, and beach-specific substrate physical properties (Fuentes & Porter 2013, Stubbs et al. 2014, Bentley et al. 2020, Laloë et al. 2020). However, these models require that some parameters are measured *in situ* for adequate calibration (e.g. moisture content, gravimetry), yet default parameters are sometimes used when no empirical measurements are available (but see Bentley et al. 2020). Additionally, implementing metabolic heating in microclimate models may be an important step forward since the heat produced by growing embryos increases the temperature of nests relative to their surrounding environment (Booth & Astill 2001, Broderick et al. 2001a), and models have to be properly parametrized for coastal environments (Bentley et al. 2020). Lastly, studies normally produce estimates of primary sex ratios from a subset of clutches, which are then used to indicate the primary sex ratio for a whole rookery and in some cases are used to infer population-level trends (e.g. Mrosovsky & Provancha 1989, Kaska et al. 2006, LeBlanc et al.

2012). In the future, including clutches laid at the beginning and end of nesting seasons, and multi-season data from a variety of beaches, will allow insights that fully capture seasonal variation. Some promising studies recently benefitted from sophisticated nesting dynamic models (Girondot 2017) to hindcast or forecast primary sex ratios of loggerhead and green turtle nesting populations (Monsinjon et al. 2019a, Laloë et al. 2020). This remains to be conducted for other marine turtle rookeries worldwide.

4.1.3. Understanding TSD under natural conditions

Despite the volume of research focussed on the effects of climate change on the sex ratio of hatchlings, several knowledge gaps still exist. First, in a key review, Wyneken & Lolavar (2015) showed that the majority of studies published to date have derived sex ratio estimates from ‘second and third level proxies’, for example estimating sex ratio from mean nest temperature or from incubation duration, respectively. Comparatively few studies have carried out hatchling gonad histology to verify sex directly (a ‘first-order proxy’) and even those that have, likely statistically under-sampled each clutch and lack evidence to suggest that the sampled individuals properly represent the sex ratio of the whole clutch in question, let alone the rookery (Wyneken & Lolavar 2015). Because of the lack of such studies, it is not clear how much variation there may be in pivotal temperatures, the transitional range of temperatures, and the slope of the relationship between temperature and sex ratio (i.e. parameters of TSD reaction norms) between individuals, rookeries, and ocean basins. How widely can an equation relating nest temperature to resultant sex ratio be applied? This question clearly reveals a gap in our understanding of TSD under natural conditions, as our assumptions mostly rely on constant-temperature incubation experiments in laboratory conditions (even sometimes relying on data from a different population). Several studies have attempted to estimate TSD reaction norms from field data, such as mean nest temperatures (e.g. Kaska et al. 1998, 2006, Öz et al. 2004, LeBlanc et al. 2012, Patrício et al. 2017) or incubation durations (e.g. Godley et al. 2001, Fuller et al. 2013, dei Marcovaldi et al. 2014, Sari & Kaska 2015). However, these approaches are likely biased since they do not account for uncontrolled sources of variation (e.g. genetic background and maternal effect) and compounding effects of fluctuating temperatures when multiple nonlinear and nonmonotonic reaction norms are

involved (known as Jensen’s inequality; Ruel & Ayres 1999, Martin & Huey 2008, Denny 2017), as it is the case for sex determination in the freshwater turtle *Chrysemys picta* (Neuwald & Valenzuela 2011). We urge future studies to bridge this gap and allow for the estimation of TSD reaction norms from *in situ* temperature data. This research area should benefit from the recent development of promising sexing techniques (Tezak et al. 2017, 2020a) that will considerably facilitate the estimation of sex ratios from *in situ* nests at broad spatial and temporal scales.

Importantly, some studies have presented evidence that nest humidity may play an underappreciated role in modifying sex ratios, and that a male bias can be produced at ‘female-producing’ incubation temperatures if clutch humidity is high (Wyneken & Lolavar 2015). This is likely due to evaporative cooling (Lolavar & Wyneken 2017, 2020); further studies will allow us to clarify the mechanism behind these observations, as this is a major avenue for future research (Sifuentes-Romero et al. 2018).

4.1.4. Reconstructing past and future nest temperature

How we trust primary sex ratio predictions under scenarios of changing climates depends on the reliability of reconstructed nest temperatures. Two approaches are commonly used to predict nest temperatures: either a correlative approach (i.e. linear relationships between sand or nest temperature and environmental variables) or a mechanistic (process-explicit) approach (i.e. heat balance equation, accounting for heat transfers via radiation, convection, conduction, and evaporation). Both approaches have limitations that require further investigation. Many studies also either predict sand temperatures at nest depth (i.e. without accounting for metabolic heating) or incubation temperatures experienced by embryos within nests. Correlative models likely provide reasonably accurate estimations of average daily temperature in the middle of the clutch (Fuentes & Porter 2013, Girondot & Kaska 2015, Monsinjon et al. 2019a, Laloë et al. 2020) but may not be useful outside of the ranges over which the original models were fitted (Fuentes & Porter 2013, Bentley et al. 2020), which reduces their applicability under scenarios of changing climates. Air temperature has been widely used for nest temperature predictions (Hays et al. 2003, Laloë et al. 2014, 2016, 2017, Esteban et al. 2016, Patrício et al. 2017, 2019), and SST may improve estimates (Fuentes et al. 2009, Girondot & Kaska 2015,

Bentley et al. 2020), while other variables (e.g. sand moisture, cloud cover, precipitation, influence of vegetation, wind speed) are yet to be accounted for. On the other hand, mechanistic models (Fuentes & Porter 2013, Stubbs et al. 2014, Cavallo et al. 2015, Whiting et al. 2018, Bentley et al. 2020, Laloë et al. 2020) hold potential for sand temperature predictions at specified depths, provided that required input data (e.g. sand physical properties, beach topography, meteorological variables) are available. However, this makes such models difficult to run at large spatial and temporal scales, since physical properties could differ greatly across nesting beaches, and local weather conditions are often at remote sites and can only be predicted with limited confidence for the future. In addition, the only model used so far for marine turtles (NicheMapR microclimate model, Kearney & Porter 2017) was initially developed for terrestrial ectotherms and thus cannot yet account for other coastal physical processes (Bentley et al. 2020), such as tidal movements and wave action.

The choice of input data used to drive a model (being correlative or mechanistic) is also a critical step. So far, the field has not considered environmental variation at spatial and temporal scales that are relevant for marine turtles. For instance, monthly mean temperatures derived from global climate datasets have previously been used to project sand temperatures (Laloë et al. 2014, 2016, 2017, Esteban et al. 2016). Yet short-term exposure to high temperatures can lead to a higher proportion of females than what would be expected from average temperatures (Georges 1989, Georges et al. 1994), and rainfall spikes throughout a nesting season can provide short periods of cooling and thus decrease incubation temperatures (Houghton et al. 2007). Daily beach-scale temperature variations have important implications for biological and ecological processes (Ruel & Ayres 1999, Martin & Huey 2008, Denny 2017, 2019), including incubation and sex determination in marine turtles. Using daily temperatures should improve both correlative and mechanistic models (Monsinjon et al. 2019a, Laloë et al. 2020). Additionally, global climate reanalysis products can be used to provide a clear picture of thermal microhabitats (Carter et al. 2015), according to species' size and ecology, thus avoiding spatial mismatches between the size of organisms and the scale at which climate data are modelled (Potter et al. 2013). We encourage future studies to (1) thoroughly characterize nesting beach microclimates that comprise the spatial and temporal distribution of clutches for a population using *in situ* temperatures and local weather data, and (2) take

advantage of the latest release of gridded climate datasets with the finest spatial ($<0.5^\circ \times 0.5^\circ$) and temporal (<daily) resolutions (e.g. ECMWF ERA5 re-analysis; Hersbach et al. 2019), for a better understanding of the physical and meteorological processes at play in such highly dynamic environments (land-sea interface). Achieving such model improvements should enhance our ability to predict primary sex ratios with better accuracy, and at finer spatio-temporal scales.

4.1.5. Population persistence under female-biased sex ratios

How seasonal primary sex ratios translate into adult sex ratios remains largely unknown and may vary within and among species (Hawkes et al. 2009, Hamann et al. 2010, 2013). Recent studies suggest that some populations with female-biased primary sex ratios have balanced or male-biased adult sex ratios (Schofield et al. 2017, Lasala et al. 2018). Importantly, whether there are sex-specific differential mortalities across age classes requires further investigation. For instance, male leatherback turtle *Dermochelys coriacea* hatchlings may exhibit higher fitness than females (Rivas et al. 2019), while adult loggerhead females might exhibit higher annual survival rates than males (Schofield et al. 2020).

If adult sex ratios were to become extremely skewed, population-wide detrimental effects, such as reduced fertilisation rates (Bell et al. 2010) and increased genetic drift via a reduction of effective population size (Girondot et al. 2004), could theoretically occur. However, the operational sex ratio (OSR), i.e. the proportion of males and females successfully breeding each year, is likely to differ from the adult sex ratio in marine turtles because males may breed annually with several females, while females do not breed every year (Hays et al. 2010a, 2014, Casale et al. 2013). The OSR is currently best estimated by genetically reconstructing parentage of nests to identify the number of male sires (Wright et al. 2012a, Phillips et al. 2013). This approach provides a robust estimation of the OSR because marine turtles, unlike freshwater and terrestrial turtles, do not generally store sperm between nesting seasons that they could use to fertilise clutches in years without males present (Phillips et al. 2013, 2014, 2017, Sakaoka et al. 2013). For instance, a ratio of 1.3 breeding males for each nesting female was determined at a fine scale using genetic reconstruction of paternity in 94 green turtle nests (from an estimated 92% of all tur-

tles nesting at the study rookery) across 3 years (Wright et al. 2012a,b). Other studies have reported similar relatively balanced to male-biased OSRs (Hays et al. 2010a, Lasala et al. 2013, 2018, Schofield et al. 2017). Additionally, multiple paternity has been demonstrated in all 7 species of marine turtles (Lee et al. 2018), varying from 9% in hawksbill turtles *Eretmochelys imbricata* (Phillips et al. 2013) to 93% in loggerhead turtles (Zbinden et al. 2007), likely as a consequence of the incidence of male–female encounters (Lee et al. 2018). It thus seems sensible to suggest that male turtles are not currently scarce at breeding grounds.

Female bias in primary sex ratios in marine turtles is frequently referred to as a vulnerable life history trait, whereas there is no evidence at present to suggest this is true. A female-biased sex ratio could benefit populations in the short-term by enhancing their growth rate (Rankin & Kokko 2007, Boyle et al. 2014a, Hays et al. 2017, Patrício et al. 2019); however, sustained warming could overrun this demographic advantage (Saba et al. 2012, Laloë et al. 2014, Santidrián Tomillo et al. 2015a). Either way, an important question is yet to be elucidated: under what range of adult sex ratios is the persistence of populations maximized? Modelling studies indicate that we can expect enhanced population growth and range expansion in reptiles with TSD under a warming scenario, assuming male dispersal and no shortage of breeding males (Boyle et al. 2014a,b, 2016). Male-biased dispersal is likely to be the rule in marine turtles, as suggested from male-mediated gene flow (Karl et al. 1992, Casale et al. 2002, Bowen & Karl 2007), and could prevent highly female-biased populations from collapsing (Doody & Moore 2010, Boyle et al. 2016). Thus, TSD in marine turtles could allow for a coadaptation mechanism, by enhancing the fecundity of a population (through female production) when hatching success is lowered under extreme high temperatures (Santidrián Tomillo & Spotila 2020). However, whether those highly female-biased populations have (or will) become population sinks (i.e. population numbers falling below replacement level) needs to be investigated. In addition, Boyle et al. (2016) suggested that 3°C warming over the next 100 yr may be a ceiling at which population declines should be expected to occur for species with TSD, but also that in reptiles with a male/female TSD reaction norm, it may be possible to model what the optimal marine turtle adult sex ratio should be. Thus, although the impacts of climate change on marine turtle primary sex ratio have been widely studied, we suggest that much work remains to be done to fully

understand how this parameter might be affected and elucidate the resultant consequences.

4.2. Hatching success

Hatching success (the proportion of eggs that produce viable hatchlings) can be highly variable within and between species, but rates in excess of 65% of eggs producing viable hatchlings appear to be normal (Bell et al. 2010). However, if even small changes to the nest environment occur at the upper end of the incubation range of temperatures, they can affect hatching success. For example, at incubation temperatures above 30°C, an increase to 31°C can decrease hatching success by up to 25% (reviewed by Howard et al. 2014). The lethal upper thermal limit that embryos can withstand and still successfully hatch appears to vary within and between species (Pike 2014). Additionally, this threshold seems to depend on the duration over which the eggs are subjected to high temperatures, and it can be modulated by rainfall and nest humidity (Lolavar & Wyneken 2017). If mean incubation temperatures are above 35°C, hatching success may be close to zero, but nests can experience higher transient temperatures (e.g. 37°C) without them being lethal (Howard et al. 2014). In the context of climate change, the lethal upper thermal limit is extremely important to determine, because it underlies modelling efforts to predict the proportion of nests that may become unviable in the future (Hawkes et al. 2007a, Laloë et al. 2017, Laloë & Hays 2017, Monsinjon et al. 2019a, Tanner et al. 2019).

A thorough characterization of thermal microhabitats should elucidate temperature-induced incubation failure, which is important because some warmer ‘female-producing’ clutches might approach lethal temperatures more often (and thus experience higher mortality rates) than cooler ‘male-producing’ clutches. For example, models of thermal tolerance that allow for the estimation of both lower and upper lethal temperature thresholds could be useful when extrapolating primary sex ratios under shifting phenology scenarios towards cooler or warmer parts of the year (Monsinjon et al. 2019a). To date, most of the published estimates of upper thermal threshold limits are from loggerhead and green turtles (e.g. Matsuzawa et al. 2002, Weber et al. 2012, Read et al. 2013), but perhaps more importantly, the mechanistic basis for decreasing hatching success with increasing mean incubation temperature is not understood for any species. It may relate to oxygen availability within the nest (Ackerman 1980) but may also relate to in-

creases in abnormalities that inhibit development (Packard et al. 1977). Surprisingly, with few exceptions (Chen et al. 2010, Cheng et al. 2015, Stewart et al. 2019), there is a lack of studies using oxygen sensors in turtle nests, and the rates of abnormality in failed hatchling turtles have yet to be synthesised across species and populations. An important research line is the possibility of increasing thermal tolerance as a response to climate change. Tedeschi et al. (2016) assessed the capacity of loggerhead embryos to adapt to increasing temperatures, by assessing the expression of heat shock-genes, which mitigate damage to cells under heat stress. They found within-clutch plasticity in gene expression and showed that this plasticity was heritable, thus demonstrating the presence of molecular mechanisms for tolerating and, potentially, adapting to future rises in incubation temperatures (Tedeschi et al. 2016).

Average humidity and accumulated precipitation also affect hatching success (Santidrián Tomillo et al. 2012, Rafferty et al. 2017, Montero et al. 2018a). At drier sites, heavy rainfall was shown to increase hatching success, while the opposite was observed at high-humidity sites (Santidrián Tomillo et al. 2015b, Montero et al. 2019). Future increases in extreme weather events with protracted rainfall may enhance hatchling production at temperate beaches and lower it at tropical beaches (Montero et al. 2019). Additionally, Rivas et al. (2018) noted that deeper nests suffered higher mortality due to increases in the water table, so interactions between biological (e.g. nest depth, location) and environmental factors should be considered.

In summary, because the eggs of marine turtles incubate at the mercy of their local environment (Miller 1997), overall patterns of hatching success are related to local climatic factors such as temperature, rainfall, inundation, and storminess (Caut et al. 2010, Santidrián Tomillo et al. 2012, Ahles & Milton 2016, Montero et al. 2018a,b, 2019), but the effect of climate appears to be variable (Santidrián Tomillo et al. 2015b) and may not entirely explain hatchling production failure (Rafferty et al. 2017). Metabolic heat can also significantly increase incubation temperatures towards the end of development, and therefore impact hatching success (Zbinden et al. 2006, Gammon et al. 2020). Future work could seek to comprehensively describe how local climate influences the incubation environment in detail, i.e. not using a single average nest temperature but describing the full variation in temperature between all eggs in a clutch, along with humidity and groundwater inundation, and consider metabolic heating as well (Gammon et al. 2020).

4.3. Hatchling morphology, survival, and performance

In both freshwater and marine turtles, incubation temperature has been shown to affect hatchling size and locomotory performance (on land and in water, Booth 2018), as well as the prevalence of scute abnormalities (Miller 1985, Reid et al. 2009, Telemeco et al. 2013). This is to be expected because the rates at which biochemical reactions take place increase at warmer temperatures (Vleck & Hoyt 1991). Maximal rates of oxygen consumption during development are higher in warmer loggerhead turtle nests (Reid et al. 2009), and embryonic development is thus likely also faster. However, because cooler nests incubate over a longer duration, it appears that more yolk is converted to somatic tissue (hatchlings have less residual yolk left at hatching), and consequently hatchlings from cooler nests appear to be marginally larger, but usually about the same mass (reviewed by Booth 2018). Additional work on this topic (Booth & Evans 2011, Maulany et al. 2012, Fisher et al. 2014, Horne et al. 2014, Sim et al. 2015, Rivas et al. 2019, Salleh et al. 2019) has suggested, however, that the effect of incubation temperature on hatchling size and locomotory performance is likely small. The impact of incubation temperature on hatchling morphology, survival, and performance has now been investigated in 5 of the 7 marine turtle species (to date there appear to be no studies on hawksbill or Kemp's ridley *Lepidochelys kempii* turtles), and the basis and consequences of these differences (e.g. whether a larger body size confers better defence against gape-limited predators) remains to be demonstrated for any population of marine turtles. The effect of moisture has been less studied, but a positive correlation between moisture and hatchling size was recently observed in natural nests (Tezak et al. 2020b).

Hatchling marine turtles are precocial and need to be capable of escaping predators from the moment they leave their nest, and thus rapid terrestrial and aquatic dispersal to offshore habitats is a key life history trait (Booth 2018). The relationship between incubation temperature and performance appears to be complex, likely an inverted 'U'-shaped relationship, where performance optima lie at intermediate temperatures (likely between 28 and 32°C; Booth 2017, 2018). This means that as ambient temperatures increase above this optimum with climate change, hatchlings (which are more likely to be female at warmer temperatures) could perform more poorly in the initial hatchling frenzy. Studies examin-

ing terrestrial dispersal tend to use 2 metrics to quantify performance: righting from dorsal recumbency (which simulates tripping over beach obstacles) and running speed. To date, the effect size measured appears to be relatively small and variable (e.g. varying between 0.08 and 11.5 s longer to right, Maulany et al. 2012, Staines et al. 2019; and between 0.5 m s⁻¹ slower and 1.5 m s⁻¹ faster, Sim et al. 2015, Rivas et al. 2019) and is almost certainly complicated by species differences and rookery to rookery variation in physiological parameters. Other reptiles (e.g. freshwater turtles, lizards, and snakes) have varying directions of change in locomotor performance as a result of warmer incubation conditions (reviewed by Booth 2006), and future comparative studies between marine turtles and other reptile groups may prove fruitful for identifying underlying drivers. For a variable that is so easy to measure, it is surprising that there are still few studies for marine turtles, on limited numbers of nests, to facilitate such a comparison.

Swimming performance in hatchling turtles has been less studied to date, with most studies focussing on green turtles (Booth et al. 2004, Burgess et al. 2006, Ischer et al. 2009, Booth & Evans 2011). Hatchlings swimming in water do not appear to exhibit symptoms of thermal stress until 41.7°C, which is outside of the range normally measured in natural nests and certainly far warmer than experienced in seawater (Drake & Spotila 2002). Hatchlings from warmer nests have between 5 and 12% higher stroke frequency (the rate at which hatchlings flap their flippers) than hatchlings from cooler nests when swimming in the same temperature water (Booth et al. 2004, Burgess et al. 2006, Ischer et al. 2009), but water temperature has a 3–4 times greater effect on stroke frequency, so the nest temperature effect is dwarfed in comparison (Booth & Evans 2011). This is because water temperature has a strong effect on whole-body metabolism in ectotherms (Ultsch 2013); for example, loggerhead turtle metabolic rates increase 2.4- to 5.4-fold for a 10°C increase in water temperature (Lutz et al. 1989, Hochscheid et al. 2004). Hatchlings from warmer nests appear to produce lower mean thrust per flipper beat than hatchlings from cool nests (Booth & Evans 2011), suggesting that some physiological property unrelated to metabolism may differ with incubation temperature – for example, that the swimming muscles of hatchlings from warmer nests may have fewer ‘fast twitch’ Type II muscle fibres, which produce greater peak force (Hill et al. 2012), or that hatchlings from warmer nests may have proportionally fewer mitochondria, or lower capillary to muscle fibre ratios (thus supplying less

oxygen to each muscle fibre). In addition, some limited evidence (Fisher et al. 2014) suggests that the proportion of time spent power stroking (the dominant propulsive swimming stroke) may be reduced with nest incubation temperature, which could suggest that hatchlings from warm nests could have less ‘slow-oxidative’ Type I muscle fibres, which produce lower peak forces, but fatigue more slowly. An understanding of how these physiological properties change with the incubation regime, and how they may be genetically encoded, will be fundamental to unravelling the downstream fitness consequences of the incubation environment. It is of note that such measurements would be necessarily invasive (requiring hatchling sacrifice) but would likely yield significant additional insights to complement the non-invasive work that has been completed.

4.4. Movements and distribution at sea

The behaviour and spatial distribution of marine turtles are largely affected by seawater temperature and ocean circulation patterns (Luschi et al. 2003, Hawkes et al. 2007b). As marine turtles migrate over thousands of kilometres (Plotkin 2003, Godley et al. 2008), and carry out variable foraging strategies throughout their life cycle (Bolten 2003), climate change impacts and potential responses may vary across ontogenetic stages and habitats.

Being ectothermic, seawater temperature can radically impact marine turtle physiology (Milton & Lutz 2003). Normal vital function is probably impaired below a thermal threshold of around 10–15°C (metabolic rates decrease, and turtles become less mobile, Schwartz 1978, Witt et al. 2007a), and colder waters can thus serve as barriers for the distribution of marine turtles (Polovina et al. 2004, McMahon & Hays 2006, Hawkes et al. 2007b). The leatherback turtle is the exception, being able to maintain its body temperature well above that of the surrounding ambient water (up to 18°C higher, Bostrom & Jones 2007), and is thus capable of foraging in colder waters (10–12°C, Witt et al. 2007b). Báez et al. (2011) found increases in stranding events among Mediterranean juvenile and adult loggerheads associated with regional decreases in SST, resulting from an increasing frequency of North Atlantic Oscillation (NAO) positive phases. Atmospheric CO₂ concentrations seem to be the underlying cause of the current positive NAO index trend, creating colder and drier conditions over the Mediterranean region (Gillett et al. 2003), so despite a generalized increase in ocean SST, some

regions will experience colder seawater in the future (Gillett et al. 2003). Griffin et al. (2019) found that warmer SST during autumn months surprisingly increased the risk of cold-stunning in Kemp's ridley turtles, because they dispersed further north to forage, but then retreated away from winter cold waters too slowly. Higher temperatures, on the other hand, can induce indirect stress by promoting the growth of pathogens and of toxic phytoplankton (Plotkin 2003); however, the seawater temperature corresponding to the upper thermal maximum in marine turtles is unknown, likely because such extremes are not experienced under present conditions. Yet recent research suggests that SST at inter-nesting sites in Southeast Asia will exceed the critical thermal maximum of leatherback turtles under future climate scenarios (Dudley & Porter 2014, Dudley et al. 2016). Increases in SST along post-breeding migration corridors may also increase basal metabolic rate of post-nesting females (Almpanidou et al. 2019), because they are ectothermic (Milton & Lutz 2003). However, this would likely be tempered by the ability of turtles to exploit thermally variable habitats at depth and in different water bodies (e.g. Schofield et al. 2009). Some species/populations may already be adapting to changing ocean temperatures; for example, Eastern Pacific olive ridley turtles *Lepidochelys olivacea* foraged further north during an El Niño year, avoiding warmer waters while seeking more productive upwelling areas (Plotkin 2010), while hawksbills in the Gulf of Arabia avoid warmer foraging areas during the summer months, when seawater temperatures exceed 33°C (Pilcher et al. 2014).

Sea surface currents near nesting beaches are known to facilitate the oceanic dispersal of post-hatchlings (Putman et al. 2010, Scott et al. 2014, Wildermann et al. 2017), likely influencing the ensuing spatial distribution of juveniles and their recruitment to suitable foraging grounds (Hamann et al. 2007). Yet small juveniles and even post-hatchlings are capable of oriented swimming (Putman & Mansfield 2015, Briscoe et al. 2016, Lalire & Gaspar 2019), allowing them to stay within preferred thermal conditions (Mansfield et al. 2014, 2017) and potentially to respond to some level to future changes. However, strong sea surface currents near the nesting beach and high-intensity storms may still mediate the initial dispersal of post-hatchlings (Hays et al. 2010b, Monzón-Argüello et al. 2012, Ascani et al. 2016, DuBois et al. 2020). Models have shown that patterns of dispersal are already likely highly variable because of short-term variation (Scott et al. 2017). For example, variations in sea surface current strength,

associated with the Pacific Decadal Oscillation was shown to impact the dispersal of first-year loggerhead turtles in relation to a high productivity oceanic front (Ascani et al. 2016), while storms were shown to influence the dispersal of post-hatchling Atlantic loggerhead turtles (Monzón-Argüello et al. 2012), and Gulf of Mexico Kemp's ridley turtles (DuBois et al. 2020). The direction of the impacts from climate-forced dispersal is not well understood, and it is unclear whether juvenile turtles will end up in sub-optimal (Monzón-Argüello et al. 2012, Ascani et al. 2016, DuBois et al. 2020), or in more favourable conditions (Ascani et al. 2016, DuBois et al. 2020). Either way, climate-forced dispersal could influence survival and thus population recruitment (Ascani et al. 2016). Notably, breeding loggerhead turtles in the Mediterranean were found to follow dispersal patterns similar to post-hatchlings, associated with prevailing currents near the nesting beach, suggesting that the initial phase of dispersal can be very important to imprint possible future foraging grounds (Hays et al. 2010b).

Multiple approaches have established our knowledge of the spatial ecology of marine turtles. Satellite tracking has become common for studying marine turtle movements (Jeffers & Godley 2016, Hays & Hawkes 2018), providing a bulk of data on their spatial distribution, connectivity, and foraging strategies. Molecular analyses have also been essential to unravel patterns of connectivity between nesting beaches and foraging areas, often coupled with ocean circulation models, allowing inferences on dispersal routes (Blumenthal et al. 2009, Putman & Naro-Maciel 2013, Putman et al. 2014). These spatial data, in combination with satellite-based environmental data, have been used to generate ecological niche models of marine turtle populations (Witt et al. 2010, Pike 2013b, Pikesley et al. 2013, Mansfield et al. 2014, Varo-Cruz et al. 2016), predicting where future suitable foraging habitats may be located in response to increasing seawater temperatures. For example, the foraging thermal niche of Atlantic leatherback turtles, and that of Atlantic and Mediterranean loggerheads, is predicted to expand northwards (Witt et al. 2010, Dudley & Porter 2014, Pikesley et al. 2015), while for Eastern Pacific leatherbacks, range contraction has been predicted (Willis-Norton et al. 2015).

Despite great technological and analytical advances, there is still need for synthetic information on the spatial distribution of marine turtles at sea at ocean scales and across life stages, to improve inferences on how they may be affected by climate

change during their marine life stage. To carry out modelling to investigate this, more data on the spatiotemporal distribution of marine turtles are required. Telemetry data can provide invaluable information (but usually only describe a limited number of individuals that may not be representative of the population-level spatial distribution, Lascelles et al. 2016), and standardised surveying (Thomas et al. 2010, Buckland et al. 2015) either by boat-based or aerial distance sampling methods (Beavers & Ramsey 1998, Eguchi et al. 2007, Lauriano et al. 2011, Fuentes et al. 2015, Williams et al. 2017, Vandeperre et al. 2019) allow for in-water estimations of both population abundance and distribution (within the survey region). Additionally, both the use of unmanned aerial vehicles and underwater video (Dunstan et al. 2020) have been proposed as cost-effective alternatives to standard surveying. We suggest that the wealth of turtle tracking data that already exist, if aggregated across the decades and ocean basins over which they have been collected (Godley et al. 2008, Hays & Hawkes 2018), could go a long way to improve our understanding on the climatic drivers of spatial distribution.

Importantly, expected increases in seawater temperature will differentially affect primary production and composition of prey communities across geographic regions, with consequences for the spatiotemporal distribution of current foraging areas (Polovina et al. 2011, Poloczanska et al. 2016). Yet, estimations of future suitable habitat under climate change have broadly relied on thermal niche modelling (Witt et al. 2010, Pikesley et al. 2015, Dudley et al. 2016), while changes in hydrological processes, which will determine the magnitude and distribution of ocean productivity, and consequently the availability of prey, have been less considered. However, the strongest impacts of increases in seawater temperature may be mediated through food availability (Stubbs et al. 2020), at least for some species. In such a scenario, turtles that find prey less available may not meet summit energy reserves for reproduction and will thus have increased remigration intervals and reduced reproductive lifetime (Stubbs et al. 2020). The opposite could potentially be possible if food availability, or its quality, were increased, as this could lead to faster growth, younger age at maturity, and more frequent breeding. This may be particularly important for species or populations with specialist diets (Witt et al. 2010, Bell 2013). Ideally, estimates of future resource availability, coupled with information on foraging strategies and diet composition, would be integrated in spatial distri-

bution forecasts. There is, however, a lack of research on marine turtle foraging habitat quality under climate change scenarios and on the potential consequences for somatic growth, limiting such integrated approaches.

4.5. Breeding patterns

Marine turtles perform cyclic migrations to breeding sites and display significant inter-population variability in the start and duration of nesting seasons (Miller 1997). Body condition determines when breeding can occur (Miller 1997, Broderick et al. 2001b), and is likely driven by resources at foraging areas which, in turn, may depend on mid- to long-term environmental conditions (Limpus & Nicholls 2000). For example, cooler waters have been shown to enhance food availability for loggerheads in the Pacific, boosting their breeding capacity (Chaloupka et al. 2008). The precise timing of nesting may depend on short-term environmental cues, such as seawater temperature (Weishampel et al. 2004, Pike et al. 2006, Hawkes et al. 2007a, Mazaris et al. 2008). Understanding how climate variables impact the breeding phenology of marine turtles is crucial, as changes in the timings of migration, courtship, and the onset and duration of nesting can exacerbate or reduce climate change impacts on the nesting beach (Pike et al. 2006, Mazaris et al. 2008, Pike 2009, Weishampel et al. 2010, Patel et al. 2016).

With the increase in research looking at phenological responses to global warming, 2 things have become clear: there are both inter- and intra-specific differences in responses, and it is not straightforward where to look for environmental drivers of breeding cycles. While previous research has focussed on environmental conditions near the nesting beach, recent work indicates that conditions at distant foraging grounds are more likely to influence the timing of migration and arrival at the breeding area for the start of courtship and nesting (Mazaris et al. 2009b, Neeman et al. 2015a, Monsinjon et al. 2019b). It is intuitive that the onset of the breeding migration is triggered by environmental conditions experienced at foraging areas (provided that suitable energetic conditions for reproduction are met), yet, once near breeding sites, where females and males aggregate for courtship and mating (Limpus 1993, Fitzsimmons et al. 1995, Arendt et al. 2012), the local seawater temperature seems to influence the timing of nesting, potentially because temperatures regulate the rate of egg maturation (Weber et al. 2011, Valverde-Cantillo

et al. 2019). Thus far, loggerhead turtle populations have consistently been found to begin nesting earlier in response to higher annual SST, both near the nesting beach (Weishampel et al. 2004, 2010, Pike et al. 2006, Hawkes et al. 2007a, Mazaris et al. 2008, 2013, Lamont & Fujisaki 2014, Patel et al. 2016), and at foraging sites (Mazaris et al. 2009b, Monsinjon et al. 2019b), albeit at different rates (Mazaris et al. 2013). Among green turtles, however, except for 1 study (Weishampel et al. 2010), no phenological changes in response to inter-annual SST near breeding sites (Pike 2009, Dalleau et al. 2012), or at foraging areas (Valverde-Cantillo et al. 2019) have been reported, and at least 1 population of leatherback turtles has demonstrated delayed onset of nesting following warmer SST at foraging areas (Neeman et al. 2015a).

Some studies have also reported a correlation between higher SST and fewer clutches (Mazaris et al. 2009b, Reina et al. 2009, Patel et al. 2016), likely as a result of fewer turtles nesting. These observations could indicate an indirect effect of seawater temperature on the availability of food resources at foraging habitats (Chaloupka et al. 2008, Neeman et al. 2015a), leading to delays in the build-up of energy reserves for reproduction (Neeman et al. 2015b, Stubbs et al. 2020). Another study found that more clutches were laid at a green turtle rookery following warmer SST during the winter prior to the nesting season (Bruno et al. 2020). As seawater temperature is likely to impact different trophic levels in different ways, depending on their prey, marine turtle populations may be differentially affected. It is also possible that increases to seawater temperature will enhance food resources for turtles particularly at higher latitudes, near the current limits of their distribution or beyond. Increases in re-migration intervals due to slower build-up of energy reserves can lead to shorter nesting seasons (Robinson et al. 2014), presumably because fewer females undertake the breeding migration (Limpus & Nicholls 2000, Neeman et al. 2015a). Conversely, nesting years with more turtles breeding lead to longer nesting seasons (Pike 2009). In fact, the size of the nesting population can be a predictor of both nesting season onset (Robinson et al. 2014) and length (Monsinjon et al. 2019b). However, because higher SST can reduce inter-nesting intervals, likely by enhancing metabolic rates and the rate of oogenesis (Weber et al. 2011, Valverde-Cantillo et al. 2019), during a warm year, the same number of clutches could be laid in a shorter period (Pike et al. 2006). Results thus far are not conclusive, as both longer (Weishampel et al. 2010, Lamont & Fujisaki 2014) and shorter nesting seasons (Pike

2009, Weishampel et al. 2010) have been observed in warmer years. Geography may account for some of the observed discrepancies, as latitudinal variation in phenological responses to SST have been observed among loggerheads, with the response of poleward populations being stronger (i.e. greater adjustment in the nesting date, Mazaris et al. 2013). Closer to the equator, on the other hand, likely due to a wider temporal range of suitable thermal conditions, populations show less sensitivity to increases in SST (Mazaris et al. 2013), or perhaps they are harder to detect. A latitudinal gradient (associated with an SST gradient) in the onset of nesting has also been observed among green turtles (Dalleau et al. 2012).

The onset and duration of the nesting season may also depend on age, as remigrant turtles tend to begin nesting earlier and lay more clutches than neophytes (Rafferty et al. 2011, Stokes et al. 2014). It is thus clear that breeding phenology depends on a diverse suite of factors, including resource availability, resource acquisition, environmental cues at both foraging and breeding sites, courtship, population demography (i.e. abundance and age of nesting females) and geography, and this complexity needs to be taken into consideration in future assessments. On the other hand, understanding the dynamic responses of breeding turtles to environmental conditions is critical to interpret the inter-annual variability in clutch numbers, and to improve estimates of population trends based on nesting data (Neeman et al. 2015a).

To date, few studies have assessed whether phenological changes by marine turtles in response to climate change will be sufficient to maintain suitable incubation conditions (Patel et al. 2016, Almpandou et al. 2018, Monsinjon et al. 2019a). At higher latitudes, earlier nesting may track current nesting thermal conditions (Patel et al. 2016, Almpandou et al. 2018, Monsinjon et al. 2019a), although this effect may be temporary (Patel et al. 2016), and dependent on the severity of future climatic change (Monsinjon et al. 2019a). On the other hand, Monsinjon et al. (2019a) estimated that under an optimistic climate warming scenario, 6 out of 7 loggerhead populations may not be able to cope with the impacts of climate warming on hatching success and primary sex ratio by adjusting their breeding phenology. A different study suggested that loggerhead turtles may not be able to track current precipitation conditions (Almpandou et al. 2018), known to also impact hatching success (Santidrián Tomillo et al. 2015b, Montero et al. 2018a) and primary sex ratio (Lolavar & Wynken 2017, 2020).

Geographic and species disparities persist in the available research on the impacts of climate change on the breeding patterns of marine turtles, which limits generalized assumptions. There is thought to be a genetic basis to the plasticity of breeding phenology (Visser et al. 2010), but this remains to be thoroughly investigated for marine turtles. Some studies have tested this hypothesis using mitochondrial DNA control region haplotypes (Dalleau et al. 2012, Mazaris et al. 2013), which trace the dispersal of female lineages, and are the most commonly used markers in marine turtle population genetics research (Bowen & Karl 2007, Tikochinski et al. 2018). However, this marker represents a very small portion of the genome, greatly limiting the chances to detect variability. Recent advances in next-generation sequencing provide reliable and relatively low-cost genomic data, which coupled with new analytical approaches allow genome-wide association studies to detect polymorphisms that are associated with observed inter-population differences in a trait, such as phenology (Visser et al. 2010, Ahrens et al. 2018). We also have yet to investigate how climate change may impact courtship behaviour and mating success (which is particularly difficult because the information on breeding males is very limited) and what may be the advantages of seasonal versus bimodal versus all-year nesting and the drivers of these different breeding patterns.

In addition, there is a lack of standard metrics to define breeding phenology parameters (e.g. the start and duration of the nesting season), making comparisons between studies almost impossible. Some applied metrics include 'median nesting date' (Pike 2009, Weishampel et al. 2010, Lamont & Fujisaki 2014, Robinson et al. 2014), 'date of first nest' (Mazaris et al. 2009b, 2013), and 'peak nesting period' (Dalleau et al. 2012). We suggest that using first nesting event can be problematic, as this reflects atypical events (outliers). Thus, for populations with nesting seasons delimited in time, we recommend using the 2.5th percentile of nesting date as a proxy for the beginning of nesting, to avoid outlying data. Using the median nesting date can also be ambiguous, as this metric is influenced both by the onset and by the duration of the nesting season (Mazaris et al. 2013) and survey effort. Furthermore, several populations have bimodal or year-round nesting (Dalleau et al. 2012), making most of these metrics impractical. Future studies could benefit from models based on a biologically meaningful description of nesting phenology dynamics, which can accommodate missing data

(e.g. due to uneven monitoring effort or to very high nesting density, Girondot 2010, 2017, Laloë et al. 2020) that are freely available (R package 'phenology'; Girondot 2020b).

4.6. Nesting area availability

The area available for marine turtles to nest is likely to be reduced by sea level rise (SLR, Fish et al. 2005, Baker et al. 2006, Fuentes et al. 2010b), with beaches in developed regions being likely the most vulnerable, since coastal development can prevent the natural movement of sediment, causing coastal squeeze and exacerbating impacts from SLR (Fish et al. 2008, Mazaris et al. 2009a, Biddiscombe et al. 2020). Reductions in available nesting area may also amplify density-dependent issues at marine turtle nesting beaches (e.g. risk of infection in clutches and accidental destruction of eggs by nesting females), and create suboptimal nesting habitats (Girondot et al. 2002, Tiwari et al. 2010). SLR may also increase exposure of clutches to saltwater inundation, ultimately affecting hatching success and hatchling fitness (Patino-Martinez et al. 2014, Pike et al. 2015). Storms (tropical storms, hurricanes, cyclones, or typhoons) can cause further impacts on marine turtle nesting beaches and their reproductive output, with storm frequency and intensity expected to increase in future warmer environments (Webster 2005, Van Houtan & Bass 2007, Fuentes & Abbs 2010, Fuentes et al. 2011a, Long et al. 2011).

Despite the potential impacts of SLR and storms on marine turtle nesting grounds and their reproductive output, only a few studies have projected how these climatic processes will impact marine turtles. This is likely a reflection of the challenges inherent in successfully predicting shoreline response to SLR and storm activities (Cooper & Pilkey 2004, Von Holle et al. 2019), and the inability to couple projections with biological information (e.g. nest site choice, responses to changes in beach morphology). Most of the studies to date (e.g. Baker et al. 2006, Mazaris et al. 2009a, Fuentes et al. 2010b, Reece et al. 2013, Varela et al. 2019, Veelenturf et al. 2020) have used the Bruun rule or 'bathtub' models to determine the potential loss of marine turtle nesting beaches to various scenarios of SLR. However, these approaches do not account for natural beach movement and sand transport, and consequent changes in beach profiles (Cooper & Pilkey 2004, Woodroffe 2008), although some studies have considered the extent to which nesting areas may shift in relation to natural and arti-

ficial physical barriers (Fish et al. 2008, Katselidis et al. 2014, Biddiscombe et al. 2020, Lyons et al. 2020). These assessments have often been coupled with data from field survey methods (e.g. beach profiles, using Emory or Abney Level methods; see Fish et al. 2005, 2008), which tend to be limited to discrete beach transects and are subject to systematic errors and low accuracy (Isaak et al. 1999), or from terrestrial and airborne light detection and ranging (LiDAR, Long et al. 2011, Yamamoto et al. 2015), which has higher accuracy, as well as cost (Varela et al. 2019). To offset some of the issues from traditional approaches, a novel combination of drone-based photogrammetry and a low-cost and portable real-time kinematic GPS has been suggested to develop the digital terrain models needed to assess the impacts of SLR on marine turtle nesting grounds (Varela et al. 2019).

Recent studies (Butt et al. 2016, Von Holle et al. 2019, Lyons et al. 2020) have taken advantage of other novel sophisticated approaches (e.g. coastal vulnerability index, storm surge models, SLR calculators) and open-access geomorphology datasets (e.g. LiDAR, digital elevation models) combined with turtle nest location data to assess the impacts of SLR on rookeries. However, these are generally developed for broad-scale assessments (e.g. continental, global); therefore, finer-scale analyses are necessary to improve current assessments of the impacts of SLR on marine turtles. Process-based models (e.g. Delft3D and XBeach) can directly simulate beach hydrodynamics and sediment transport, and provide more robust assessments of the potential impacts of SLR on marine turtle nesting areas. For example, these models account for non-erodible portions of the beach (due to shoreline protection strategies such as sea walls, groynes, and other hard sea defences), which will become more prevalent as sea level rises and storms become more frequent, and evaluate how current or proposed installation of these interventions could alter the risk of habitat loss under various scenarios of SLR and storm activity, which remains a big gap in our knowledge.

In addition to the uncertainty in how SLR/storms will affect specific nesting beaches, there is still considerable uncertainty on how marine turtles will respond to changes in beach profiles, and the availability of nesting areas as well as the effects of synergistic and cumulative impacts from other climatic pressures (e.g. temperature, rainfall, Fuentes et al. 2011a). The threat of SLR/storms coupled with contemporary anthropogenic threats (e.g. coastal devel-

opment or pollution), may weaken the ability of marine turtles to cope with climate change (Reece et al. 2013, Fuentes et al. 2016a, Biddiscombe et al. 2020, Fuentes et al. 2020). While marine turtles can buffer effects from individual storm events, by laying multiple clutches spaced throughout the nesting season (Dewald & Pike 2014, Fuentes et al. 2019), climate change scenarios suggest that this threat will become of greater concern in the future (Fuentes & Abbs 2010, Fuentes et al. 2019). Therefore, there is a need to understand the magnitude of the potential impact from storms at a rookery level (e.g. loss of eggs and habitat) and across populations. Some studies have looked at the exposure of marine turtle nesting beaches to storms (Fuentes et al. 2011a, 2019, Dewald & Pike 2014), but these do not usually quantify the actual loss in turtle reproductive output, or they focus on single nesting beaches (for examples, see Foley et al. 2006, Caut et al. 2010, Long et al. 2011, Ehrhart et al. 2014). Future research should focus on the long-term impact of storms and implications at a population level. Such assessments would benefit from improvements in our understanding of how well eggs can withstand inundation. Recent studies have found that short periods of inundation (1–6 h) did not significantly reduce hatching success (Pike et al. 2015, Limpus et al. 2020), and that embryos may be more vulnerable at the beginning and at the end of development (Limpus et al. 2020). Tolerance thresholds could then be integrated with inundation models, such as wave run-up models, to better identify areas at significant risk of wave exposure from SLR/storms (Ware et al. 2019).

As nesting beaches become unsuitable or unavailable, marine turtles may respond by shifting their range to climatically suitable areas (Hamann et al. 2013, Abella Perez et al. 2016, Mainwaring et al. 2017). Some studies also suggest that marine turtles may respond to changes in beach profiles (due to SLR/storms) through nest-site selection, as some populations seem to favour elevated sites for nesting, increasing clutch survival (Santos et al. 2017, Patricio et al. 2018). To date, only a few studies have explored potential range shifts as suitability of nesting beaches changes, and predicted that some populations may be able to shift their nesting distribution as climate change progresses (McMahon & Hays 2006, Pike 2013a, Butt et al. 2016, Fuentes et al. 2020). Newly colonized areas must provide the necessary conditions for egg incubation (Katselidis et al. 2012) and hatchling dispersal, but other factors will influence the potential for rookery establishment, such as the presence of other hazards.

This is important because range shifts may result in increased exposure to anthropogenic threats, such as coastal development (Pike 2013a, Biddiscombe et al. 2020, Fuentes et al. 2020). Our current lack of understanding of the synergistic effects of multiple climatic processes with other anthropogenic factors hinders our ability to identify suitable areas that will allow turtle nesting to persist (Fuentes et al. 2013). Thus, a future emphasis should be on coupling predicted range shift studies with assessments of exposure to threats with considerations to the interconnected nature of impacts and responses for a multitude of processes.

4.7. Emerging diseases and pathogens

Infectious disease outbreaks have increased in some marine taxa in the last few decades (e.g. Fisher et al. 2012, Altizer et al. 2013, Sanderson & Alexander 2020), potentially driven by either climatic or anthropogenic factors, but likely by a combination of both (Fey et al. 2015). It is clear that stressors such as these exacerbate the impact of disease (Hing et al. 2016) and that climate change, particularly warming temperatures, ocean acidification, changes in precipitation, and storm damage, may alter marine disease dynamics (Harvell et al. 2009, Tracy et al. 2019). To date there is no clear evidence of recent increases in marine turtle diseases (Tracy et al. 2019), but this may also be due to a lack of baselines, and/or limited research in this field (Tracy et al. 2019).

One of the major diseases of marine turtles is fibropapillomatosis (FP), a neoplastic disease characterized by external and internal tumours, which affects all 7 species, and is reported globally (Jones et al. 2016). FP tumours, if sufficiently numerous and large, can impede sight, swimming, feeding, and breathing, and can suppress organ function, leading to death (Herbst 1994). FP is linked to infection by a herpesvirus, the chelonid herpesvirus 5 (ChHV5, Patrício et al. 2012, Alfaro-Núñez et al. 2014, Page-Karjian et al. 2015); however, the virus transmission route is not clear, and environmental factors may also play a role in disease expression (Van Houtan et al. 2010). Although widespread, FP currently does not seem to pose a major threat to marine turtles (Patrício et al. 2016), but if warmer seawater were to promote tumour growth (which remains to be empirically demonstrated, but appears possible; Herbst 1994, 1995, Foley et al. 2005), outbreaks could increase in severity in the future.

The prevalence of fungal infectious diseases has increased in marine turtles in recent decades (Phillott & Parmenter 2001, Fisher et al. 2012, Gleason et al. 2020), with a newly emerging fungal disease reported worldwide to affect marine turtle clutches, the 'sea turtle egg fusariosis' (STEF, Gleason et al. 2020). It appears to be caused by the *Fusarium solani* species complex, a group of at least 26 common soil fungi that colonize plant materials in the division Ascomycota (Short et al. 2013), 2 of which have been shown to be particularly virulent, *F. falciforme* and *F. keratoplasticum* (Sarmiento-Ramírez et al. 2014). The fusarium species infect incubating eggs, creating yellowish-blue infection zones that become necrotic, eventually leading to embryo death (Gleason et al. 2020). Pathogenic fusarium species have also been isolated from healthy eggs, indicating that they may be normally present, but unremarkable unless stressors weaken the host immune system (Sarmiento-Ramírez et al. 2014). Notably, tidal inundation was shown to correlate with STEF prevalence, leading to higher clutch mortality (Sarmiento-Ramírez et al. 2014), implying that future SLR and storm surges may influence disease spread. Additionally, future loss of nesting area may increase nest density (Patrício et al. 2019), favouring pathogen spread among neighbouring clutches (Sarmiento-Ramírez et al. 2017).

Climate change can also alter host–pathogen interactions, either by impairing host immune systems or by altering the virulence of pathogens, and this has been documented in shellfish, coral, and some fish species (Burge et al. 2014), but not yet in marine turtles. Warming seas may also allow pathogens to increase their range, while simultaneously, poleward shifts in host species range in response to climate change may bring them into more frequent contact with known or novel pathogens (Cohen et al. 2018). Marine diseases may also impact foraging habitats on which marine turtles depend, for example seagrass meadows (Sullivan et al. 2018) and coral reefs (Precht et al. 2016, Tracy et al. 2019), but much work remains to demonstrate how and at what magnitude climate change may impact these habitats, and determine what capacity marine turtles have to broaden their diets. Future research should focus on understanding which environmental factors favour the colonization and infection of clutches by pathogenic fungal species, and which factors promote FP tumour growth. Disease monitoring using standard operational protocols should also be encouraged to improve baselines, essential to detect change, under future climatic conditions.

5. STRATEGIES TO REDUCE CLIMATE CHANGE IMPACTS

Faced with the certainty of future climate change, it seems logical that strategies to reduce the potential negative impacts of climate change on marine turtles should be investigated. Here we distinguish 'intervention', which we define as the direct manipulation of the ecological processes of turtles, and 'mitigation', which is the reduction of stressors on marine turtles in order to give them the best possible opportunity to adapt by themselves. Interventions that have been proposed so far include relocating nests to hatcheries or artificial incubators, and manipulating incubation temperatures using shade, water sprinklers, native vegetation, or the addition of sediment with different colour (and therefore albedo) and grain sizes (Table 1; Kamel & Mrosovsky 2006, van de Merwe et al. 2006, Fuentes & Cinner 2010, Fuentes et al. 2012, 2016b, Patino-Martinez et al. 2014, Wood et al. 2014, Hill et al. 2015, Jourdan & Fuentes 2015, Liles et al. 2019). Mitigations that have been proposed include identifying and legally protecting extant and future suitable nesting beaches (e.g. male-producing beaches and/or areas with low risk of inundation and erosion; Baptistotte et al. 1999, dei Marcovaldi et al. 2016), establishing marine protected areas (MPAs) to protect both dynamic habitats (i.e. habitats that may change in space and/or time) and the marine turtles that occupy them (Maxwell et al. 2020), as well as mitigating other anthropogenic stressors (Fuentes et al. 2013).

It seems sensible to suggest that mitigation activities can and should be used widely to help reduce the impact of climate change and other stressors to marine turtles. However, whether any interventions would be helpful or wise to employ is still influenced by our understanding of their associated effectiveness, feasibility, and risks (see summary Table 2 in Fuentes et al. 2012, Jourdan & Fuentes 2015). For example, to assess the utility of interventions related to changes in sex ratio, ideally we should know what primary sex ratio and OSR would be 'optimal' in the population that we are managing, and the resulting consequences of manipulating sex ratio on population dynamics and evolutionary potential (Fuentes et al. 2012). On the one hand, if too few males are produced for the population to remain fertile, it risks becoming extirpated (see Section 2.1). On the other hand, if we assume that the survivorship between male and females is equal, if the proportion of females is reduced in lieu of manipulation for males, the population growth rate might slow, because the finite rate of pop-

ulation increase is set by the proportion of females (Boyle et al. 2014a), which can eventually reduce the capacity of the population to adapt. Thus, manipulation of primary sex ratios may be risky, and lacks an adequate knowledge base at present to be widely, safely implemented (Santidrián Tomillo & Spotila 2020). Similarly, to determine the need for interventions to address impacts from nest inundation and wash-over associated with rises in precipitation, sea level, and storm activities, we need to be able to predict the spatiotemporal threat of inundation/wash-over at individual beaches and the consequent risk to incubating eggs, based on embryonic tolerances (Ware et al. 2019). This information must be weighed against information on the risks of intervening (e.g. relocating, Ware & Fuentes 2018).

Direct strategies may become necessary at some sites, as the negative effects of climate change become more extreme (Prober et al. 2019). For this, decisions will need to be made at a site level and with consideration of the environmental, social, economic, and cultural conditions of specific locations (Fuentes et al. 2012). As intervention strategies are trialled, it is critical that information about their effectiveness is documented, so that managers at other sites can learn, and an adaptive management approach can be taken (Fuentes et al. 2016b). Importantly, any approach should be based on our best understanding of the population level impacts of, for example, manipulating sex ratio, and consider the long-term (e.g. >100 yr) persistence of marine turtles. This should also be set against the risk of creating 'maladapted' phenotypes and altering the gene pool by carrying out inappropriate intervention (see Mrosovsky 2006). Thus, it is suggested that we should not intervene with incubating clutches until we know what the consequences are, and instead we should prioritize the protection of areas that will have climatically suitable conditions for incubation over the long-term and that will have reduced impact by SLR (Fuentes et al. 2020), including minor rookeries, especially if they have male-producing conditions (dei Marcovaldi et al. 2016). As climate change progresses and temperatures become extreme, causing high mortality rates and low production, there might be a shift in management goal from obtaining OSRs versus preserving hatching productivity. However, if the vast majority of eggs are failing due to habitat conditions (e.g. low beach profile leading to inundation of clutches, or extremely high incubation temperatures), it might indicate that a beach is probably no longer suitable for incubation, so the efficacy of increasing the production of hatchlings that might

Table 1. Potential strategies to mitigate the direct impacts of climate change on marine turtles, and knowledge gaps in relation to the effectiveness, and ecological risks of implementing strategies. Information presented in the last two columns was adapted from Fuentes et al. (2012)

Metric	Impacted life stages	Observed and projected impacts	Climatic drivers	Strategies to reduce climate change impacts	Knowledge gaps
(1) Sex ratio	- Hatchlings	- Change in sex ratio - Destabilization of population dynamics - Reduction of effective population sizes	- Increases in air and sea surface temperatures - Altered rainfall and humidity regimes - Sea level rise - Extreme weather events (cyclones and floods)	- Prevent removal of beach vegetation - Re-vegetation or planting native vegetation - Identify and legally protect beaches that have climatically suitable environment and/or produce higher proportions of male hatchlings - Manipulate incubation temperature <i>in situ</i> using water sprinklers, shade, or by adding lighter sediment to the beach - Move nests to areas with suitable conditions, hatcheries, or incubators	- Current hatchling sex ratios at key nesting beaches, and intra-beach variability in these ratios - Pivotal temperature and upper thermal threshold for each sea turtle species and for key populations - Level of plasticity and heritability in temperature-dependent sex determination - Optimal primary and operational sex ratios for each sea turtle species and for key populations - How much sex ratios should be manipulated to maintain optimal sex ratio - Optimal incubation environments for successful hatching for different species - Effects of cooling nests with sprinklers on rates of fungal infection - Impact of different manipulating interventions on nest temperature, and how this varies spatially and temporally at key nesting sites - Effects of watering on the temperature and moisture of the nesting environment and whether this affects sex ratios and hatching success - Thermal properties of different sediments and how they affect hatching success and sex ratios - Amount of sand, colours, and grain sizes required to change the thermal profile of nesting beaches
(2) & (3) Hatching success & hatchling condition failure	- Eggs - Hatchlings	- Changes in hatching morphology, physiology, and performance - Low hatching success /	- Changes in sea surface temperature - Changes in wind and ocean circulation - Changes in ocean stratification - Ocean acidification	Marine protected areas (dynamic, seasonal or permanent)	- Optimal design for marine protected areas (MPAs) to protect marine turtles across different life stages and under a changing climate - Effectiveness of MPAs in reducing the impacts of climate change
(4) Movements and distribution at sea	- Hatchlings - Juveniles - Sub-adults - Adults	- Changes in hatchling dispersal - Changes in recruitment of juveniles to foraging sites - Changes in adult foraging and nesting distribution - Decrease in survival and population recruitment - Changes to the spatio-temporal distribution of foraging areas - Changes in abundance or location of food	- Changes in sea surface temperature - Changes in wind and ocean circulation - Changes in ocean stratification - Ocean acidification		

Table 1 (continued)

(5) Breeding patterns	<ul style="list-style-type: none"> - Eggs - Hatchlings - Nesting females 	<ul style="list-style-type: none"> - Changes in the timings of migration, courtship, onset and duration of nesting - Changes in nesting intervals and reproductive output 	<ul style="list-style-type: none"> - Whether changes in breeding patterns can ameliorate impacts of climate change - Direction of changes in breeding patterns
(6) Nesting beach availability	<ul style="list-style-type: none"> - Eggs - Hatchlings - Nesting females 	<ul style="list-style-type: none"> - Loss of nesting beach - Amplification of density-dependent issues (i.e. Allee effect) - Suboptimal nesting habitats, with increased risk of inundation - Distributional shifts 	<ul style="list-style-type: none"> - Ability of shorelines to respond to sea level rise and storm activities - Sediment transportation within a nesting beach with climate change - Risks associated with hard and soft engineering structures to prevent beach movement and erosion - Effects of hard and soft engineering structures on the natural morphological shift of nesting beaches and their response to sea level rise and storm activity
	<ul style="list-style-type: none"> - Sea level rise - Extreme weather events (cyclones and floods) 	<ul style="list-style-type: none"> - Establish rolling easements (voluntary agreement limiting amount/type of development on property) - Incorporate climate change into land-use planning - Establish or enforce existing setback regulations - Ban and remove permanent shoreline-hardening structures - Plan urban growth to redirect development away from nesting areas - Beach replenishment - Use hard engineering structures - Install offshore breakwaters 	

return to a 'doomed' beach should be evaluated. Persistence of suitable nesting habitat is crucial for the reproduction of marine turtles and is one of the key factors influencing the resilience of marine turtles to climatic changes (Fuentes et al. 2013).

Although substantial knowledge gaps remain to efficiently manage climate-change-related threats to incubating eggs, larger knowledge gaps remain in relation to turtles at sea (Table 1). Large and mobile MPAs have been suggested to protect dynamic habitats and the migratory marine species that occupy them, such as marine turtles, as climate change progresses (Davies et al. 2017, Maxwell et al. 2020). However, design of such protected areas relies on robust modelling of how marine turtles might respond to change, and whether MPAs would be effective in reducing the impacts from climate change (Lawler et al. 2010, Fuentes et al. 2012, 2016b). Until we address some of these uncertainties, we suggest focussing on enhancing marine turtle resilience by reducing other threats that they currently face (Robinson et al. 2009, Witt et al. 2010, Fuentes et al. 2013, Reece et al. 2013). The main challenge will be to account for the cumulative and synergistic nature of climate-related impacts and existing threats to marine turtles (Fuentes et al. 2011b, Reece et al. 2013).

6. RESEARCH PRIORITIES

Based on the knowledge gaps identified in Section 4, key research questions were formulated and are summarized in Box 1. Here we highlight what we see as the key priorities that urgently need to be addressed and provide suggestions where research might be best applied.

6.1. Understanding sex ratios under climate change and associated impacts

Despite decades of meaningful research, many of the current estimates of primary sex ratios may not accurately reflect the reality, given that most studies have not taken into account the large variability of natural environments throughout the full duration of nesting seasons or have used proxies with inherent limitations or do not adequately cover the beaches used by the population. What the primary sex ratios will be in the future, and how they will vary between species, rookeries, and individuals, are key questions to understand the resilience of marine turtles to climate change, which remain largely unanswered. We

Box 1. Priority research questions to improve our understanding of how climate change will impact marine turtles, for each parameter expected to be impacted, and for strategies to reduce the impact of climate change

Nest area availability

How will nesting turtles respond to changing beach profiles and inundation of current nesting areas?
 What are the synergetic impacts of shoreline protection strategies and sea level rise to nesting areas?
 What are the long-term impacts of more frequent and intense storm activity?
 What areas will be available for marine turtles as climate change progresses?
 Will adaptive shifts in nesting location lead to changes in other threats?

Sex ratios

What is the variability in temperature-dependent sex determination reaction norms between individuals, rookeries, and species?
 What is the role of nest humidity in determining sex ratio?
 How can models used to reconstruct nest temperature be improved?
 How can we better predict beach microclimates?
 What spatial and temporal scales are relevant to predict incubation temperature?
 How do seasonal primary sex ratios translate into adult sex ratios?
 How many males are needed to sustain populations? Is there evidence of male limitation?
 What are the long-term consequences of skewed sex ratios on population dynamics and genetics?

Hatching success

Why do clutches fail at high temperatures?
 What is the impact of the oxygen–temperature interaction on clutch success?
 What is the lethal upper thermal limit for marine turtle clutches?
 Why does the lethal upper thermal limit vary between species and populations?
 Can the lethal critical thermal limit of embryos change as a result of natural selection?
 How tolerant are marine turtle eggs to inundation?

Hatchling morphology, survival, and performance (hatchling condition)

Is the effect of incubation temperatures on hatchling locomotion meaningful to survival?
 Do larger hatchlings from cooler incubation conditions have a reduced individual chance of predation?
 How does the muscle phenotype of hatchlings vary with incubation temperature?

Movements and distribution at sea

What will be the impact of climate change on hydrological processes?
 How will climate change impact foraging grounds?
 How will climate-forced dispersal influence recruitment to juvenile/adult foraging grounds?
 Will adaptive shifts in foraging location lead to changes in other threats?

Breeding patterns

How does latitude/local climate relate to phenological responses to climate change?
 What are the drivers of seasonal, bimodal, and year-round nesting strategies?
 How is courtship timing and duration affected by climate factors?
 Will phenological changes be sufficient to maintain suitable incubation conditions?
 Is there a genetic basis for phenological behaviour?

Emerging diseases and pathogens

Are diseases/infections of marine turtles increasing due to climate change?
 Does fibropapillomatosis prevalence/severity increase with temperature?
 What climate conditions favour the survival of egg fungal pathogens?

Strategies to reduce climate change impacts

What are the effectiveness, feasibility of implementation, and ecological risks associated with strategies to reduce impacts from climate change?

thus recommend a re-estimation of primary sex ratios globally, using improved metrics, sampling design, and modelling approaches (see Section 2.1), and a continuation of research on non-lethal sexing techniques (Tezak et al. 2020a). The effect of humidity on primary sex ratios also deserves more attention, particularly to clarify if there is a direct effect of water uptake on the regulation of sex-determining genes or if, otherwise, this is an indirect effect of evaporative

cooling. Of extreme importance is to determine what the demographic consequences of extremely female-skewed primary sex ratios are, i.e. how these translate into OSRs. Is population growth to be expected in the short-term and collapse in the long-term? This will be fundamental to inform intervention strategies, namely if management of incubation environments is necessary, and if so, under what conditions. Another priority is to investigate to which extent

male abundance limits female fecundity (Boyle et al. 2014a) and the importance of timed courtship. While male turtles are much less tractable to study (i.e. they never come ashore), given their wide-scale distribution, indirect approaches can be immediately applied, such as estimating the proportion of infertile eggs within clutches (as a proxy for fertilisation success; Phillott & Godfrey 2020) combined with genetic assessments of effective sex ratios (Lasala et al. 2018). Notwithstanding, the lack of information on this demographic group (adult males) must be addressed, particularly given their role for population persistence under future climate change. For this purpose, the Global Male Sea Turtle Initiative was created, to promote the study of male marine turtles worldwide (García-Cruz et al. 2018).

6.2. Understanding climate change impacts on embryo and hatchling survival

Severe weather conditions (extreme high incubation temperatures, storm surges, and protracted inundation), are often predicted to cause clutch mass mortality; however, the lethal upper thermal limits of some species are yet to be estimated, and the tolerance of marine turtle clutches has rarely been studied (but see Pike et al. 2015 and Limpus et al. 2020). Reports on these parameters are essential, assessing variability between species and populations and the influence of environmental factors (e.g. clutch size, nest depth, and sediment type). More consideration should be given to the role of the oxygen–temperature interaction on the thermal tolerance of embryos and on hatchling muscle performance (Liang et al. 2015, Booth 2017, Stubbs & Mitchell 2018), as a warmer climate may simultaneously increase oxygen consumption rates, while contributing to oxygen depletion (e.g. due to SLR/storm-related inundation or to metabolic activity of nearby eggs at high nest density sites). Additionally, improved models of beach sediment movement in response to SLR are critical for robust estimations of clutch flooding/nesting area loss. The information relative to the impacts of diseases and pathogens is also scarce, and despite the increase in fungal infections among incubating clutches, there is a lack of baselines precluding the estimation of change under future conditions, and more importantly, there is no clear understanding of how pathogens will respond under a warmer climate. There is likewise a need for research on the downstream consequences of the incubation environment on hatchlings; particularly, it is critical to discern if

body size has an impact on the relative predation risk, and if the amount of yolk reserves is important for dispersal and survivorship.

6.3. Assessing the potential for adaptation

Understanding the capacity for physiological adaptation to future climate change is a major priority; specifically, studies should assess the plausibility for adaptation of critical thermal limits of incubation through natural selection, suggested by plasticity in the expression of genes that mitigate cell damage under heat stress (heat-shock genes, Tedeschi et al. 2016). Possibly, however, marine turtles will respond more rapidly to adverse climatic conditions by shifting their spatiotemporal distribution and/or changing their nesting/foraging behaviour, but there is still limited information on their expected responses to climate change, and even more so, on the efficacy of such responses (Fuentes et al. 2020). Future research should thus assess how nesting females and foraging animals respond to climate-related changes, such as rising sand temperatures, altered beach profiles, inundation of current nesting areas, and increasing seawater temperatures, taking into account site-specific sensitivities (e.g. Dalleau et al. 2012, Mazaris et al. 2013). Genome-wide association studies will also be key to assess if relevant behaviours (e.g. nest-site choice, phenological responses to temperature) have a genetic basis, and are thus susceptible to evolution by natural selection. Perhaps even more important will be to quantify the efficiency of potential (and observed) responses to climate change. For instance, will marine turtles shift their distributions to areas where anthropogenic disturbance is high (Fuentes et al. 2020)? Will phenological changes be sufficient to maintain suitable incubation conditions (Monsinjon et al. 2019a)? Answering these questions will be critical to anticipate the need for mitigation strategies. Lastly, a key action is to identify (and legally protect) beaches that will become (or remain) suitable for nesting under climate change. This may imply surveying beaches with current very little to no nesting, yet it may be the single most important strategy to enhance the resilience of these animals in the long-term.

6.4. Understanding climate change impacts on foraging ecology

The lack of information regarding the impacts of climate change on foraging grounds and the interac-

tions between food availability and the somatic growth of marine turtles is a considerable obstacle to predicting the responses of marine turtles to future conditions. Somatic growth is a key demographic parameter, as it will impact the age at maturity, and thus the reproductive output of populations. Decreases in somatic growth among Pacific green turtle foraging aggregations have been associated with an El Niño event, leading to cooler SST and lower net productivity (Chaloupka et al. 2004). In the Western Atlantic, on the other hand, declining somatic growth rates across multiple foraging grounds and 3 marine turtle species (green turtles, hawksbills, and loggerheads), occupying different trophic positions, have been associated with warming SST (Bjorndal et al. 2013, 2016, 2017), and the authors suggested that indirect effects of the seawater temperature on net productivity may be driving these declines. Recent research has further highlighted that food limitation due to climate change is likely to have the strongest impact on population persistence among herbivorous green turtle populations (Stubbs et al. 2020), but more research is needed, encompassing more populations and wider geographic scales. The additional layers of trophic complexity for carnivorous and omnivorous species like ridley, flatback *Natator depressus* and loggerhead turtles may make such modelling efforts more difficult. It is fundamental to assess how the distribution and abundance of food resources will change under future climate scenarios. For instance, some seagrass species are predicted to decline with increases in seawater temperatures (Jordà et al. 2012), but there is insufficient information to make predictions at a global level (Unsworth et al. 2019). Some food resources may become more abundant under future climate change (Bell et al. 2013), which, coupled with faster metabolism, could increase food intake and enhance growth rates, and lead to lower age at maturity and thus to longer reproductive periods and higher breeding rates. We need basic knowledge on how climate change will impact hydrological processes, such as ocean circulation and mixing, turbidity, upwelling regimes, water column stratification, and the distribution of frontal and convergence zones, as these processes, combined with changes in SSTs and in water acidity, will affect ocean productivity and consequently, the availability of food for marine turtles. This type of assessment will benefit from collaborations between transdisciplinary research teams. It is also essential to study the diet and foraging plasticity of different species and populations, as opportunistic diets should increase resilience, while a combination of a

specific diet with declines of a major food source is cause for concern.

6.5. Final remarks

Following their 120 million years of existence (since early Cretaceous), marine turtles have survived major past climate changes (Scheyer et al. 2014), including the dramatic changes leading to the Cretaceous-Paleogene mass extinction (~66 Mya), responsible for the disappearance of 75% of life on earth (Schulte et al. 2010). Yet, they now face a much faster rate of change (IPCC 2018, Cheng et al. 2019) along with several human-induced threats that may act synergistically with climate change impacts (Fuentes et al. 2013, Rees et al. 2016). Even if marine turtles survive as a group, species with restricted distribution ranges (i.e. flatback and Kemp's ridley turtles), and individual populations that have been depleted (Hamann et al. 2010), are likely to be most vulnerable. Some populations may be more resilient, however, having spatial and temporal microrefugia that allow for optimal incubation conditions, and may also exhibit foraging plasticity (Abella Perez et al. 2016, Patrício et al. 2019). As the knowledge gaps identified here are addressed, our understanding of what the future will look like for marine turtles will increase. Importantly, future research efforts should be global in scope, rectifying current geographic and species biases (Jeffers & Godley 2016), with more research funded and supported in Africa, Asia, and Central and South America. New techniques, enhanced data sharing, and meta-analytic approaches will all afford excellent possibilities for breaking down the barriers to understanding what the impacts of climate change will be on this charismatic group, and how these impacts may be effectively reduced.

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