

Global patterns for upper ceilings on migration distance in sea turtles and comparisons with fish, birds and mammals

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Summary

1. Some animals migrate huge distances in search of resources with locomotory mode (flying/swimming/walking) thought to drive the upper ceilings on migration distance. Yet in cross-taxa comparisons, upper ceilings on migration distance have been ignored for one important group, sea turtles.

2. Using migration distances recorded for 407 adult and 4715 juvenile sea turtles across five species, we show that for adult cheloniid turtles, the upper ceiling on species migration distances between breeding and foraging habitats (1050–2850 km across species) is similar to that predicted for equivalent-sized marine mammals and fish.

3. In contrast, by feeding in the open ocean, adult leatherback turtles (*Dermochelys coriacea*) and juveniles of all turtle species can travel around 12 000 km from their natal regions, travelling across the widest ocean basins. For juvenile turtles, this puts their maximum migration distances well beyond those expected for equivalent-sized marine mammals and fish, but not those found in some similar sized birds.

4. Post-hatchling turtles perform these long-distance migrations to juvenile foraging sites only once in their lifetime, while adult turtles return to their breeding sites every few (generally ≥ 2) years. Our results highlight the important roles migration periodicity and foraging mode can play in driving the longest migrations, and the implications for Marine Protected Area planning are considered in terms of sea turtle conservation.

Key-words: biologging, Fastloc GPS, migration, movement ecology, movement models, tracking

Introduction

There has been prolonged debate about the evolution of migration across animals with diverse life histories (Alexander 1998; Hein, Hou & Gillooly 2011), and migration forms an important component of the broader area of movement ecology (Nathan 2008). Migration is often described as the to-and-fro movement between regions where conditions (e.g. foraging/breeding conditions/temperature) are alternately favourable and unfavourable, so that it is better for animals to move between locations in some repeatable manner rather than remain continuously in one place (Dingle & Drake 2007; Holt & Fryxell 2011). Often this to-and-fro migration occurs over an annual

cycle. Classic examples of these to-and-fro annual migrations include birds that may travel 100s or 1000s of km to take advantage of seasonally available resources, and in some cases, these movements span both the northern and southern hemisphere (Shaffer *et al.* 2006; Egevang *et al.* 2010). For example, satellite-tracked Arctic terns (*Sterna paradisaea*) perform the longest documented animal migrations between their seasonal habitats in the Arctic and Antarctic >17 000 km apart (Egevang *et al.* 2010). In the marine realm, there are also a number of notable long-distant swimmers, including baleen whales that migrate to-and-fro between tropical calving grounds in winter and high-latitude feeding areas in the summer (>8000 km apart; Rasmussen *et al.* 2007). In the terrestrial realm, migrants such as Arctic caribou (*Rangifer tarandus*) and wildebeest (*Connochaetes taurinus*) travel between sites

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several hundred kilometres apart to avoid poor winter conditions and/or profit from good summer conditions (Fancy *et al.* 1989; Murray 1995).

For flying birds/insects, swimming mammals/fish and terrestrial mammals, meta-analyses show migration distances increase with species body mass, albeit with different relationships among flyers, swimmers and walkers: for their body size, flyers travel furthest followed by swimmers and then walkers (Alexander 1998; Hein, Hou & Gillooly 2011). Such relationships stimulate questions on the processes that drive maximum migration distances. Alexander (1998) considered the interplay between energy utilization during migration, speed of migration and energy gain after completing migration to model potential migration distances across different taxa. For example, if animals travel quickly and the cost of migration is relatively small, then they may have sufficient time to build up reserves after travelling to allow annual migration (Alexander 1998). The model of Hein, Hou & Gillooly (2011) is centred around equations that relate the cost of locomotion to mode of locomotion (swimming, flying and walking), body size and movement speed. While this biomechanical model has great strength for predicting the observed general patterns of maximum migration distance, there remain a number of features related to specific aspects of the biology of individual taxa that may remain important, as evidenced by the considerable variation in migration distance not explained by the biomechanical model. For example, the model formulation of Hein, Hou and Gillooly (2011) suggests that the number of refuelling stops during migration will influence the ceiling of migration distance. We use a paradigmatic group of long-distance travellers, the sea turtles, which were not considered in the Hein, Hou and Gillooly (2011) analysis, to explore two aspects of the biology of migrants that might be expected to be important determinants for maximum migration distance. First, we consider the periodicity of migration. The general paradigm is that migrants complete to-and-fro migration each year. Hence, there must be sufficient time to refuel within this annual cycle. However, sea turtles do not migrate every year, but instead take several years to refuel between migrations (Hughes 1995). Second, we consider the importance of the extent of refuelling during migration trips by distinguishing species and life-history stages of sea turtle that fast vs. those that continually forage during long-distance journeys.

Given the huge international efforts over the last decade devoted to satellite tracking sea turtles and also, to a lesser extent, to document the extent of juvenile movements using genetic mixed stock analysis (see for example Bowen & Karl 2007; Shillinger *et al.* 2008; Block *et al.* 2011), it is timely to review the distance that sea turtles migrate. We used satellite tracking and molecular mixed stock analysis of >5000 individual sea turtles across five species to establish where their upper ceiling on migration distance lies compared to other walking, flying and swimming migrants. Hence, we help complete the picture of how sea turtle

migration distances compare to those of other vertebrates while taking into consideration the roles of breeding periodicity/migration frequency (annual vs. non-annual), feeding mode during migration (feeding vs. fasting) and locomotory mode (swimming, flying, walking) in driving migration distances.

Materials and methods

ADULT MIGRATORY DISTANCES

For adult hard-shelled sea turtles (family Cheloniidae), we used papers in the peer-review literature where maps clearly displayed the post-nesting migratory routes of ≥ 3 individuals successfully satellite tracked to spatially discrete foraging sites (see Table S1a and references in Supporting information). Only turtles that showed a period of residence, typically weeks or months at their final destinations, were considered successfully tracked to foraging grounds. While Cheloniidae species typically migrate to spatially discrete neritic foraging habitats, a couple of turtles were tracked to less discrete oceanic foraging habitats (e.g. loggerhead turtles from Cape Verde; Hawkes *et al.* 2006). Satellite transmissions confirmed that these individuals had reached their general foraging areas off the West coast of Africa as tags transmitted for prolonged periods (several months to >1 year) in these offshore waters. Hence, for these turtles, their final locations were used to represent the general vicinity of their foraging habitats. Other turtles believed to be foraging oceanically (e.g. green turtles tracked south from the Galapagos Islands; Seminoff *et al.* 2008) were not included in this analysis as their final foraging habitats could not be confirmed. Tags from these turtles either stopped transmitting while turtles were still travelling at speeds of 25–50 km per day or, at most, only two successive Argos fixes at the same oceanic locations where transmitted before tag transmissions ceased. Leatherback turtles (*Dermochelys coriacea*) are the only species of the family Dermochelyidae. Unlike Cheloniidae species, adult leatherbacks do not migrate to discrete foraging sites where they remain for long periods, but instead they continue to travel throughout the interval between breeding seasons (e.g. Fossette *et al.* 2010). Hence, for leatherbacks, we could not use migratory end points to identify foraging grounds. Consequently, to compare travel distances of adult turtles, we measured the great-circle distance (assuming travel around intervening land masses) between breeding grounds and the point at which turtles were furthest from their breeding grounds.

For >99% of the tracked cheloniid turtles, great-circle distance measurements revealed that final foraging destinations also coincided with the point of maximum displacement from nesting sites. So for two loggerhead turtle (*Caretta caretta*) populations where the furthest locations of their tracks could not be determined (because individual tracks could not be identified in the spaghetti tracking plots of a large number of individuals; Hawkes *et al.* 2006; Girard, Tucker & Calmettes 2009), we instead measured the distance to final foraging locations, which were clearly identifiable. For leatherback turtles, we only used populations where ≥ 3 individuals were tracked for a period of at least 4 months before satellite transmissions stopped. When the duration of the satellite tracking period was unknown, tracks that had clearly ended too prematurely to obtain accurate information on distance travelled (typically just a few km from the nesting site while individuals were still in transit to foraging sites or believed to be performing interesting movements) were not used. In studies where individual leatherback tracks could not be identified in the spaghetti tracking plots of large numbers of tracked turtles, we instead measured distances to clearly defined high-use foraging areas, areas of concentrated and prolonged foraging activity by one or multiple

individuals (Shillinger *et al.* 2008; Benson *et al.* 2011). Where it was unclear how many turtles had migrated to each high-use foraging area, the number of tracked turtles was divided by the number of high-use areas to best utilize these valuable extensive data sets to gain information on migration distances (Shillinger *et al.* 2008).

JUVENILE MIGRATORY DISTANCES

All sea turtles except the geographically restricted flatback turtle (*Natator depressus*) have a juvenile oceanic phase (Musick & Limpus 1997). Hatchlings enter the sea and disperse widely in oceanic currents for a period commonly known as the 'lost years', until they are seen again upon arrival in coastal foraging habitats as young juveniles. Due to natal philopatry and the resultant genetic isolation among nesting populations, population-specific mtDNA markers are routinely used to assign juvenile turtles captured at juvenile feeding grounds to their respective rookery of origin (Bowen & Karl 2007). Due to the evolving nature of this technique and the continual updating of mtDNA data bases as genetic data from additional turtle rookeries are obtained for each juvenile foraging ground, we used only the most recent publication where mixed stock analyses had been conducted to determine the origin of and hence displacement distance of juvenile turtles. In the same way as adult turtles, displacement distances between foraging and nesting grounds were determined by great-circle distances assuming travel around land masses (see Table S1b and references in Supporting information). These juvenile movements between nesting grounds and foraging sites may only occur once in each direction in an individual's life and hence are not 'to-and-fro' migrations like those shown by adults. For simplicity, here we use the term 'migration' to describe both the to-and-fro movements of adults and these movements of juveniles.

Across taxa meta-analysis

The majority of satellite tracking studies contained data on the carapace measurements of individual turtles. Carapace measurements were converted to body mass (kg) based on species-specific carapace length and mass equations (van Dam & Diez 1998; Jones *et al.* 2008; Wabnitz & Pauly 2008). In a few instances where the sizes of satellite-tracked individuals were not available, we used either (i) the mean size of the satellite-tracked turtles from that site or (ii) the mean size of the nesting population at that site (see Table S1). Using R software (R Development Core Team 2009), Mann–Whitney–Wilcoxon tests were used in pairwise comparisons to determine whether migration distances differed significantly between cheloniid species, between adult leatherbacks and cheloniid species and between adult and juvenile turtles within species. For hard-shelled turtles, we used percentile regression to objectively fit a function to the upper ceiling of migration distance vs. body size. We created a series of size bins (25-kg increments) and then determined the 97.5 percentile of the values for migration distance within each bin. The choice of a particular percentile threshold will have some influence on the function fitted for the upper ceiling of migration distance. We therefore conducted a sensitivity analysis to show that our conclusions were not changed by varying the percentile values between 90% and 99%. We chose the 97.5 percentile on the basis of statistical convention (i.e. the 95% confidence interval; e.g. Bradshaw, McMahon & Hays 2007). For comparison of sea turtle migration distances with other groups, migration distances for other swimmers (marine mammals and fish), walkers (terrestrial mammals) and flyers (birds and insects) were taken from a recent meta-analysis (Hein, Hou & Gillooly 2011) of species maximum recorded migration distances (typically displacement).

Results

ADULT SEA TURTLES

There were significant differences in the migration distances across adult sea turtle species (Fig. 1a,b; Table S1a, Supporting information). For adults, mean migration distances (\pm SD) were 4138 ± 1966 km for leatherbacks, 806 ± 602 km for green turtles (*Chelonia mydas*), 618 ± 445 km for loggerhead turtles, 327 ± 387 km for hawksbill turtles (*Eretmochelys imbricata*) and 482 ± 286 km for olive ridley turtles (*Lepidochelys olivacea*). Maximum migration distances were c. 11 000 km (Benson *et al.* 2011), 2850 km (Hays *et al.* 2002a), 2150 km (Broderick *et al.* 2003), 1630 km (Van Dam *et al.* 2008) and 1050 km, respectively (Whiting, Long & Coyne 2007). Within the cheloniid turtles, in order of descending mean/maximum migration distance, migration distances were significantly different between green turtles and loggerhead turtles ($n = 194$, $W_1 = 7120$, $P = 0.04$), loggerhead turtles and hawksbill turtles ($n = 110$, $W_1 = 1050$, $P < 0.001$), and hawksbill and olive ridley turtles ($n = 40$, $W_1 = 526$, $P = 0.04$; Fig. 1b). Migration distances for leatherback turtles were significantly further than all the cheloniid turtles combined ($n = 407$, $W_1 = 278891$, $P < 0.001$; Fig. 1a). Phylogeny thus appears to have an important influence on adult migration distances. Across adult cheloniid turtles (i.e. excluding leatherback turtles), there was a weak linear relationship between migration distance and body mass: \log_{10} distance (km) = $0.49 \times \log_{10}$ turtle body mass (kg) + 1.69 ($n = 234$, $r^2 = 0.03$, $F_{232} = 7.26$, $P < 0.01$). However, the percentile regression indicated that the upper ceiling of migration distance did not increase significantly with body size ($n = 234$, $F_{1,4} = 0.04$, $P = 0.84$). A weak linear relationship between migration distance and body mass was also evident for leatherback turtles [body mass: \log_{10} distance (km) = $0.72 \times \log_{10}$ turtle body mass (kg) + 1.77 ($n = 173$, $r^2 = 0.03$, $F_{171} = 6.24$, $P < 0.01$)].

Shown in Figure 1 are some examples of special cases for adult migration distance in cheloniid turtles, for example, small turtles that migrated relatively long distances and large turtles that migrated relatively short distances. For example, three small (c. 40 kg) loggerhead turtles from Cyprus migrated c. 2000 km (Broderick *et al.* 2003), while large (c. 150 kg) green turtles nesting on the Cocos (Keeling) Islands were non-migratory (Whiting *et al.* 2008). Also highlighted are the longest migrations shown by adult cheloniid turtles; green turtles from Ascension Island which migrated up to 2850 km (Hays *et al.* 2002a).

JUVENILE SEA TURTLES

Migration distances travelled by juvenile turtles were of the same order of magnitude as leatherback turtles (Fig. 1a, Table S1b, Supporting information). The mean

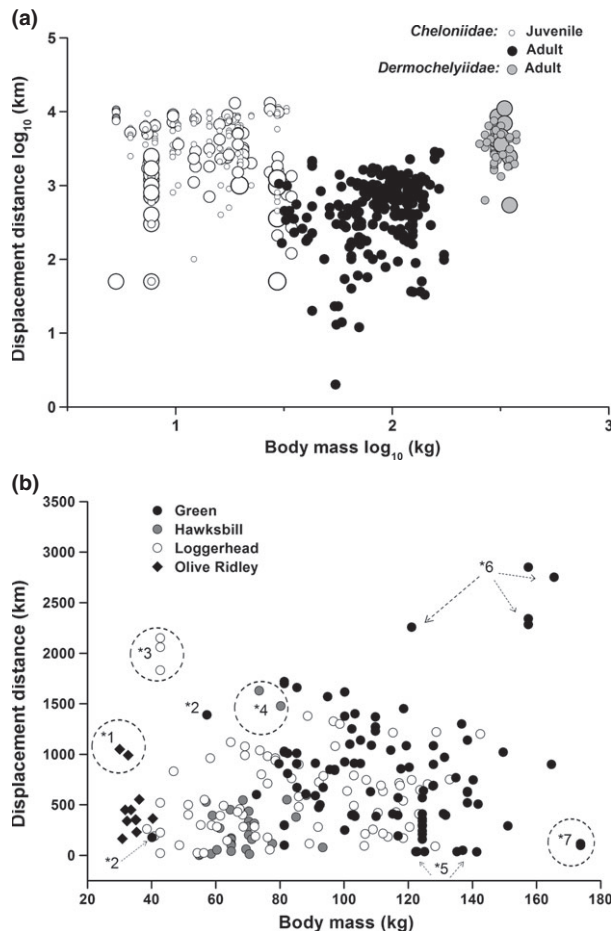


Fig. 1. The distances between breeding sites and foraging sites for adult and juvenile sea turtles. Adult data come from satellite-tracked individuals (see Table S1a, Supporting information). Juvenile data come from genetic mixed stock analysis linking haplotypes on foraging grounds to potential source breeding grounds (see Table S1b, Supporting information). (a) Data for all turtles. Data points for hard-shelled adult turtles are based on each satellite-tracked individual turtle. For leatherback turtles, small points represent data from a single individual, and medium-sized points represent the mean distances travelled by 5–16 individuals. For juvenile turtles, the small points represent the distances travelled by <10 individuals, medium-sized points represent the distances travelled by ≥ 10 to <100 individuals, and large points represent the distances travelled by ≥ 100 to <1000 individuals. (b) Only data for adult hard-shelled turtles. Asterisks denote points of interest; *1. two Olive Ridley turtles that migrated *c.* 1000 km from North Australia (McMahon, Bradshaw & Hays 2007; Whiting, Long & Coyne 2007), *2. the smallest satellite-tracked green turtle that did not migrate far from the Galapagos Islands, and a small Galapagos green turtle that migrated >1000 km after nesting are both highlighted (Seminoff *et al.* 2008), *3. three small loggerhead turtles from Cyprus that migrated *c.* 2000 km (Broderick *et al.* 2003), *4. the only two Hawksbill turtles that migrated >1000 km (both from Puerto Rico; Van Dam *et al.* 2008), *5 non-migratory green turtles from the Cocos (Keeling) Islands (Whiting *et al.* 2008), *6. green turtles from Ascension Island, which performed the longest migrations of up to 2850 km (Hays *et al.* 2002a) and *7. two large green turtles tracked from Thailand, which did not migrate far (Yasuda *et al.* 2006).

(\pm SD) distances travelled by juvenile green turtles, loggerhead turtles and hawksbill turtles were 4557 (\pm 2525) km, 4993 km (\pm 3627) km and 2675 km (\pm 3212) km,

respectively. Within species, migration distances of juvenile turtles were significantly different to adult turtles (green turtles: $n = 1540$, $W_1 = 39367$, $P < 0.001$; hawksbill turtles: $n = 698$, $W_1 = 5637$, $P < 0.001$; loggerhead turtles: $n = 2686$, $W_1 = 47511$, $P < 0.001$). The maximum migration distances of >13 000 km were obtained by juvenile loggerhead turtles that travelled from Australia to Peru (Boyle *et al.* 2009). Loggerhead turtles from the Mediterranean, Mexico and southern Florida travelled >10 000 km (Casale *et al.* 2008; Reis *et al.* 2010). The maximum distances recorded for juvenile green turtles were >9000 km from West Africa to the southeast USA, and juvenile greens from Ascension Island, eastern Brazil, Costa Rica, Mexico and Florida all travelled >8000 km (Monzón-Argüello *et al.* 2010). Juvenile hawksbill turtles from Mexico, Belize and Costa Rica travelled >10 000 km to foraging grounds off West Africa (Monzón-Argüello *et al.* 2011). Phylogeny also appears to influence juvenile migration distances as migration distances were significantly different between juvenile green and loggerhead turtles ($n = 4032$, $W_1 = 4854108$, $P < 0.001$), juvenile loggerhead and hawksbill turtles ($n = 3274$, $W = 928319$, $P < 0.001$), and juvenile green turtles and hawksbill turtles ($n = 2096$, $W_1 = 562336$, $P < 0.001$).

THEORETICAL CONSIDERATIONS

Is this observed maximum migration distance of *c.* 2850 km for adult cheloniid turtles close to the physiological maximum for a sea turtle that does not feed while away from the foraging grounds? Figure 2 sets out some of the considerations that dictate when migration will be profitable. Quantifying the various rates of energy gain and expenditure inherent in these theoretical body condition trajectories is not straightforward in sea turtles. Almost nothing is known about the maximum fuel stores, the rate of energy loss when at the breeding grounds and the rate of energy gain on the foraging grounds. However, we can crudely estimate, using best guesses to parameterise the energy balance calculations, whether 2850 km lies close to the physiological maximum that can be sustained by fuel stores. Green turtles nesting at Ascension Island are around 150 kg (Hays *et al.* 2002b), and a study of one species of turtle, the leatherback, revealed that turtles weigh *c.* 25% more on their foraging grounds than on their nesting beaches (James, Ottensmeyer & Myers 2005). If we assume a maximum fat load to sustain migration of 25% of the total body weight, then for a 150-kg turtle, we obtain a fat store of around 37.5 kg. The weight loss of female green turtles during nesting season at Ascension Island has been measured by repeat weighing individuals and averages 0.22 kg per day (Hays *et al.* 2002b). These empirical data provide a good starting point for the energy/fat balance calculations. During the nesting season, female turtles at Ascension Island rest for around 40% of their time during which their energy expenditure has been estimated from dive durations at 0.018 L O₂ kg⁻¹ per h (Hays *et al.*

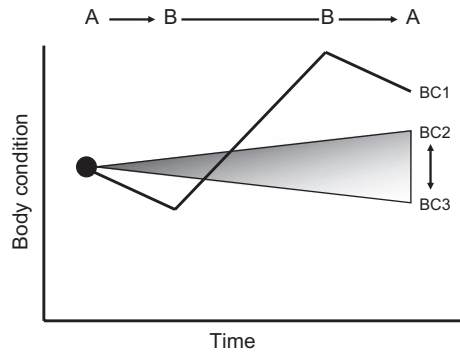


Fig. 2. Theoretical considerations for when migration will be feasible between two sites A and B for a sea turtle that loses body condition when migrating. The same considerations apply to other migrants that travel between breeding and foraging grounds. Circle shows body condition of an individual at the end of the breeding season. Shaded area shows a range of body condition trajectories if the animal remains at the breeding ground A. The solid line shows the body condition of an animal that migrates to site B. In this situation, body condition initially declines as the animal travels to site B, but then improved conditions at site B lead to a greater rate of increase in body condition compared to if the animal remained at site A. Consequently, even after the animal migrates back to site A, its body condition (BC1) is better than if it had not migrated (range BC2 to BC3).

2000), which is close to that predicted from allometric predictions based on minimal metabolic rates measured for turtles ashore on beaches (Prange & Jackson 1976). The energy content of an egg laid by a green turtle at Ascension Island is 279.5 kJ, the mean clutch size is around 110 eggs, and individuals are thought to produce around 3 clutches per nesting season over about 40 days (Hays *et al.* 2000, 2002b). Direct observations and satellite tracking have shown that prior to the nesting season, green turtles are at Ascension Island for around 30 days to mate and that the Brazil–Ascension Island ocean crossings take around 80 days (i.e. 40 days each way). Key uncertainties in fat utilization calculations are the metabolic rate of turtles when they are non-resting during the nesting seasons (i.e. 60% of their time), their metabolic rate during the 30-day mating season and their metabolic rate during the 80-day oceanic crossings. If we assume these metabolic rates are 2 \times , 2.5 \times and 3.5 \times the resting metabolic rate (RMR), respectively (these values are reasonable given the difference between RMR and field metabolic rates (Hulbert & Else 2004), then the measured weight loss of 0.22 kg per day translates to a weight loss of 8.6 kg during the 39-day nesting season, 4.8 kg during the 30-day mating season and 17.9 kg during the 80-day oceanic crossings, that is, total weight loss of 31.3 kg, which is close to the assumed maximum fat load of 37.5 kg, that is, fuel stores seem to impose an upper ceiling on migration distance for adult cheloniid turtles. Clearly, these calculations are very speculative given the dearth of information on metabolic rates of migrating turtles and maximum fat stores.

COMPARISONS BETWEEN SEA TURTLES AND OTHER TAXA

The maximum migration distances of adult turtles were comparable, and within the 95% predictive intervals, to those of equivalent-sized swimming fish and marine mammals (Fig. 3). Adult leatherback turtles (size 330 kg) that travelled the furthest from their breeding areas (11 000 km; Benson *et al.* 2011) had migration distances comparable to the largest fish such as the whale shark (*Rhincodon typus*, mass, 34 000 kg; maximum migration distance, 13 000 km; Eckert & Stewart 2001), the great white shark (*Carcharodon carcharias*, mass, 550 kg; maximum migration distance, 11 000 km; Bonfil *et al.* 2005), the basking shark (*Cetorhinus maximus*, mass, 3900 kg; maximum migration distance, 9500 km) (Gore *et al.* 2008) and the bluefin tuna (*Thunnus thunnus*, mass, 240 kg; maximum migration distance, 9500 km). However, the maximum migration distance for juvenile sea turtles was significantly greater than that predicted for equivalent-sized swimming fish and marine mammals: for a 19-kg loggerhead turtle, the maximum migration distance was 13 040 km (Boyle *et al.* 2009) compared to a 95% predictive interval for an equivalent-sized fish or marine mammal of 1379 km (95% predictive limit 241–7899 km; 95% confidence limit 1002–1897 km). Hence, while Hein, Hou & Gillooly (2011) modelled the maximum migration distances travelled across a broad size range of walking, swimming and flying migrants, we extended this work by including data from sea turtles. Adult turtle migration distances were in the predicted range of equivalent-sized marine mammals and fish, while juvenile sea turtles

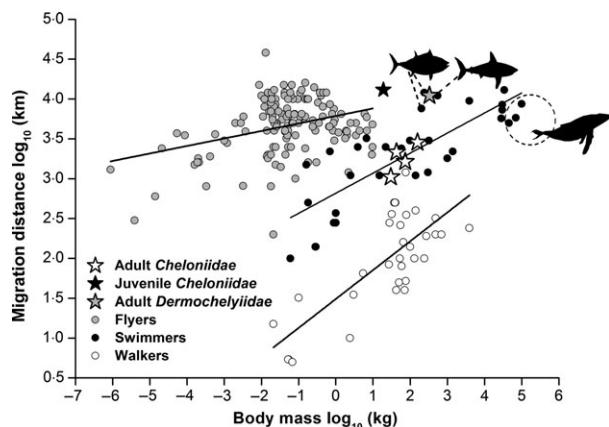


Fig. 3. Maximum migration distances for sea turtles (our study) compared to other swimming, walking and flying migrants (Hein, Hou & Gillooly 2011). The upper migratory ceilings for adult turtles (10 000, 2850, 2150, 1630 and 1050 km for leatherback turtles, green turtles, loggerhead turtles, hawksbill turtles and olive ridley turtles (Hays *et al.* 2002a; Broderick *et al.* 2003; Whiting, Long & Coyne 2007; Van Dam *et al.* 2008; Benson *et al.* 2011), respectively) lie within the 95% predictive limits for other swimmers. However, the migration ceiling for juvenile sea turtles (13 040 km travelled by a 19-kg loggerhead turtle; Boyle *et al.* 2009) lies beyond the 95% predictive limit for other swimmers.

migrated further than predicted for these other swimming taxa.

Discussion

In the most general terms, our inclusion of sea turtles in the cross-taxa meta-analysis reaffirms the general impression that, for their body size, migration distance is greatest in flyers, intermediate in swimmers and shortest in walkers. However, within sea turtles, there were clear differences in migration distances across juveniles vs. adult cheloniid turtles and also adult cheloniid turtles vs. adult leatherback turtles and between cheloniid turtles. If an upper ceiling on migration distance exists in sea turtles, we expect that (i) this ceiling will be evident in the empirical data, for example, some trans-ocean basin migration distances will not be evident by adults travelling between breeding and foraging sites, (ii) animals that do not need to complete this regular to-and-fro migration (e.g. immature turtles that do not return to juvenile development habitats once reaching maturity) may forage much further from their natal sites than adults on their regular breeding migrations and (iii) individuals that do not fast while travelling to and from their breeding grounds may be freed of an upper ceiling migration distance constraint and instead conduct much larger migrations than adults that fast. Our findings are consistent with all these expectations. Our results suggest that despite only breeding every few years, for adult cheloniid sea turtles, there is an upper ceiling on migration distance of around 2850 km. In contrast, juvenile sea turtles and leatherbacks can travel across the widest ocean basins. Essentially for the later two groups, it is only the width of the World's oceans and their thermal tolerance (McMahon & Hays 2006; Witt, Penrose & Godley 2007) that constrains their maximum migration distance.

Given the caveats with the energy/fat balance calculations, one possibility that remains is that the observed ceiling of migration distance in cheloniid sea turtles does not represent a physiological performance maximum, but rather that there is never any need for cheloniid sea turtles to migrate further because there are no suitable breeding grounds that are further than this distance from foraging grounds. If this hypothesis is correct, then we might expect that juveniles would similarly always forage within 2850 km of their breeding grounds, but this was clearly not the case. Juvenile turtles can forage >13 000 km from their breeding grounds. For example, juvenile loggerhead turtles from natal areas in Australia undergo transoceanic migrations to foraging grounds as far away as Peru respectively (Boyle *et al.* 2009). It should be noted that the molecular analysis reveals the direct-line one-way distance between nesting areas and foraging areas for juveniles. These distances therefore are not the total distance travelled by juveniles or necessarily the furthest distance that an individual travels from the nesting area. However, given the large number of these molecular studies, it is likely that our analysis does capture the maximum straight-line dis-

tance between nesting and foraging areas for juveniles. Certainly ocean currents may be instrumental in the transoceanic dispersal of hatchling turtles. As Hein *et al.* (2011) note, species that interact strongly with currents may deviate from model predictions on migration distance. Hatchling turtles reside near the ocean surface, and although they may show some limited directional swimming, their movement trajectory is dominated by surface currents (Scott, Marsh & Hays 2012a,b). As they drift and grow, the swimming ability of juvenile turtles improves. So while some hatchlings are displaced by both ocean currents and storms to unsuitable distant sites and are doomed never to return to breed (Witt, Penrose & Godley 2007; Monzón-Argüello *et al.* 2012), there is direct satellite tracking evidence that juvenile turtles tracked from distant foraging grounds do undertake long oceanic journeys from these distant sites back to their breeding grounds (Eckert *et al.* 2008; Peckham *et al.* 2011). For example, Eckert *et al.* (2008) tracked a 54-kg juvenile loggerhead turtle, which travelled >8000 km from the South coast of Spain to the coast of Nicaragua over a period of 363 days, while Peckham *et al.* (2011) tracked juvenile turtles travelling across the Pacific from foraging grounds off the coast of Baja California back towards their natal area of Japan (>10 000 km apart). In a unique satellite tracking study, Nichols *et al.* (2000) tracked a 95-kg captive-reared adult-sized loggerhead turtle from its release (and initial capture site) off the coast of Baja California back to its natal Japanese nesting region. This individual was captured in its juvenile foraging grounds (weighing just 4 kg) and then kept in captivity for 10 years; hence, this transoceanic migration is regarded as a delayed juvenile return migration as opposed to a typical to-and-fro adult breeding migration. Juveniles can presumably forage at such distant sites because they remain at these sites for many years and then only make one return journey to take up residence at new coastal subadult foraging grounds much closer to their breeding sites. So the situation for juvenile sea turtles differs from that of adults who conduct their to-and-fro breeding migrations every few years. Furthermore, juvenile sea turtles probably feed en route during these long journeys. For example, juvenile loggerhead turtles have a broad range of prey and likely feed on a range of pelagic invertebrates including crustaceans (e.g. pelagic crabs) and molluscs (Witherington 2002) as well as dead animals encountered.

It remains surprising why such long-distance migrations (>10 000 km) are not evident in small fish (Schmidt 1922). One possibility is that the small fish are simply not amenable to direct tracking (e.g. with satellite tags) and that indirect efforts such as mark-recapture/genetics analysis have currently underestimated the true extent of movements. Support for this possibility comes from recent tracking results from small fish. For example, inferred from the distribution of larvae, the spawning grounds of European eels (*Anguilla anguilla*) are thought to be in the Sargasso Sea >6000 km away from the European Shelf (Schmidt 1922,

1923). However, it is only recently that satellite tracking has started to directly document the long-distance migrations of adult eels to these spawning grounds (Aarestrup *et al.* 2009). The developing eel larvae, like hatchling turtles, seem to depend largely on ocean currents for their movement as they travel back to Europe (e.g. Bonhommeau *et al.* 2009).

In addition to juveniles, adult leatherback turtles can also travel to sites very distant from their breeding grounds (Benson *et al.* 2011). Importantly, leatherbacks are open ocean foragers, consuming a variety of gelatinous zooplankton. Hence, when they are travelling in the open ocean away from their breeding sites, their body condition is not necessarily declining during open ocean crossings. In other words, leatherback turtles do not conform to the general paradigm for adult sea turtles of a discrete time during travel away from foraging grounds where they do not feed and so must lose body condition. Their poleward movements are constrained by sea surface temperature, with leatherbacks unable to tolerate water temperatures <15°C for extended periods, and hence, their broad-scale movements can span the width, but not the length, of ocean basins as they cannot penetrate into polar regions (McMahon & Hays 2006). This environmental niche provides a limit to the geographical areas occupied by leatherbacks, compared to groups such as large whales that are more eurythermal and can hence travel between tropical and polar regions (Rasmussen *et al.* 2007). Hence, the areas occupied by migrating swimmers, walkers and flyers may be the result of their capacity to travel different distances from their breeding sites along with their environmental tolerances.

The maximum distances travelled by adult leatherbacks away from breeding sites (11 000 km) are comparable to the distances travelled by some of the largest fish such as great white sharks and bluefin tuna. As with leatherback turtles, these fish are presumably foraging en route, and hence, the upper ceiling for their long-distance movements is not simply driven by body reserves. For example, tracking data for great white sharks travelling from South Africa to Australia show regular deep diving to 900 m alternating with periods at the surface consistent with foraging for pelagic fish and cephalopods (Bonfil *et al.* 2005). Similarly, there is evidence that some fish that travel long distances also do not breed every year. For example, bluefin tuna tracked using light-based geolocator tags may show several years of residence in the western Atlantic and then NE Atlantic before returning to their breeding grounds in the Mediterranean (Block *et al.* 2005).

Conclusions

In short, our results suggest that freed of the constraint of fasting during long-distance movements, leatherback turtles and juvenile turtles may travel very large distances (>10 000 km) across oceans from their natal regions akin to some large fish, but that in contrast, for adult cheloniid

turtles, the tendency to fast during migration between breeding and foraging sites seems to constrain their migration distance to below 3000 km. While these non-annual breeding migrations of adult cheloniid species should increase their capacity to migrate longer distances (as they have longer to replenish energy reserves), this 3000-km migratory ceiling suggests that foraging mode during migration ultimately caps the attainable travel distances on these regular (albeit non-annual) to-and-fro migrations. Finally, our results may have implications for marine conservation planning. In recent years, some huge ocean areas that host populations of endangered sea turtles have been designated as marine protected areas (MPAs) including Papahānaumokuākea Marine National Monument in the Pacific and the British Indian Ocean Territory MPA, which encompass 360 000 km² and 639 661 km², respectively (Gerber *et al.* 2011; Sheppard *et al.* 2012). However, even these largest MPAs are unlikely to encompass the extent of movements undertaken by juvenile sea turtles originating from nesting beaches within those MPAs. Hence, our results suggest that in addition to MPA designation, there is also ongoing need for basin-wide conservation measures (e.g. methods to reduce sea turtle by-catch) to protect sea turtles.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. (a) Adult satellite tracking data. (b) Juvenile mixed stock analysis data.