

MARINE CONSERVATION

Global sea turtle conservation successes

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We document a tendency for published estimates of population size in sea turtles to be increasing rather than decreasing across the globe. To examine the population status of the seven species of sea turtle globally, we obtained 299 time series of annual nesting abundance with a total of 4417 annual estimates. The time series ranged in length from 6 to 47 years (mean, 16.2 years). When levels of abundance were summed within regional management units (RMUs) for each species, there were upward trends in 12 RMUs versus downward trends in 5 RMUs. This prevalence of more upward than downward trends was also evident in the individual time series, where we found 95 significant increases in abundance and 35 significant decreases. Adding to this encouraging news for sea turtle conservation, we show that even small sea turtle populations have the capacity to recover, that is, Allee effects appear unimportant. Positive trends in abundance are likely linked to the effective protection of eggs and nesting females, as well as reduced bycatch. However, conservation concerns remain, such as the decline in leatherback turtles in the Eastern and Western Pacific. Furthermore, we also show that, often, time series are too short to identify trends in abundance. Our findings highlight the importance of continued conservation and monitoring efforts that underpin this global conservation success story.

INTRODUCTION

Worldwide declines in mammal, bird, reptile, amphibian, and fish abundance have prompted concerns that the planet is experiencing a sixth mass extinction (1). Factors implicated in these declines include over-exploitation (for example, fishing, hunting, and poaching), habitat loss, disease, introduction of invasive species, and climate change (2, 3). Set against this backdrop, conservation measures have been introduced at various levels, ranging from intergovernmental agreements [for example, Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) and Convention on Migratory Species] to national and local conservation programs, including marine and terrestrial protected areas (4). Although these measures often lead to conservation success stories, it is more difficult to reverse population declines of broadly distributed groups (that is, migratory species) of conservation concern [for example, the study of Butchart *et al.* (5)].

Sea turtles are a classic example of a broadly distributed group that has historically suffered population declines, as a result of, for example, bycatch and harvesting adults and eggs (6). These declines have motivated worldwide conservation efforts since the 1950s (7, 8). Efforts included various beach protection measures, strict fisheries bycatch regulations [for example, turtle excluder devices (TEDs) (9, 10)], and the establishment of marine protected areas (7). Over the last 10 years, reports for individual sea turtle nesting sites (rookeries) include both conservation success stories, with long-term increases in the abundance of females and their nest numbers (9, 11, 12), and declines, leading to imminent, likely localized extinctions (8, 13). These trajectories in abundance at nesting sites have been synthesized in species assessments through the International Union for Conservation of Nature (IUCN), which broadly categorizes the conservation status of species (14). Six of the seven sea turtle species are currently listed as vulnerable, endangered, or critically endangered; however, the Hawaiian green turtle subpopulation was recently listed as “least concern” in 2012, reflecting a long-term increase in the size of this population (9).

The flatback turtle (*Natator depressus*) remains data-deficient (14). Understanding trends at individual nesting sites helps enhance conservation initiatives at the local scale, potentially highlighting emerging threats. In comparison, regional and global assessments present a holistic view of population trends and viability, facilitating management decisions at political levels.

The IUCN is constantly improving and updating assessments on the status of the seven sea turtle species, with the most recent assessment being Kemp’s ridleys (*Lepidochelys kempii*) in 1996, green turtles (*Chelonia mydas*) in 2004, hawksbills (*Eretmochelys imbricata*) and olive ridleys (*Lepidochelys olivacea*) in 2008, leatherbacks (*Dermochelys coriacea*) in 2013, and loggerheads (*Caretta caretta*) in 2015. Here, we provide a complementary assessment of the status of all species of sea turtles using all available published time series. The most recent IUCN updates (leatherbacks in 2013 and loggerheads in 2015) made their assessments by comparing the mean number of nests per year at the nesting sites calculated over 5 years in the past versus 5 years nearer the present. Hence, these time series of nesting numbers span at least 10 years. Data from individual nesting sites are then combined at regional and global scales. This way of comparing the mean nesting numbers between two periods is a useful and pragmatic approach developed because the complete time series of annual nest numbers are often not available in the public domain. Here, we build on information available from the IUCN listings by sourcing time series available in the public domain of annual nest numbers for individual nesting sites globally and for all seven species. By using annual time series, we are able to identify significant trends at each site. This approach has the advantage that the full time series are rich in information but has the disadvantage that full annual time series are not available for all the sites included in the IUCN assessments. Therefore, we view our approach as complementing the IUCN assessments.

Here, we complement the IUCN work and provide important messages for global efforts to help protect sea turtles. We compile trends for each species from the scale of individual nesting sites to regional management units (RMUs) developed by Wallace *et al.* (15). RMUs represent discrete groups of nesting sites in certain areas that are distinct from one another based on genetics, distribution, movement, and demography. They have been recommended as the

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unit for population management, and are analogous to the IUCN Red List's subpopulations, which are the level at which the most recent sea turtle assessments have been conducted. We consider whether initial abundance at a nesting site is linked to the trend in the trajectory of abundance and, in this way, consider whether Allee effects exist, that is, an inability of nesting sites with low abundance to recover. We consider the length of time series that are required to detect significant trends in abundance. In particular, we assess whether short time series (for example, <10 years; not currently used by the IUCN) sometimes have value. Finally, we quantify how much long-term monitoring is required to detect trends in some cases where interannual variability in nesting numbers is high.

RESULTS

We obtained 299 time series of annual abundance with 4417 individual records of annual nesting numbers. The number of time series assessed for each species included 32 for hawksbill turtles, 83 for green turtles, 103 for loggerhead turtles, 6 for flatback turtles, 54 for leatherback turtles, 19 for olive ridley turtles, and 2 for Kemp's ridley turtles. For loggerheads and leatherbacks, 58 of the 103 time series and 32 of the 54 time series, respectively, were not included in the recent IUCN assessments of change in abundance. For the other five species, our analysis of trends in abundance within RMUs considers time series extending to 2010 or beyond and hence updates the most recent IUCN assessments.

At the level of individual time series, we found 95 significant increases in abundance and 35 significant decreases. In a few cases ($n = 7$), previously nonsignificant trends in abundance became significant when we merged data obtained from 2 or 3 years to reduce the impact of masked interannual variability in numbers. The probability of detecting a significant change in abundance increased as the time series lengthened (Fig. 1A). For example, when time series were 6 to 9 years, we found a significant trend in abundance for time series in 0.24 cases (21 of 89), but this proportion increased to 0.62 (41 of 66) when time series were >21 years. Notably, there was no significant increase or decrease in abundance for many time series. Of the 299 time series, many have not been updated recently. For example, the last year of the published time series did not extend beyond 2009 in 118 cases (Fig. 1B). For time series where there was a significant increase or decrease in abundance over time, the growth rate was not lower when initial nesting numbers were low (Fig. 1C). One well-known example of a high growth rate for a time series where abundance was initially low is for green turtles nesting at French Frigate Shoals, Hawaii (RMU 35), where nesting numbers have grown by around an order of magnitude (approximately 200 to 2000 nests) between 1973 and 2012.

To provide an up-to-date picture of abundance trends, we focused on time series where the most recent published annual abundance estimate was 2010 or later. We then selected time series where there was a significant upward or downward trend in abundance and calculated the annual growth rate for these sites. We then calculated the mean growth rate within each RMU, weighting this mean growth rate to the abundance at the end of each time series (see Materials and Methods). In this way, we determined the overall trend in abundance for each RMU. There were 17 RMUs where there was a significant trend in abundance, with 12 increasing and 5 decreasing. Across species, the number of RMUs in which the trend in abundance was upward rather than downward was one of one RMUs for hawksbills, four of five RMUs for green turtles, three of three RMUs for loggerhead

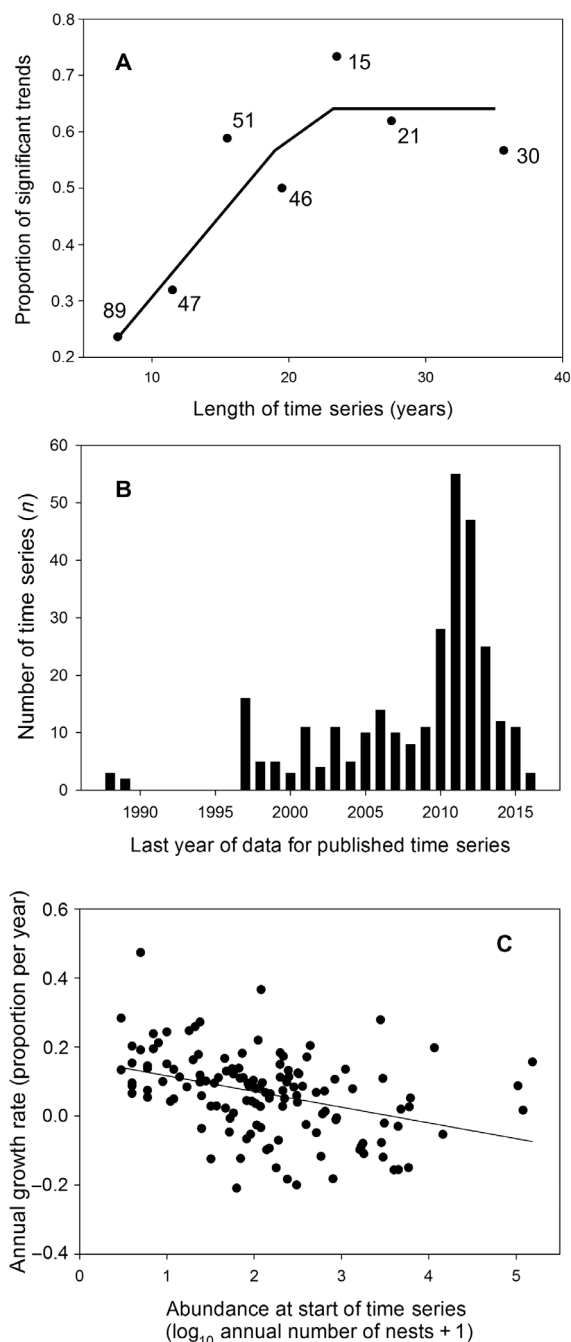


Fig. 1. Trends in abundance at individual nesting sites. (A) The proportion of time series that showed significant upward or downward trends in the nesting abundance versus the length of the time series. We pooled individual time series in 4-year intervals, except for those >30 years, which we combined to ensure relatively even sample sizes within each class (sample sizes indicated by number next to each point). A model of a linear increase in the ability to detect a significant trend for time series up to 21 years followed by an invariant (0.62) ability to detect a trend explained 76% of the variance ($F_{1,5} = 12.2$, $r^2 = 0.76$, $P < 0.01$). (B) For individual time series of annual nesting abundance that were ≥ 6 years long, the last year of the published time series. (C) The mean annual growth rate for individual time series versus the abundance at the start of the time series (using the mean nesting numbers for the first 3 years of monitoring). There was a weak ($r^2 = 0.15$) but significant ($P < 0.01$) tendency for growth rate to be lower when the initial abundance in a time series was higher. However, across time series that differed hugely in levels of abundance, high growth rates were found.

turtles, zero of one RMUs for flatback turtles, one of three RMUs for leatherback turtles, two of three RMUs for olive ridley turtles, and one of one RMUs for Kemp's ridley turtles (Fig. 2 and table S1).

Some examples of increases in abundance within RMUs include olive ridley turtles in RMU 7 (northeast Indian Ocean), where the mean annual growth rate was 0.088, and green turtles in RMU 46 (South Central Atlantic), where the mean annual growth rate was 0.052. Exceptions to the general pattern for integrated levels of abundance to be increasing included RMUs 55 (Pacific East) and 56 (Pacific West) for leatherback turtles, where the annual growth rates were -0.156 and -0.08 , respectively, and RMU 60 (Pacific Southwest) for flatback turtles, where the mean annual growth rate was -0.021 .

DISCUSSION

Our results both support and complement the IUCN assessments of the status of sea turtles. The IUCN Red List is based on a range of criteria, of which changes in abundance are only one, to provide a particular category listing. Our approach focused solely on trends in abundance. Although we used different data sets and methods to the IUCN, focusing on time series of abundance that are in the public domain and population trends, many of our key conclusions add support to the recent IUCN assessments that highlight many encouraging population trends, as well as some worrying population declines. There are good reasons for evaluating abundance trends over different spatial scales. RMUs are often considered as semi-independent management units for sea turtles that are distinct from one another based on genetics, distribution, movement, and demography, so declines in abundance within an RMU are unlikely to be supplemented by immigration from other RMUs (15). Hence, determining abundance trends for RMUs as a whole, as we have done, is important. However, many conservation organizations operate at sites where nesting numbers can be small compared to the overall abundance within that RMU as a whole. In these cases, trends at a site with low abundance will often not affect the abundance trajectory for the RMU as a whole. However, that does not mean that conservation efforts at these small sites are unimportant. They are and may drive

long-term population increases and provide a range of environmental benefits and ecosystem services at local levels (16–18). For these reasons, we have considered trends in abundance both at the level of individual time series and within RMUs as a whole. For individual time series, our results show that significant upward trends outweigh significant downward trends and that upward trends are not impeded for time series where nest numbers are initially low, that is, there appears to be an absence of Allee effects, a pattern that contrasts with some other endangered species (19–22). These findings provide an important message for local conservation efforts, showing that they can be and are being effective for different species globally. A classic example of recovery from initially low nesting numbers concerns green turtles at French Frigate Shoals, Hawaii (9). The spectacular recovery of this population is testimony to effective conservation and has led to the IUCN listing this subpopulation as least concern in 2012. A lack of Allee effect in sea turtles may be linked to the fact that male-female encounters are facilitated for time series where abundance is low because both males and females often return to fairly small breeding areas close to nesting beaches (23). Therefore, although the probability of male-female encounters on widely dispersed foraging grounds may be relatively low, this probability is relatively high when individuals are concentrated at their breeding grounds. In addition, at the nesting sites where numbers are initially very low, immigration from nearby sites might sometimes aid population recovery, with this immigration possibly explaining some exceptionally high annual growth rates (>0.3) that we reported. Our analysis could be extended by considering the distance to the neighboring nesting sites and the density of turtles, because these factors may influence, for example, male-female encounters and hence levels of egg fertility.

Conservation concerns are acute for Eastern and Western Pacific leatherbacks, which were listed as “critically endangered” by the IUCN in 2013 (13, 24, 25). We reiterate these concerns. Furthermore, there may be long lags between increased mortality during certain life stages and the reduction in nesting numbers with, for example, low hatchling success potentially taking several decades to be detected through low nesting numbers. This scenario is currently occurring on Raine Island, Australia, which is the world's largest green turtle nesting site (26). In contrast, the IUCN lists the Northwest Atlantic Ocean leatherback as

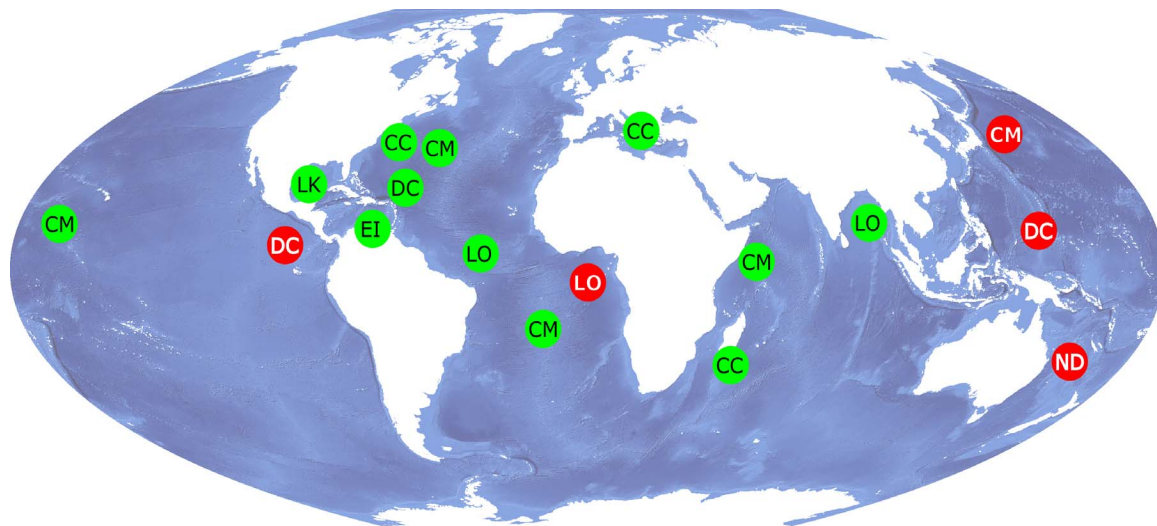


Fig. 2. Trends in the nesting abundance of sea turtles integrated within RMUs. Plot symbols reflect species, colors reflect upward (green) or downward (red) trends, and symbol size represents mean growth rate. CC, *C. caretta* (loggerhead turtle); CM, *C. mydas* (green turtle); DC, *D. coriacea* (leatherback sea turtle); EI, *E. imbricata* (hawksbill turtle); LK, *L. kempii* (Kemp's ridley); LO, *L. olivacea* (olive ridley); ND, *N. depressus* (flatback turtle).

least concern, and here, we found an increasing population size, with a mean annual growth rate of 0.109. Likewise, our analyses support the recent IUCN assessments for loggerhead turtles, in which RMUs listed as least concern have positive growth rates. The Southwest Indian Ocean loggerhead subpopulation is listed by the IUCN as “near threatened,” despite the positive growth rate reported both in this study and by the IUCN. Here, the designation is based on the small number of nesting sites within that RMU and its isolation. In addition to reiterating the messages from the recent IUCN assessments for leatherback and loggerhead turtles, our analysis informs on other species of sea turtle where the IUCN assessment are 10 years old or more. Here, we find some increases in abundance for RMUs such as hawksbill turtles in the Western Atlantic, green turtles in the Atlantic and Indian Oceans, and olive ridley turtles in the Western Atlantic and Northeast Indian Ocean. The last IUCN assessment for flatback turtles was completed in 1996, with this species being listed as “data-deficient.” We showed that in one area, RMU 60 (Australia), there has been a decline in abundance. However, we note that available time series in the public domain may often not capture information that has been collected on trends in abundance at some nesting sites. Encouragingly, data sets that are helping to fill these data gaps are continually being published [for example, the study of Groom *et al.* (27)], so an improved assessment of the conservation status of flatback turtles may soon be possible. This same issue of data availability also likely applies to other species, with the likelihood that often abundance time series will not be in the public domain. Here again, the increasing availability of data in the future will help improve assessments of population status.

We show that detecting significant increases or decreases in abundance is easier in time series that are longer and that, in many cases, the most recent estimates of abundance at nesting sites have not been updated for at least a decade. These patterns highlight both the importance of long-term monitoring, as well as the importance of reporting the outcomes of monitoring effort. It is well known that often there is considerable interannual variability in nesting numbers with sea turtles (28). This phenomenon occurs because females generally do not breed in successive years, and variability in foraging conditions may drive the proportion of a population that attains sufficient body condition to breed (29). As the extent of interannual variability in nesting numbers increases, it becomes harder to detect trends in abundance over time. Whereas the IUCN uses a minimum of 10 years of abundance data for individual nesting sites, our analysis shows that, in some cases, time series may be <10 years and still provide meaningful information on significant decreases or increases in the abundance of nests at sites. For example, across species, we found 21 significant trends in the nesting abundance at sites with <10 years of data. These findings highlight how shorter time series may sometimes have value, in particular, where the extent of interannual variability in nesting numbers is low and the rate of change in abundance at sites is high. However, we also show that significant trends were more evident in longer time series. This finding alludes to a more worrying message. Essentially, a nesting site may sometimes be in decline for many years before it becomes evident. The key conservation message is that long time series are particularly important for detecting population trends, and so, it is important that continued monitoring occurs to lengthen available time series. Our findings show that after about 20 years of monitoring, the proportion of time series with detectable increases or decreases in abundance remained constant at around 0.62, most likely because abundance at the remaining sites was fairly stable. Note that sea turtle recovery may sometimes take a long time, for example, where increased egg survival needs to propagate through to adult

numbers. Long-term support for conservation is often hard to obtain but is needed to deliver sustained conservation success.

For many individual nesting sites, the most recent published values are now >10 years old. In the intervening years, these populations may have increased, decreased, or remained stable, and even over short periods, important changes can occur. Updated time series will lead to improved estimates of population trajectories, both at individual nesting sites and within RMUs. For example, the literature on biological time series is rich with examples of new discoveries that have been made both because new approaches have been applied to existing data and new (for example, longer) data sets emerge [for example, the previous studies (30–34)]. Therefore, we encourage others to look further at long-term trends in the abundance of sea turtles, and we are sure that they will be able to expand and improve our analyses. We also applaud all the efforts of sea turtle conservation biologists to report the outcomes of their monitoring [for example, the previous studies (9, 13, 24, 35) but also see tables S2 and S3 for a full listing of published articles]. An important development in helping this reporting of monitoring data has also been the emergence of new conservation journals [for example, the studies of Groom *et al.* (27) and Piacenza *et al.* (36)]. However, it is important to be aware of the data gaps that remain. For example, at some sites where annual abundance values are not reported, there is nonetheless strong evidence for population recovery, such as for nesting hawksbill turtles in the Solomon Islands, located within RMU 12 (Southwest Pacific), and the green turtles nesting in the Aves Island Wildlife Refuge in Venezuela, located across RMUs 47 and 50 (Atlantic South Caribbean and Northwest Atlantic, respectively) (37, 38). Major information gaps also remain on the abundance trends of different life stages, including juveniles and adult males, and hence on information such as adult sex ratios (39).

Several factors have likely contributed to the recent growth in abundance at many sea turtle nesting sites (12). Historically, adult females were harvested while nesting onshore, along with their eggs (13). Eggs are also consumed by various predators, including crabs, foxes, and raccoons (16). Consequently, most conservation efforts have focused on reducing illegal harvesting and caging or relocating nests to hatcheries to maximize protection (7) and, potentially, population recovery. For example, positive impacts of improved egg survival have been modeled at several nesting sites, such as the U.S. Virgin Islands and Tortuguero, Costa Rica (40, 41). The reduced harvesting of turtles at sea [for example, green turtles in Hawaii (9)] and reduced bycatch of turtles in fishing gear might have also helped population recoveries, for example, the use of TEDs, along with the modification of hook types in long-line fisheries (10) and international conservation agreements including CITES, which prohibits trade in sea turtle products. Encouraging trends of sea turtle population resilience and recovery often reflect the long-standing efforts of conservation programs, with even simple measures helping to boost population recovery (12). For example, efforts to limit the harvesting of sea turtles and their eggs at Tortuguero, Costa Rica date back to the late 1950s (42). In the Hawaiian Archipelago, the recovery of green turtles was facilitated by the protection of turtles at both nesting beaches and foraging habitats through the enforcement of the U.S. Endangered Species Act dating back to 1978 (43). Similarly, strong recovery patterns have been detected for leatherback and green turtles nesting on the index beaches of Florida, following the implementation of more than 35 years of monitoring and conservation effort (16, 44).

The underlying effectiveness of the varied conservation measures implemented to help the recovery of sea turtle populations contrasts

with many other taxa where disease, invasive species, and habitat loss represent major drivers of population declines and tend to be very difficult to mitigate (2, 3). In some cases, trophic cascades might also operate. For instance, the general increase in green turtle populations could be attributed to the decline in their key predator, tiger sharks, due to overfishing (45). Broad-scale differences in environmental conditions might also have an effect. For example, Atlantic leatherback populations are relatively healthy, whereas Pacific populations continue to decline [our study and the studies of Martínez *et al.* (13) and Santidrián Tomillo *et al.* (24)], with these differences possibly being associated with differences in foraging conditions between the two ocean basins (46). Increasing sand temperatures, as part of global climate change, might increase the proportion of female turtles being produced and, potentially, nesting numbers (47), although rising temperature might ultimately also threaten sea turtles by increasing mortality in the nests (39, 48).

In conclusion, by focusing on time series of abundance in the public domain and using different methods from those used in the IUCN assessments, our results support and extend current knowledge on the status of global sea turtle populations. In particular, we highlight both encouraging population trends at the RMU level and some worrying population declines, particularly because these populations are unlikely to be supplemented by immigration from other RMUs. An encouraging message derived from our study is that even nesting sites with low abundance have the potential to recover. Because many conservation organizations operate at sites where nesting numbers can be small, this finding highlights the value of local conservation work, which often involves community-based programs. We hope our work encourages others to assess patterns of long-term change in the abundance of sea turtles, including the use of new data analysis methodologies, helping to extend the work of the IUCN. As time series lengthen and more data sets become available, the ability to provide comprehensive assessment of the status of species will improve.

MATERIALS AND METHODS

Global database on sea turtle population trends

We used a range of literature sources to assemble a database on global trends in population abundance for all seven species at nesting sites globally. The seven extant species of sea turtles are loggerhead (*C. caretta*), green (*C. mydas*), leatherback (*D. coriacea*), hawksbill (*E. imbricata*), olive ridley (*L. olivacea*), Kemp's ridley (*L. kempii*), and flatback (*N. depressus*) turtles. The sources included research articles published in peer-reviewed scientific journals and gray literatures (that is, symposium proceedings, annual, interannual and regional monitoring reports and newsletters, and Internet sources); we further extracted citations from the available IUCN reports. Only sources with sufficient information to demonstrate temporal trends in nest numbers were used. For pragmatic reasons, we selected a minimum of 6-year data to detect trends, although longer time series are required for robust results, as shown in Results.

We used raw data on the number of breeding females and/or nests laid annually where available or digitized nesting trends presented in graphs from various literature sources where raw numbers were unavailable. In a small proportion of cases (31 of 299 time series and 11 time series that contained data beyond 2010), where the original data sets reported the number of nesting females, these values were multiplied by 3 [that is, a value that has been assumed as the mean number of nests per female for sea turtles (49)] so that all analyses were conducted using estimated nest numbers. This assumption of three

clutches per female had no impact on the trends we identified nor on our overall conclusions. We also note that the estimates of clutch frequency for sea turtles remain problematic. For example, recently, satellite tags have been used to show that the mean number of clutches laid by females is likely very often underestimated by traditional foot patrols of nesting beaches (50). The more extended use of satellite tracking data will help to improve the conversion of data between the total number of nests and the total number of nesting females. The database was made up of both distinct sites and sites grouped by human delineations, such as county, state, country borders, or regional borders (table S3).

Trends in geographically distinct population segments (RMUs)

To assess long-term population trends at the regional level, we grouped the assimilated time series into RMUs, which are geographically distinct population segments, originally delineated by Wallace *et al.* (15). These regional population units are used to assimilate biogeographical information (that is, genetics, distribution, movement, and demography) of sea turtle nesting sites, providing a spatial basis for assessing management challenges. A total of 58 RMUs were originally delineated for the seven sea turtle species. We obtained a map of the spatial arrangement of the RMUs from the State of the World's Sea Turtles mapping application (<http://seamap.env.duke.edu/swot>) (51, 52). We then assigned each time series in our analyses to the appropriate RMU by overlapping its location with the RMU polygons. The reference name and coding of each RMU followed the original description provided in the supporting information of the study by Wallace *et al.* (15). A total of 15 nesting sites (loggerheads, $n = 1$; green turtles, $n = 3$; leatherbacks, $n = 3$; and olive ridley, $n = 8$) were located within the boundaries of two RMUs and were designated RMUs on the basis of their geographical location, their relative distance to each RMU.

In addition to examining trends in abundance for individual time series, we also aggregated abundance across time series within individual RMUs. To do this, we first selected time series where the most recent abundance estimate was 2010 or later. In this way, we included the most recent data. For sites where there were significant upward or downward trends in abundance, we used these fitted trend lines to estimate the abundance each year. This procedure removed interannual variability in nesting numbers. For sites where there was no significant trend in abundance, we applied the mean annual nesting number to all years. We then summed the abundance of individual time series within each RMUs to assess changes in abundance for RMUs as a whole. For one site (table S2, site 115), we obtained a significant decline in the first part of the series followed by an increase in the series, but overall, there is no monotonic change; thus, it was designated as no significant change.

Statistical analyses

We used linear regression models to detect directional upward or downward trends in each time series. To reduce the impact of interannual variability on detecting trends where no significant trends were detected, we reran the analyses by averaging nesting data by two and three successive years for these nesting sites. To validate the findings of the regression models, we further applied a nonparametric Mann-Kendall test (53, 54) to detect significant directional upward or downward trends in each time series using Kendall's tau rank correlation. Kendall's tau rank correlation was calculated in R (55), using the packages Kendall (56) and wq (57).

The annual growth rate for each nesting site was calculated from the mean abundance in the last 3 years of each time series (N_L) compared

to the mean abundance in the first 3 years of the same time series (N_F) and the length of the time series (n years) using Eq. 1

$$\text{Annual growth rate } (r) = \left(\frac{N_L}{N_F} \right)^{\left(\frac{1}{n-3} \right)} - 1 \quad (1)$$

We then determined the mean annual growth rate within RMUs for each species, weighting this mean growth rate to the documented abundance at the end of the time series. For example, if there were 10,000 nests at the end of time series A and an annual growth rate of 0.1 and time series B had 300 nests and an annual growth rate of 0.4, then the mean annual growth rate for that RMU would be $[(10,000 \times 0.1) + (300 \times 0.4)] / (10,000 + 300) = 0.109$.

Allee effect

To delineate whether the Allee effect affects sea turtle recovery, we examined the growth rates reported over each data set against the initial abundance reported. To validate the output of the analysis, we further regressed the number of nests at a given site ($1 + \log_{10}$ number of nests) reported over the first year against the slope of change for abundance ($1 + \log_{10}$ number of nests) produced by using linear models. Twelve time series with significant trends were excluded from this analysis due to covering a large area of disconnected sites, although their inclusion or not did not affect the outcomes of the analysis.

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at <http://advances.sciencemag.org/cgi/content/full/3/9/e1600730/DC1>

table S1. The mean growth rate within individual RMUs, weighted to the nesting abundance at the end of the time series.

table S2. Details of the 299 time series on the nesting abundance: Nonsignificant trends marked as 0, upward significant trends marked as 1, and downward trends marked as 2.

table S3. List of sea turtle nesting sites and sources.

REFERENCES AND NOTES

1. A. D. Barnosky, N. Matzke, S. Tomiya, G. O. U. Wogan, B. Swartz, T. B. Quental, C. Marshall, J. L. McGuire, E. L. Lindsey, K. C. Maguire, B. Mersey, E. A. Ferrer, Has the Earth's sixth mass extinction already arrived? *Nature* **471**, 51–57 (2011).
2. S. N. Stuart, J. S. Chanson, N. A. Cox, B. E. Young, A. S. L. Rodrigues, D. L. Fischman, R. W. Waller, Status and trends of amphibian declines and extinctions worldwide. *Science* **306**, 1783–1786 (2004).
3. W. J. Ripple, J. A. Estes, R. L. Beschta, C. C. Wilmers, E. G. Ritchie, M. Hebblewhite, J. Berger, B. Elmhagen, M. Letnic, M. P. Nelson, O. J. Schmitz, D. W. Smith, A. D. Wallach, A. J. Wirsing, Status and ecological effects of the world's largest carnivores. *Science* **343**, 1241484 (2014).
4. M. R. W. Rands, W. M. Adams, L. Bennun, S. H. Butchart, A. Clements, D. Coomes, A. Entwistle, I. Hodge, V. Kapos, J. P. W. Scharlemann, W. J. Sutherland, B. Virá, Biodiversity conservation: Challenges beyond 2010. *Science* **329**, 1298–1303 (2010).
5. S. H. Butchart, M. Walpole, B. Collen, A. Van Strien, J. P. W. Scharlemann, R. E. A. Almond, J. E. Baillie, B. Bomhard, C. Brown, J. Bruno, K. E. Carpenter, G. M. Carr, J. Chanson, A. M. Cheney, J. Csirke, N. C. Davidson, F. Dentener, M. Foster, A. Galli, J. N. Galloway, P. Genovesi, R. D. Gregory, M. Hockings, V. Kapos, J. F. Lamarque, F. Leverington, J. Loh, M. A. McGeoch, L. McRae, A. Minasyan, M. Hernández Morcillo, T. E. E. Oldfield, D. Pauly, S. Quader, C. Revenga, J. R. Sauer, B. Skolnik, D. Spear, D. Stanwell-Smith, S. N. Stuart, A. Symes, M. Tierney, T. D. Tyrrell, J.-C. Vié, R. Watson, Global biodiversity: Indicators of recent declines. *Science* **328**, 1164–1168 (2010).
6. J. B. C. Jackson, M. X. Kirby, W. H. Berger, K. A. Bjorndal, L. W. Botsford, B. J. Bourque, R. H. Bradbury, R. Cooke, J. Erlandson, J. A. Estes, T. P. Hughes, S. Kidwell, C. B. Lange, H. S. Lenihan, J. M. Pandolfi, C. H. Peterson, R. S. Steneck, M. J. Tegner, R. R. Warner, Historical overfishing and the recent collapse of coastal ecosystems. *Science* **293**, 629–637 (2001).
7. M. Hamann, M. Godfrey, J. Seminoff, K. Arthur, P. Barata, K. Bjorndal, A. Bolten, A. Broderick, L. Campbell, C. Carreras, P. Casale, M. Chaloupka, S. K. F. Chan, M. S. Coyne, L. B. Crowder, C. E. Diez, P. H. Dutton, S. P. Epperly, N. N. FitzSimmons, A. Formia, M. Girondot, G. C. Hays, I. J. Cheng, Y. Kaska, R. Lewison, J. A. Mortimer, W. J. Nichols, R. D. Reina, K. Shanker, J. R. Spotila, J. Tomás, B. P. Wallace, T. M. Work, J. Zbinden, B. J. Godley, Global research priorities for sea turtles: Informing management and conservation in the 21st century. *Endanger. Species Res.* **11**, 245–269 (2010).
8. B. P. Wallace, A. D. DiMatteo, A. B. Bolten, M. Y. Chaloupka, B. J. Hutchinson, F. A. Abreu-Grobois, J. A. Mortimer, J. A. Seminoff, D. Amorcho, K. A. Bjorndal, J. Bourjea, B. W. Bowen, R. Briseño Dueñas, P. Casale, B. C. Choudhury, A. Costa, P. H. Dutton, A. Fallabrino, E. M. Finkbeiner, A. Girard, M. Girondot, M. Hamann, B. J. Hurley, M. López-Mendilaharsu, M. A. Marcovaldi, J. A. Musick, R. Nel, N. J. Pilcher, S. Troëng, B. Witherington, R. B. Mast, Global conservation priorities for marine turtles. *PLOS ONE* **6**, e24510 (2011).
9. J. N. Kittinger, K. S. V. Houtan, L. E. McClenachan, A. L. Lawrence, Using historical data to assess the biogeography of population recovery. *Ecography* **36**, 868–872 (2013).
10. R. L. Lewison, L. B. Crowder, D. J. Shaver, The impact of turtle excluder devices and fisheries closures on loggerhead and Kemp's ridley strandings in the western Gulf of Mexico. *Conserv. Biol.* **17**, 1089–1097 (2003).
11. G. C. Hays, Good news for sea turtles. *Trends Ecol. Evol.* **19**, 349–351 (2004).
12. M. Chaloupka, K. A. Bjorndal, G. H. Balazs, A. B. Bolten, L. M. Ehrhart, C. J. Limpus, H. Suganuma, S. Troëng, M. Yamaguchi, Encouraging outlook for recovery of a once severely exploited marine megaherbivore. *Glob. Ecol. Biogeogr.* **17**, 297–304 (2008).
13. L. S. Martínez, A. R. Barragán, D. G. Muñoz, N. García, P. Huerta, F. Vargas, Conservation and biology of the leatherback turtle in the Mexican Pacific. *Chelonian Conserv. Biol.* **6**, 70–78 (2007).
14. International Union for Conservation of Nature (IUCN), The IUCN Red List of Species (IUCN, 2016); www.iucnredlist.org/.
15. B. P. Wallace, A. D. DiMatteo, B. J. Hurley, E. M. Finkbeiner, A. B. Bolten, M. Y. Chaloupka, B. J. Hutchinson, F. A. Abreu-Grobois, D. Amorcho, K. A. Bjorndal, J. Bourjea, B. W. Bowen, R. B. Dueñas, P. Casale, B. C. Choudhury, A. Costa, P. H. Dutton, A. Fallabrino, A. Girard, M. Girondot, M. H. Godfrey, M. Hamann, M. López-Mendilaharsu, M. A. Marcovaldi, J. A. Mortimer, J. A. Musick, R. Nel, N. J. Pilcher, J. A. Seminoff, S. Troëng, B. Witherington, R. B. Mast, Regional management units for marine turtles: A novel framework for prioritizing conservation and research across multiple scales. *PLOS ONE* **5**, e15465 (2010).
16. L. Ehrhart, W. Redfoot, D. Bagley, K. Mansfield, Long-term trends in loggerhead (*Caretta caretta*) nesting and reproductive success at an important western Atlantic rookery. *Chelonian Conserv. Biol.* **13**, 173–181 (2014).
17. S. B. Weber, N. Weber, J. Ellick, A. Avery, R. Frauenstein, B. J. Godley, J. Sim, N. Williams, A. C. Broderick, Recovery of the South Atlantic's largest green turtle nesting population. *Biodivers. Conserv.* **23**, 3005–3018 (2014).
18. K. A. Bjorndal, J. B. C. Jackson, *10 Roles of Sea Turtles in Marine Ecosystems: Reconstructing the Past*, vol. 2 of *The Biology of Sea Turtles*, P. L. Lutz, J. A. Musick, J. Wyneken, Eds. (CRC Press LLC, 2002), pp. 259–273.
19. J. A. Hutchings, Thresholds for impaired species recovery. *Proc. R. Soc. B* **282**, 20150654 (2015).
20. P. A. Stephens, W. J. Sutherland, Consequences of the Allee effect for behaviour, ecology and conservation. *Trends Ecol. Evol.* **14**, 401–405 (1999).
21. C.-M. Hung, P.-J. L. Shaner, R. M. Zink, W.-C. Liu, T.-C. Chu, W.-S. Huang, S.-H. Li, Drastic population fluctuations explain the rapid extinction of the passenger pigeon. *Proc. Natl. Acad. Sci.* **111**, 10636–10641 (2014).
22. A. Kuparinen, D. M. Keith, J. A. Hutchings, Allee effect and the uncertainty of population recovery. *Conserv. Biol.* **28**, 790–798 (2014).
23. G. Schofield, V. J. Hobson, M. K. S. Lilley, K. A. Katselidis, C. M. Bishop, P. Brown, G. C. Hays, Inter-annual variability in the home range of breeding turtles: Implications for current and future conservation management. *Biol. Conserv.* **143**, 722–730 (2010).
24. P. Santidrián Tomillo, E. Vélez, R. D. Reina, R. Piedra, F. V. Paladino, J. R. Spotila, Reassessment of the leatherback turtle (*Dermodochelys coriacea*) nesting population at Parque Nacional Marino Las Baulas, Costa Rica: Effects of conservation efforts. *Chelonian Conserv. Biol.* **6**, 54–62 (2007).
25. B. P. Wallace, M. Tiwari, M. Girondot, *Dermodochelys coriacea* (The IUCN Red List of Threatened Species 2013: E.T6494A43526147, 2013); <http://dx.doi.org/10.2305/IUCN.UK.2013-2.RLTS.T6494A43526147.en>.
26. C. J. Limpus, J. D. Miller, C. J. Parmenter, D. J. Limpus, The green turtle, *Chelonia mydas*, population of Raine Island and the northern Great Barrier Reef: 1843–2001. *Mem. Queensl. Mus.* **49**, 349–440 (2003).
27. R. A. Groom, A. D. Griffiths, M. Chaloupka, Estimating long-term trends in abundance and survival for nesting flatback turtles in Kakadu National Park, Australia. *Endanger. Species Res.* **32**, 203–211 (2017).
28. G. C. Hays, The implications of variable remigration intervals for the assessment of population size in marine turtles. *J. Theor. Biol.* **206**, 221–227 (2000).
29. A. C. Broderick, F. Glen, B. J. Godley, G. C. Hays, Variation in reproductive output of marine turtles. *J. Exp. Mar. Biol. Ecol.* **288**, 95–109 (2003).

30. S. L. Hinder, G. C. Hays, M. Edwards, E. C. Roberts, A. W. Walne, M. B. Gravenor, Changes in marine dinoflagellate and diatom abundance under climate change. *Nat. Clim. Chang.* **2**, 271–275 (2012).
31. P. S. Jørgensen, K. Böhning-Gaese, K. Thørup, A. P. Tøttrup, P. Chylarecki, F. Jiguet, A. Lehikoinen, D. G. Noble, J. Reif, H. Schmid, C. van Turnhout, I. J. Burfield, R. Foppen, P. Voříšek, A. van Strien, R. D. Gregory, C. Rahbek, Continent-scale global change attribution in European birds-combining annual and decadal time scales. *Glob. Chang. Biol.* **22**, 530–543 (2016).
32. C. Sguotti, C. P. Lynam, B. García-Carreras, J. R. Ellis, G. H. Engelhard, Distribution of skates and sharks in the North Sea: 112 years of change. *Glob. Chang. Biol.* **22**, 2729–2743 (2016).
33. W. J. Chivers, A. W. Walne, G. C. Hays, Mismatch between marine plankton range movements and the velocity of climate change. *Nat. Commun.* **8**, 14434 (2017).
34. E. Willis-Norton, E. L. Hazen, S. Fossette, G. Shillinger, R. R. Rykaczewski, D. G. Foley, J. P. Dunne, S. J. Bograd, Climate change impacts on leatherback turtle pelagic habitat in the Southeast Pacific. *Deep Sea Res. Part II Top. Stud. Oceanogr.* **113**, 260–267 (2015).
35. P. Santidrián Tomillo, V. S. Saba, G. S. Blanco, C. A. Stock, F. V. Paladino, J. R. Spotila, Climate driven egg and hatchling mortality threatens survival of Eastern Pacific leatherback turtles. *PLOS ONE* **7**, e37602 (2012).
36. S. E. Piacenza, G. H. Balazs, S. K. Hargrove, P. M. Richards, S. S. Heppell, Trends and variability in demographic indicators of a recovering population of green sea turtles *Chelonia mydas*. *Endanger. Species Res.* **31**, 103–117 (2016).
37. R. J. Hamilton, T. Bird, C. Gereniu, J. Pita, P. C. Ramohia, R. Walter, C. Goerlich, C. Limpus, Solomon islands largest hawksbill turtle rookery shows signs of recovery after 150 years of excessive exploitation. *PLOS ONE* **10**, e0121435 (2015).
38. D. A. Prieto-Torres, J. Hernández-Rangel, Breeding biology and hatching success of *Chelonia mydas* (Testudines: Cheloniidae) in Aves Island Wildlife Refuge, Venezuela, during the 2010 reproductive season. *Rev. Biol. Trop.* **63**, 1059–1070 (2015).
39. G. C. Hays, A. D. Mazaris, G. Schofield, J.-O. Laloë, Population viability at extreme sex ratio skews produced by temperature dependent sex determination. *Proc. R. Soc. B* **284**, 20162576 (2017).
40. Turtle Expert Working Group, An assessment of the leatherback turtle population in the Atlantic Ocean (NOAA Technical Memorandum NMFS-SEFSC-555, 2007), 116 p; www.sefsc.noaa.gov/turtles/TM_555_DcTEWG.pdf.
41. Sea Turtle Conservancy (STC); <https://conserveturtles.org/stc-programs-research-tortuguero-season-reports/>.
42. K. A. Bjørndal, J. A. Wetherall, A. B. Bolten, J. A. Mortimer, Twenty-six years of green turtle nesting at Tortuguero, Costa Rica: An encouraging trend. *Conserv. Biol.* **13**, 126–134 (1999).
43. G. H. Balazs, M. Chaloupka, Thirty-year recovery trend in the once depleted Hawaiian green sea turtle stock. *Biol. Conserv.* **117**, 491–498 (2004).
44. Fish and Wildlife Research Institute, Florida Fish and Wildlife Conservation Commission; <http://myfwc.com/research/wildlife/sea-turtles/nesting/>.
45. T. B. Atwood, R. M. Connolly, E. G. Ritchie, C. E. Lovelock, M. R. Heithaus, G. C. Hays, J. W. Fourqurean, P. I. Macreadie, Predators help protect carbon stocks in blue carbon ecosystems. *Nat. Clim. Chang.* **5**, 1038–1045 (2015).
46. H. Bailey, S. Fossette, S. J. Bograd, G. L. Shillinger, A. M. Swithenbank, J.-Y. Georges, P. Gaspar, K. P. Strömberg, F. V. Paladino, J. R. Spotila, B. A. Block, G. C. Hays, Movement patterns for a critically endangered species, the leatherback turtle (*Dermochelys coriacea*), linked to foraging success and population status. *PLOS ONE* **7**, e36401 (2012).
47. J.-O. Laloë, J. Cozens, B. Renom, A. Taxonera, G. C. Hays, Effects of rising temperature on the viability of an important sea turtle rookery. *Nat. Clim. Chang.* **4**, 513–518 (2014).
48. V. S. Saba, C. A. Stock, J. R. Spotila, F. V. Paladino, P. Santidrián Tomillo, Projected response of an endangered marine turtle population to climate change. *Nat. Clim. Chang.* **2**, 814–820 (2012).
49. H. F. Hirth, Some aspects of the nesting behavior and reproductive biology of sea turtles. *Am. Zool.* **20**, 507–523 (1980).
50. N. Esteban, J. A. Mortimer, G. C. Hays, How numbers of nesting sea turtles can be over-estimated by nearly a factor of two. *Proc. R. Soc. B* **284**, 20162581 (2017).
51. C. Y. Kot, E. Fujioka, A. D. DiMatteo, B. P. Wallace, B. J. Hutchinson, J. Cleary, P. N. Halpin, R. B. Mast, The State of the World's Sea Turtles Online Database: Data provided by the SWOT Team and hosted on OBIS-SEAMAP [Oceanic Society, Conservation International, IUCN Marine Turtle Specialist Group (MSTSG), and Marine Geospatial Ecology Lab, Duke University, 2015]; <http://seamap.env.duke.edu/swot>.
52. State of the World's Sea Turtles (SWOT), SWOT reports vol. I (2006); vol. II (2007); vol. III (2008); vol. IV (2009); vol. V (2010); vol. VI (2011); vol. VII (2012); vol. VIII (2013); vol. IX (2014); vol. X (2015); <http://seamap.env.duke.edu/swot>.
53. H. B. Mann, Nonparametric tests against trend. *Econometrica* **13**, 245–259 (1945).
54. M. G. Kendall, *Rank Correlation Methods* (Griffin, ed. 4, 1976).
55. R Core Team, R: A language and environment for statistical computing (R Foundation for Statistical Computing, 2013); www.R-project.org/.
56. A. I. McLeod, Kendall rank correlation and Mann-Kendall trend test (R Package Kendall, 2005); <https://cran.r-project.org/web/packages/Kendall/Kendall.pdf>.
57. A. D. Jassby, J. E. Cloern, wq: Some tools for exploring water quality monitoring data (R package version 0.4.5, 2015); <http://cran.r-project.org/package=wq> [accessed January 2016].

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