

Population characteristics and seasonal migrations of leatherback sea turtles at high latitudes

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ABSTRACT: Efforts to model populations of the leatherback sea turtle *Dermochelys coriacea* and design appropriate conservation measures for this endangered species have been hindered by a lack of information on in-water (vs. nesting) population characteristics. We present the first synthesis of population characteristics of leatherbacks at high latitudes. During 8 seasons of fieldwork (1999 to 2006) off Nova Scotia, Canada, we collected biological data from 152 turtles, including 127 live-captured individuals. The size-class distribution mainly represented large sub-adult and adult individuals (mean curved carapace length = 148.1 cm). Mean body mass was 392.6 kg (range: 191.9 to 640 kg). We found a significantly female-biased sex ratio (1.86 females:1 male) among mature turtles. We expect that there may be geographical variation in sex ratios of foraging populations reflecting breeding periodicity, distance from nesting areas, and associated migration patterns. Tag recoveries from 25 leatherbacks captured off Canada reveal nesting origins throughout South and Central America and the Caribbean. Recapture data suggest that although some female turtles proceed to Canadian waters within several months of nesting (in the same calendar year), entry into high-latitude coastal waters of the western Atlantic may more regularly occur later in the nesting remigration interval. Comparison of data from leatherbacks off Canada with those from a foraging population at similar latitudes off France reveals unequal size-class distributions, which may reflect the different thermal regimes in these areas.

KEY WORDS: *Dermochelys coriacea* · Population characteristics · Size · Foraging · Canada · France · Sex ratio · Tag recapture · Nesting origins · Remigration interval · Sea surface temperature

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INTRODUCTION

When realistic population models are available for endangered species, they can help predict changes in population size over time and in response to specific perturbations, and they can also indicate when and where conservation efforts may be most effective (Shuter et al. 1998, Crouse 1999, Bjørndal et al. 2005). The utility of such models is enhanced by integrating comprehensive information on life history parameters, including growth, maturation, fecundity, and potential differences in the mortality and geographic distributions of various ages and/or size classes (Chaloupka 2002, Mazaris et al. 2005). Unfortunately, for many marine vertebrates much of this information is lacking, making their conservation and management especially challenging.

Although the leatherback turtle *Dermochelys coriacea* is the most widely distributed of all sea turtles, with individuals undertaking extensive migrations between tropical and temperate waters (Hays et al. 2004, James et al. 2005b,c), most efforts to study this species have focused on nesting beaches. Research on leatherback nesting ecology (Girondot & Fretey 1996, Reina et al. 2002, Rivalan et al. 2005) has facilitated modeling of nesting trends in some colonies (Spotila et al. 2000, Girondot et al. 2002, Troëng et al. 2004, Dutton et al. 2005). However, more comprehensive, predictive modeling of the dynamics of the broader leatherback population at ocean-basin scales requires improved mortality estimates for different segments of the population (Lewison et al. 2004, Kaplan 2005) and integration of other critical life history parameters, many of which have not been previously documented.

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Given the imperiled status of leatherback populations worldwide (Spotila et al. 1996, 2000), there is an urgent need to define these parameters. Collection of field data from in-water studies of leatherbacks is essential to this process, as capturing turtles at sea enables more representative sampling of the population than do studies based on nesting beaches.

Coastal and slope waters of the NW Atlantic above 38°N provide high-use foraging habitat for leatherbacks (James et al. 2005c). Waters off Nova Scotia, Canada, are particularly important to this species, as indicated by the large seasonal aggregation of turtles that occurs there (James et al. 2006). Fisheries interactions are an important source of injury and mortality for leatherbacks in temperate waters (Godley et al. 1998, Lewison et al. 2004, James et al. 2005c); however, the implications of such interactions cannot be assessed without knowledge of the sources of the turtles that are affected, their size and sex.

In the present study we present the first synthesis of data on the population size structure, sex ratios, origins, and remigration intervals of leatherbacks at high latitudes of the Atlantic. This information is needed to construct population dynamics models that can be used both to assess conservation risks to this species and to guide appropriate management actions.

MATERIALS AND METHODS

At-sea field research. We identified periods of peak leatherback occurrence in coastal areas of Nova Scotia from patterns of sightings reported by fishers, tour boat operators, and other mariners (Martin & James 2005) and conducted field research at these times. Field studies were undertaken in 2 areas of the Scotian Shelf. The first encompasses shelf waters off the SW coast of mainland Nova Scotia (approx. 44°N, 64°W). The second area corresponds to waters off the NE tip of Cape Breton Island, near the mouth of the Gulf of St. Lawrence (approx. 47°N, 60°W). Field studies took place off Cape Breton Island during the summers of 1999 to 2006 and off mainland Nova Scotia during the summers of 2001 to 2006.

Leatherbacks were captured at or near the sea surface using a breakaway hoop-net (for more details see James et al. 2005c). Curved carapace length (CCL) and curved carapace width (CCW) were collected from most turtles, but not all, as poor sea conditions and other logistical challenges occasionally hindered measurement of captured individuals. When sea conditions permitted, some turtles were brought aboard using a stern-mounted ramp and were weighed with a digital hanging scale (Model TL6000; Intercomp). To minimise measurement error, one of us (M. C. James)

examined and recorded morphometrics of all individuals.

Sexual dimorphism in tail length was used to assign sex to leatherbacks. We have observed markedly longer tails, with a greater distance between the cloaca and the posterior tip of the carapace, among mature male vs. female leatherbacks (James 2004). Consistent with other species of sea turtle, such sexual dimorphism becomes increasingly evident with increasing carapace size (Godley et al. 1998, Heithaus et al. 2005). To reduce potential error associated with visually sexing leatherbacks of smaller size classes, we assigned sex only to turtles of ≥ 145 cm CCL. While some female Atlantic leatherbacks reach sexual maturity before attaining a CCL of 145 cm (Stewart et al. in press), studies of multiple Atlantic nesting populations suggest that this reflects the minimum size at maturity for most turtles (Boulon et al. 1996); therefore, we follow Eckert's (2002) classification of leatherbacks < 145 cm CCL as juveniles.

To determine if turtles had been previously tagged, the rear flippers were inspected for metal tags and the right and left shoulder musculature and neck were scanned for the presence of passive integrated transponders (PITs) using a hand-held PIT reader (Dutton & McDonald 1994). Readers capable of detecting multiple brands of PITs, including those most commonly implanted in leatherbacks (i.e. AVID and Trovan) were used. Unmarked turtles were equipped with flipper tags (Monel No. 49, National Band and Tag) and a PIT in the right shoulder muscle (AVID encrypted or unencrypted and/or Trovan ID100).

Nesting origins were determined both by capture of previously tagged turtles at sea off Nova Scotia and by reported sightings of turtles bearing Canadian flipper tags or PITs on nesting beaches. The remigration interval between nesting seasons for most female Atlantic leatherbacks is 2 yr, although 3 yr remigration intervals are also common (Girondot & Fretey 1996). We expect that relatively few female leatherbacks venture directly to Canadian shelf waters post nesting because of considerable overlap in the peak nesting season in the western Atlantic (Girondot & Fretey 1996) and the primary foraging period in Canadian waters (June to October) (James et al. 2005b, 2006). To clarify the extent to which mature female leatherbacks encountered in Canadian shelf waters represent turtles that have proceeded directly to Canadian waters in the same calendar year (< 6 mo) following nesting, we considered time between tagging and recapture.

Examination of stranded turtles. Dead leatherbacks found floating at sea or entangled in fishing gear and all leatherbacks reported dead on the shoreline (stranded) were examined and subject to necropsy when possible. In all cases, CCL and CCW were recorded.

Sex was confirmed through examination of gonads in necropsied leatherbacks. Sexual dimorphism in tail length was used to assign sex to live-captured turtles of ≥ 145 cm CCL. Dead turtles recovered directly from fishing gear were weighed using a digital hanging scale (Model TL6000; Intercomp). As the weights of stranded leatherbacks may reflect compromised physical condition prior to death, these were not included in our analyses.

Morphometrics of high-latitude leatherback populations in the NW and NE Atlantic. Records of live and dead leatherbacks at similar latitudes in the NE Atlantic (off the coast of France) have been collected and summarised annually for over 2 decades by R. Duguy and colleagues (Aquarium de La Rochelle); however, corresponding morphometric data have not been synthesised. To assess potential morphometric differences between high-latitude leatherback foraging populations in the NW vs. NE Atlantic for the period 1998 to 2006, we compared CCL data for turtles from shelf waters off Canada with those reported from France (Duguy et al. 1999, 2000, 2001, 2002, 2003, 2004, 2005, 2006, 2007). Consistent with the methods we used in Canada, we calculated adult sex ratio of leatherbacks from France by compiling data from turtles of ≥ 145 cm CCL.

For leatherbacks in Canada, we compared the relationship between carapace length and width ($n = 115$) and length and mass (present study: 1998 to 2006, $n = 16$; Bleakney 1965 and unpubl data, $n = 5$; Threlfall 1978, $n = 1$; D'Amours 1983, $n = 1$) using linear regression. Although there is similar measurement error in carapace length and width, we assumed that the measurement error is relatively small compared to variation between individuals. Similar analyses were not performed on data from France, as the published weights ($n = 5$) were principally limited to stranded individuals, and no carapace widths were available.

Patterns of sea surface temperature in foraging areas. For the period 1998 to 2006, we extracted the dates of all reported live leatherback sightings in waters off France (Duguy et al. 1999, 2000, 2001, 2002, 2003, 2004, 2005, 2006, 2007) and Nova Scotia (James et al. 2006) to assess seasonal distributions of leatherbacks in these areas. Average monthly sea surface temperature (SST) (4 km resolution), was obtained from Advanced Very High Resolution Radiometer Oceans Pathfinder data (1998–2005) and Moderate Resolution Imaging Spectroradiometer data (2006) (Physical Oceanography Distributed Active Archive Center, NASA Jet Propulsion Laboratory; <http://podaac.jpl.nasa.gov>) for continental shelf waters (< 200 m) encompassing leatherback sightings (1998 to 2006) in Canada and France. SST data for Canada were collected from an area bounded by 69 to 59° W longitude and 42.5 to 47.5° N latitude, excluding waters of the northern half of the Gulf of Maine (including the Bay of Fundy) and waters of the Gulf of St. Lawrence west of 62° W. SST data for France were collected from an area bounded by 5 to 1° W longitude and 44 to 48° N latitude. SST data were averaged to yield monthly SST estimates for the years 1998 to 2006. To evaluate if SST was higher off France than Atlantic Canada, we fit a mixed effect maximum likelihood model to the mean monthly SSTs for the 2 areas.

RESULTS

We captured 127 leatherbacks during field research off the coast of Nova Scotia during the summers of 1999 to 2006 (Table 1). While most turtles received a single PIT (AVID encrypted, $n = 40$; AVID unencrypted, $n = 15$; Trovan ID100, $n = 9$), 48 turtles received 2 PITs (AVID unencrypted and Trovan ID100). We did not implant PITs in 16 leatherbacks, including

Table 1. *Dermochelys coriacea*. Summary data of live capture and tagging of leatherback turtles off Nova Scotia, Canada, 1999 to 2006. Values in parentheses: no. of additional turtles recaptured (these were originally marked on nesting beaches). PIT: passive integrated transponder

Year	No. captured	No. of PITs applied			No. flipper-tagged	PIT reader used
		AVID encrypted	AVID unencrypted	Trovan ID100		
1999	3	3	0	0	0	AVID 1001 Multi Mode
2000	4	3	0	0	0	AVID 1001 Multi Mode
2001	15	13	0	0	12	AVID Powertracker IV
2002	11	10	0	(1)	10 (1)	AVID Powertracker VI
2003	28	11 (1)	13 (1)	0	26 (2)	AVID Powertracker VI
2004	24	0	9 (1)	16 (4)	23 (1)	AVID Powertracker VI
2005	20	0	20	20	18 (2)	AVID Powertracker VI + Trovan LID500
2006	22	0	21	21 (1)	21 (1)	AVID Powertracker VI + Trovan LID500
Total	127	40 (1)	63 (2)	57 (6)	110 (7)	

10 bearing PITs previously applied on nesting beaches. We equipped 110 turtles with flipper tags.

Measurements of CCL were obtained from 120 turtles off Nova Scotia, including 99 live-captured turtles and 21 found dead at sea or on the shore. Corresponding measurements of CCW were obtained from 115 of these. The size-class distribution in Canadian coastal waters (CCL range = 111.8 to 171.8 cm) principally comprised large sub-adult and adult individuals (Fig. 1). Only 1 turtle with a CCL < 125 cm was captured. We found that for the period 1998 to 2006, the mean CCL for leatherbacks in Canadian waters was significantly larger (Welch 2-sample *t*-test, $p < 0.0001$) than that corresponding to 82 turtles measured by Duguay et al. (1999, 2000, 2001, 2002, 2003, 2004, 2005, 2006, 2007) off France (mean CCL \pm 95% CI: Canada = 148.1 ± 4.4 cm, France = 139.8 ± 12.2 cm; Fig. 1). Moreover, data from France revealed a significantly broader size-class distribution than was the case for the turtles measured in Canada (Levene's test, $p < 0.0001$, Fig. 1).

There was a strong relationship between the logarithms of CCL and CCW for leatherbacks in Canadian waters: $\log(\text{CCW}) = 0.065 + 0.922 \times \log(\text{CCL})$; $r^2 = 0.80$. The ratio of CCL to CCW did not differ significantly between sexes and was not significantly different from isomorphic growth (slope 95% CI = 0.837 to 1.01) (Fig. 2). Mean mass of 23 leatherbacks from Canadian waters, including 16 turtles we measured and 7 turtles measured in previous studies, was 392.6 kg (range: 191.9 to 640 kg). The equation describing the relationship ($r^2 = 0.67$) between CCL and mass for Canadian turtles was $\log(\text{mass}) = -4.96 + 3.46 \times \log(\text{CCL})$ (Fig. 3).

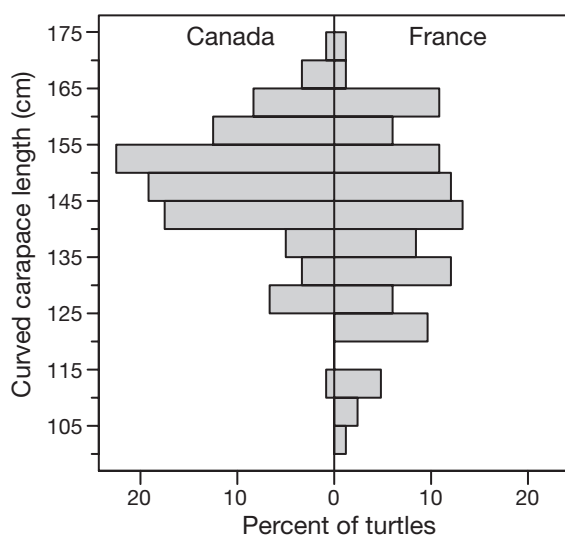


Fig. 1. *Dermochelys coriacea*. Size-frequency distribution at high latitudes: turtles measured in Canada (1998 to 2006; $n = 120$) and France (1998 to 2006; $n = 82$). French data from Duguay et al. (1999, 2000, 2001, 2002, 2003, 2004, 2005, 2006, 2007)

The adult sex ratio among live-captured, stranded and entangled turtles in Atlantic Canada was 1.86 females: 1 male ($n = 80$, 1998 to 2006), representing a significant female bias (exact binomial test, $p = 0.007$, 95% CI = 0.53 to 0.75). In contrast, data from a smaller sample of turtles from France ($n = 28$) yielded a male-biased adult sex ratio (0.78 females:1 male). The sex ratios in Canada vs. France were significantly different (Fisher's exact test, $p = 0.025$).

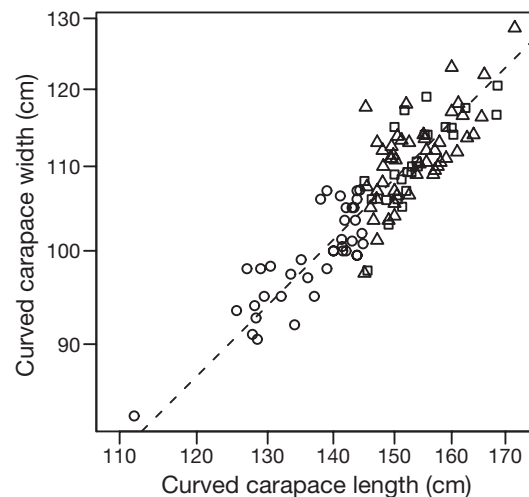


Fig. 2. *Dermochelys coriacea*. Relationship between curved carapace length and width in Canadian waters. (□) Males; (Δ) females; (○) juveniles. Dashed line is 1:1 line through mean of data

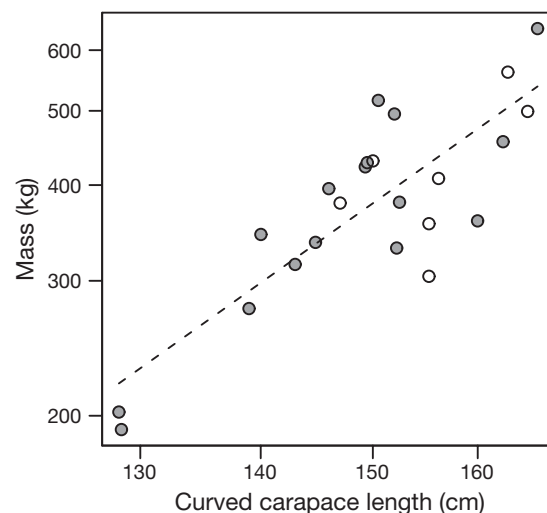


Fig. 3. *Dermochelys coriacea*. Relationship between curved carapace length (CCL) and mass in Canadian waters. (●) Turtles measured in Canada during this study (1998 to 2006, $n = 16$); (○) turtles measured in Canada prior to this study (Bleakney 1965 and unpubl. data, $n = 5$; Threlfall 1978, $n = 1$; D'Amours 1983, $n = 1$); dashed line: length – mass equation $\log(\text{mass}) = -4.96 + 3.46 \times \log(\text{CCL})$. For 2 Canadian records CCL was derived from straight carapace length using the equation of Tucker & Frazer (1991)

Mean monthly SSTs were significantly higher in France than Canada in all months (all p -values < 0.001), ranging between 7.6°C higher in March to 2.3°C higher in August. Temporal distribution of leatherback sightings were similar between Atlantic Canada and France, with most reports corresponding to the summer months (July to September), when SST approaches seasonal highs (Fig. 4).

Nesting origins

Nesting origins for 25 leatherbacks captured off Nova Scotia were confirmed through tag recoveries. The tag recoveries correspond to 15 turtles originally tagged on nesting beaches and 10 originally tagged in Canadian waters. All tag recoveries in Canada were from live-captured turtles. Five females previously tagged on nesting beaches were identified by the presence of 1 or more flipper tags only, 7 by the presence of a PIT only, and 3 by the presence of both a PIT and a flipper tag. Recapture data demonstrate that turtles utilising Canadian foraging

habitat represent nesting populations in a minimum of 10 countries in South and Central America and the Caribbean, including Suriname, French Guiana, Guyana, Venezuela, Trinidad, Grenada, Colombia, Panama, Costa Rica, and Puerto Rico (Fig. 5). Three turtles captured in Canadian waters had nesting histories encompassing multiple countries: French Guiana and Suriname (2 turtles) and Costa Rica and Panama (1 turtle).

Migration to high latitudes during nesting remigration interval

Only 1 tagged turtle was recaptured off Nova Scotia in the same calendar year in which nesting occurred (149 d after being observed at Matura Beach, Trinidad, Fig. 6). If we assume a minimum nesting remigration interval of 2 yr, we can infer that 15 turtles did not nest in the season immediately preceding their capture in Canadian waters (Fig. 6). Because of longer intervals between recaptures, we could not infer inter-nesting year for 10 turtles.

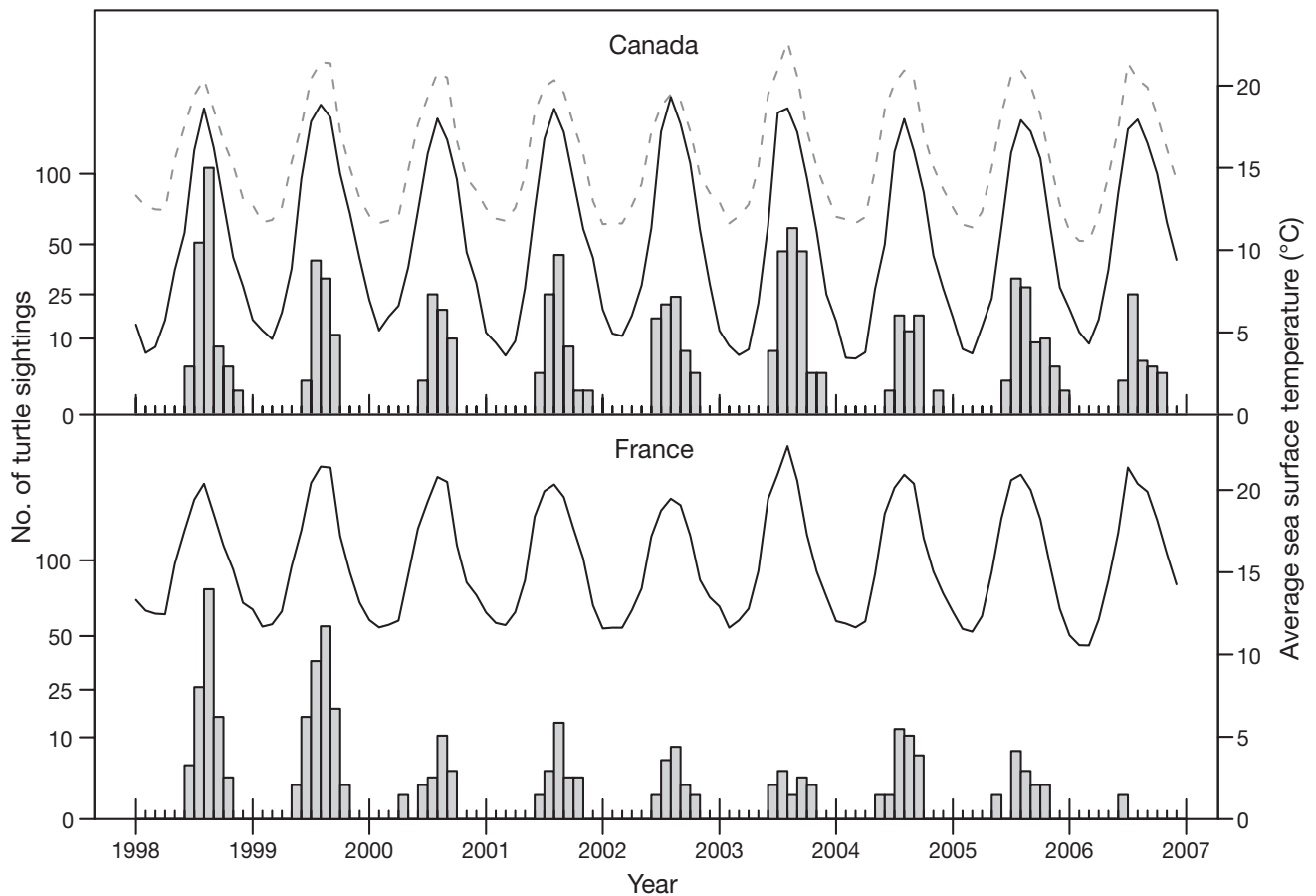


Fig. 4. *Dermochelys coriacea*. Monthly frequency of sightings (bars) and mean monthly sea surface temperature (continuous lines) off Nova Scotia, Canada, and France (1998 to 2006). Mean monthly sea surface temperature off France is repeated in top panel (dashed line) to facilitate comparison

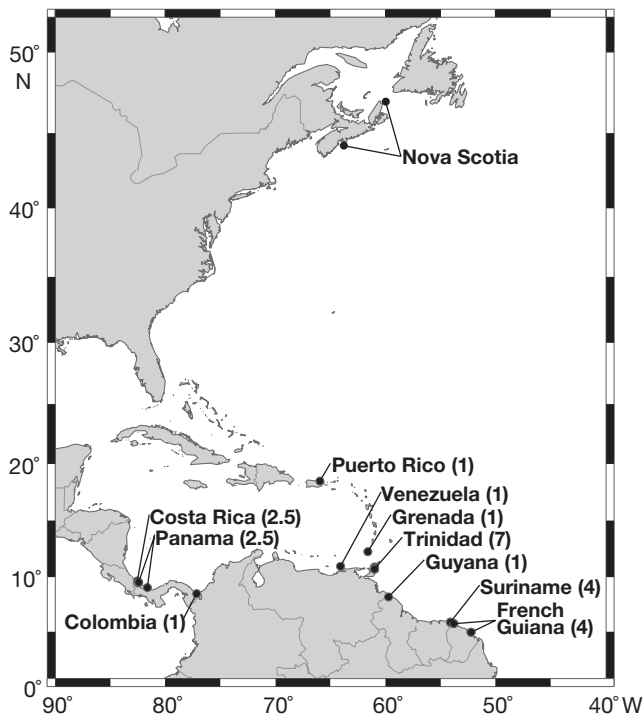


Fig. 5. *Dermochelys coriacea*. Nesting origins of 25 turtles encountered in Canadian waters, 2001 to 2006. Nos. in parentheses: no. of turtles recorded for each country. Turtles confirmed as nesting in 2 countries (French Guiana/Suriname $n = 2$, Costa Rica/Panama $n = 1$) were accorded value of 0.5 for each of the relevant countries. Black circles off Nova Scotia denote 2 principal areas of at-sea field research

DISCUSSION

Body size at high latitudes

Comparison of carapace lengths for turtles from foraging areas at similar latitudes, but opposite sides of the Atlantic, reveals differences in size-class distributions, with a larger mean CCL and narrower size-class distribution associated with turtles off Canada's coast. For leatherbacks, an enhanced capacity to exploit foraging opportunities in cold waters is partially related to body size and the ratio of volume to surface area (Paladino et al. 1990). Therefore, as ambient ocean temperatures rise, we might expect a corresponding increase in the number of smaller-sized turtles present. The occurrence of more turtles of smaller size classes in waters off France than off Canada may, therefore, reflect differences in the thermal regimes of these areas, as SST is consistently warmer off France than off Canada throughout the year (Fig. 4). Further evidence for larger mean carapace lengths associated with foraging areas characterised by generally cooler SSTs comes from Witt et al. (2007, this volume), who report a latitudinal gradient in body size for leatherbacks in the NE Atlantic.

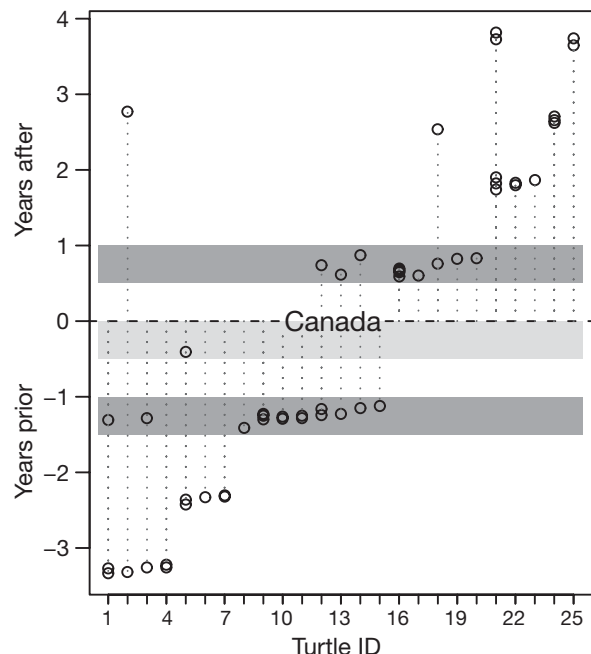


Fig. 6. *Dermochelys coriacea*. Time between capture in Canadian shelf waters (dashed line) and observations on nesting beaches (O) for 25 leatherback turtles; y-axis represents time prior to (below zero) and after (above zero) capture in Canada (zero). Assuming minimum nesting remigration interval of 2 yr for Atlantic leatherbacks, turtles observed nesting during periods indicated by dark grey bars would be precluded from nesting in season immediately prior to their capture in Canada (light grey bar)

It is unlikely that leatherbacks of smaller size classes than those reported here utilise coastal temperate foraging areas of the NW or NE Atlantic, consistent with the reported distribution of juvenile leatherbacks of <100 cm CCL being constrained to waters warmer than 26°C (Eckert 2002). Alternatively, an absence of smaller-sized leatherbacks at higher latitudes may reflect potential changes in the diet of leatherbacks as they mature, with prey distributions targeted by smaller turtles being limited to warmer, pelagic waters and exploitation of larger coastal cnidarians accompanying seasonal recruitment into shelf foraging areas once turtles exceed a specific carapace length. Such dietary shifts coincident with size-specific changes in habitat use have been documented in other species of sea turtle, including loggerhead and green turtles (Bjorndal 1997).

In-water sex ratios

Lazell (1980) hypothesised that in any given year there would be insufficient time for many female leatherbacks to migrate far north after nesting, where-

as males would be free of such constraints, resulting in a preponderance of males in foraging areas off the NE United States and Canada. Consistent with Lazell's (1980) hypothesis, our tag recapture data suggest that many females may not reach Canadian shelf waters in the months immediately following nesting, and recent satellite tracking of male leatherbacks has indicated that many are capable of completing annual migrations to high-latitude feeding areas, even in breeding years (James et al. 2005a). However, the female-biased adult sex ratio we derived for turtles in Canadian waters contradicts Lazell's (1980) prediction of a male-biased population in northern waters.

Satellite telemetry suggests that breeding remigration intervals may be shorter for male versus female leatherbacks and that males may also depart from breeding areas earlier than females (James et al. 2005a). Given these sex differences in behaviour and the variable distances separating different foraging areas from nesting and breeding sites, there may be geographic differences in in-water adult sex ratios of leatherbacks. For example, a higher proportion of mature females may occur in foraging areas at lower latitudes, as these areas can be more readily reached in the months immediately following nesting. If this is true, the adult sex ratio data from coastal Nova Scotia could underestimate the degree to which the Atlantic-wide population of adult turtles is female-biased. Alternatively, if the overall population sex ratio approximates 1:1, because male Atlantic leatherbacks journey to waters off nesting beaches to breed more frequently than females (James et al. 2005a), we predict that more southerly habitats may contain higher numbers of mature males than females. However, larger sample sizes and results from in-water studies of this species in other areas are recommended before drawing conclusions regarding geographic variation in adult sex ratios.

We speculate that long-term trends in the sex ratios of northern foraging populations of leatherbacks may involve an increasing female bias resulting from both global warming, which would augment female hatching production through elevated nest incubation temperatures (Davenport 1997), and enhanced female survival associated with reduction of slaughter on nesting beaches throughout the Atlantic.

Migration to high latitudes during nesting remigration interval

Satellite telemetry studies indicate that females in their inter-nesting years, sub-adults, and many mature males undertake annual return movements between tropical waters and high-latitude (north of 38°N) coastal feeding areas off Canada and the NE United

States (James et al. 2005a,c). However, the proportion of mature females that move directly to these northern shelf waters in the first few months following nesting is not known. Although 1 turtle in this study (Fig. 5), another reported by Goff et al. (1994), and 2 turtles satellite-tagged in Florida (Eckert et al. 2006) demonstrated that some leatherbacks do make rapid, post-nesting migrations to Canadian coastal waters, our recapture data suggest that many females may not venture that far north in the same calendar year in which nesting has occurred. This may be particularly true for turtles nesting late in the season (as the annual foraging period in Canadian waters overlaps with the peak nesting season in the western Atlantic), and for turtles from more distant nesting areas. For example, a larger proportion of females from nesting colonies in the northern Caribbean (e.g. Puerto Rico, British Virgin Islands) and Florida may proceed to shelf waters off Canada's coast in the spring or summer following nesting than of females departing beaches in Central America (e.g. Panama) or South America (e.g. French Guiana). Currently, there are insufficient numbers of tag recaptures available to test hypothesised differences in the degree to which turtles from various nesting colonies migrate north to Canadian waters in the same year as nesting. However, other data can be used to clarify patterns of migration to northern latitudes. For example, Hays et al. (2006) used satellite telemetry to conclude that leatherbacks from Grenada are unable to reach coastal high-latitude feeding areas in the same year that they nested.

Nesting origins

Prior to our initiation of dedicated leatherback field research in Atlantic Canada, there was only 1 reported recovery of a tagged turtle (from French Guiana) in Canadian waters (Goff et al. 1994). The tag recapture data we present here demonstrates that leatherbacks from beaches across South and Central America and the Caribbean forage in Canadian waters. Satellite telemetry has also recently shown that turtles from Florida, USA, are among those that occur off Canada's coast (Eckert et al. 2006). Leatherbacks nesting in the eastern Atlantic have not yet been encountered in Canadian waters. This may simply reflect a lower probability of finding these turtles due to lower tagging effort and/or smaller nesting populations in the eastern vs. western Atlantic, or could indicate use of alternative foraging destinations by turtles nesting in Africa. Some leatherbacks tagged in Gabon do cross the Atlantic to forage; however, no turtles from African nesting colonies have yet been reported in western Atlantic waters north of the equator (Billes et al. 2006).

Standardisation of tagging protocols

A lack of standardisation in tagging protocols across leatherback nesting beaches, coupled with continued exclusive use of non-permanent marking techniques (i.e. flipper tags) in some areas prohibits universal recognition of previously tagged turtles. This has created serious obstacles to clarifying key life history parameters that influence population demographics. For example, as researchers on different beaches are not equally likely to use PITs or PIT readers (of the 10 reported recaptures of turtles marked in Canada with both flipper tags and PITs, only 2 PITs were reported from the nesting beach), the extent to which leatherback females distribute nests between beaches remains poorly understood. Similarly, until tagging equipment, protocols and effort are standardised among nesting beach monitoring programs, it will be difficult to assess the relative proportion of turtles from different nesting areas represented in the Canadian foraging population. Greater promise in answering this question is likely to come from matching foraging turtles to nesting stocks through genetic analyses (Dutton et al. 1999).

As leatherbacks from multiple nesting beaches aggregate in Canadian waters, we have taken measures to maximise detection of individuals previously tagged with varying technologies. For example, since 2001 we have used PIT readers designed to decode multiple PIT types (Table 1). This has probably increased PIT detection rates; however, given the inconsistent performance of many multi-tag readers (Epperly et al. in press) and the fact that flipper tags are not permanent (Rivalan et al. 2005), our recapture data must underestimate the proportion of previously tagged turtles we have encountered off Nova Scotia. For similar reasons (plus the added challenge that many nesting beach monitoring projects remain unable to detect multiple brands of PIT or have yet to implement the use of PITs at all), we expect that there is a low rate of tag detection in nesting individuals originally marked by our research group. Moreover, incompatibility of PIT technologies has resulted in turtles bearing Canadian flipper tags and 1 brand of PIT later receiving a second, different brand of PIT, while nesting.

In addition to applying flipper tags, we have also equipped all turtles with both Trovan and AVID PITs since 2004 to increase detection of Canadian-tagged individuals by nesting beach personnel. While these represent the 2 most common brands of microchip used to mark this species (Epperly et al. in press), until PIT readers capable of detecting 1 or both of these technologies become standard equipment on all monitored beaches, PITs in many turtles tagged in Canada will go unnoticed.

CONCLUSIONS

Leatherbacks show fidelity to broad temperate foraging zones, returning to northern waters on the same side of the Atlantic in subsequent years (James et al. 2005b,c). Our comparison of high-latitude leatherback populations in the NW and NE Atlantic demonstrates that foraging populations that share at least some common nesting origins (Fretey & Girondot 1996, Girondot & Fretey 1996, Troëng et al. 2004) can have different population characteristics that may be influenced by many factors, including proximity to nesting centres and environmental conditions.

Beyond demonstrating fidelity to the eastern or western Atlantic, there is evidence for further segregation among high-latitude leatherback populations. For example, leatherbacks that forage in the region of the Grand Banks (Witzell 1998) may comprise a separate group of individuals from those that occur in shelf waters off Nova Scotia (James et al. 2005c). If foraging subpopulations exist, each may be subject to different sources and levels of anthropogenic mortality. Therefore, to evaluate the effects of such threats on broader leatherback populations (e.g. at the scale of Atlantic or Pacific stocks), further definition of nesting origins, sex ratios and size-class distributions of turtles from multiple areas of the species' range is critical.

At-sea field research confirms that leatherbacks from multiple nesting colonies aggregate annually off Canada's Atlantic coast. Therefore, Canadian efforts to promote recovery of this endangered reptile have global implications and should include participation in international sea turtle conservation initiatives and reduction of incidental capture of leatherbacks in Canadian fisheries.

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LITERATURE CITED

- Billes A, Fretey J, Verhage B, Huibregts B and 5 others (2006) First evidence of leatherback movement from Africa to South America. *Mar Turtle Newsl* 111:13–14
- Bjorndal KA (1997) Foraging ecology and nutrition of sea turtles. In: Lutz PL, Musick JA (eds) *The biology of sea turtles*, Vol 1. CRC Press, Boca Raton, FL, p 199–231
- Bjorndal KA, Bolten AB, Chaloupka MY (2005) Evaluating trends in abundance of immature green turtles, *Chelonia mydas*, in the Greater Caribbean. *Ecol Appl* 15:304–314
- Bleakney JS (1965) Reports of marine turtles from New England and Eastern Canada. *Can Field-Nat* 79:120–128
- Boulon RH, Dutton PH, McDonald DL (1996) Leatherback turtles (*Dermodochelys coriacea*) on St. Croix, US Virgin Islands: fifteen years of conservation. *Chelonian Conserv Biol* 2: 141–147
- Chaloupka M (2002) Stochastic simulation modelling of southern Great Barrier Reef green turtle population dynamics. *Ecol Model* 148:79–109
- Crouse DT (1999) Population modeling and implications for Caribbean hawksbill sea turtle management. *Chelonian Conserv Biol* 3:185–188
- D'Amours D (1983) Une tortue luth (*Dermodochelys coriacea*) dans les eaux côtières du Québec. *Nat Can* 110:481
- Davenport J (1997) Temperature and the life-history strategies of sea turtles. *J Therm Biol* 22:479–488
- Duguy R, Morinière P, Meunier A (1999) Observations de tortues marines en 1998 (Atlantique). *Ann Soc Sci Nat Charente-Marit* 8:911–924
- Duguy R, Morinière P, Meunier A (2000) Observations de tortues marines en 1999 (Atlantique et Manche). *Ann Soc Sci Nat Charente-Marit* 8:1025–1034
- Duguy R, Morinière P, Meunier A (2001) Observations de tortues marines en 2000 (Atlantique et Manche). *Ann Soc Sci Nat Charente-Marit* 9:17–25
- Duguy R, Morinière P, Meunier A (2002) Observations de tortues marines en 2001 (Atlantique et Manche). *Ann Soc Sci Nat Charente-Marit* 9:161–172
- Duguy R, Morinière P, Meunier A (2003) Observations de tortues marines en 2002 (Atlantique et Manche). *Ann Soc Sci Nat Charente-Marit* 9:265–273
- Duguy R, Morinière P, Meunier A (2004) Observations de tortues marines en 2003 (Côtes Atlantiques). *Ann Soc Sci Nat Charente-Marit* 9:361–366
- Duguy R, Morinière P, Meunier A (2005) Observations de tortues marines en 2004 (Côtes Atlantiques). *Ann Soc Sci Nat Charente-Marit* 9:461–466
- Duguy R, Morinière P, Meunier A (2006) Observations de tortues marines en 2005 (côtes Atlantiques Françaises). *Ann Soc Sci Nat Charente-Marit* 9:607–611
- Duguy R, Morinière P, Meunier A (2007) Observations des tortues marines en 2006 (Golfe de Gascogne). *Ann Soc Sci Nat Charente-Marit* 9:695–698
- Dutton DL, Dutton PH, Chaloupka M, Boulon RH (2005) Increase of a Caribbean leatherback turtle *Dermodochelys coriacea* nesting population linked to long-term nest protection. *Biol Conserv* 126:186–194
- Dutton P, McDonald D (1994) Use of pit tags to identify adult leatherbacks. *Mar Turtle Newsl* 67:13–14
- Dutton PH, Bowen BW, Owens DW, Barragan A, Davis SK (1999) Global phylogeography of the leatherback turtle (*Dermodochelys coriacea*). *J Zool* 248:397–409
- Eckert SA (2002) Distribution of juvenile leatherback sea turtle *Dermodochelys coriacea* sightings. *Mar Ecol Prog Ser* 230: 289–293
- Eckert SA, Bagley DA, Kubis S, Ehrhart LM, Johnson C, Stewart KR, DeFreese D (2006) Internesting, and post-nesting movements and foraging habitats of leatherback sea turtles (*Dermodochelys coriacea*) nesting in Florida. *Chelonian Conserv Biol* 5:239–248
- Epperly S, Belskis L, Stokes L (in press) Using passive integrated transponder (PIT) RFID equipment. Proceedings of the 25th Annual Sea Turtle Symposium. NOAA Tech Memo NMFS-SEFSC
- Fretey J, Girondot M (1996) Première observation en France métropolitaine d'une tortue Luth, *Dermodochelys coriacea* baguée en Guyane. *Ann Soc Sci Nat Charente-Maritime* 8: 515–518
- Girondot M, Fretey J (1996) Leatherback turtles, *Dermodochelys coriacea*, nesting in French Guiana, 1978–1995. *Chelonian Conserv Biol* 2:204–208
- Girondot M, Tucker AD, Rivalan P, Godfrey MH, Chevalier J (2002) Density-dependent nest destruction and population fluctuations of Guianan leatherback turtles. *Anim Conserv* 5:75–84
- Godley BJ, Gaywood MJ, Law RJ, McCarthy CJ and 5 others (1998) Patterns of marine turtle mortality in British waters (1992–1996) with reference to tissue contaminant levels. *J Mar Biol Assoc UK* 78:973–984
- Goff GP, Lien J, Stenson GB, Fretey J (1994) The migration of a tagged leatherback turtle, *Dermodochelys coriacea*, from French Guiana, South America, to Newfoundland, Canada, in 128 days. *Can Field-Nat* 108:72–73
- Hays GC, Houghton JDR, Myers AE (2004) Pan-Atlantic leatherback turtle movements. *Nature* 429:522
- Hays GC, Hobson VJ, Metcalfe JD, Righton D, Sims DW (2006) Flexible foraging movements of leatherback turtles across the North Atlantic Ocean. *Ecology* 87:2647–2656
- Heithaus MR, Frid A, Wirsing AJ, Bejder L, Dill LM (2005) Biology of sea turtles under risk from tiger sharks at a foraging ground. *Mar Ecol Prog Ser* 288:285–294
- James MC (2004) *Dermodochelys coriacea* (leatherback sea turtle) penis display. *Herpetol Rev* 35:264–265
- James MC, Eckert SA, Myers RA (2005a) Migratory and reproductive movements of male leatherback turtles (*Dermodochelys coriacea*). *Mar Biol* 147:845–853
- James MC, Myers RA, Ottensmeyer CA (2005b) Behaviour of leatherback sea turtles, *Dermodochelys coriacea*, during the migratory cycle. *Proc R Soc Lond Ser B* 272:1547–1555
- James MC, Ottensmeyer CA, Myers RA (2005c) Identification of high-use habitat and threats to leatherback sea turtles in northern waters: new directions for conservation. *Ecol Lett* 8:195–201
- James MC, Sherrill-Mix SA, Myers RA (2006) Canadian waters provide critical foraging habitat for leatherback sea turtles. *Biol Conserv* 133:347–357
- Kaplan IC (2005) A risk assessment for Pacific leatherback turtles (1). *Can J Fish Aquat Sci* 62:1710–1719

- Lazell JD (1980) New England waters: critical habitat for marine turtles. *Copeia* 2:290–295
- Lewison RL, Freeman SA, Crowder LB (2004) Quantifying the effects of fisheries on threatened species: the impact of pelagic longlines on loggerhead and leatherback sea turtles. *Ecol Lett* 7:221–231
- Martin KE, James MC (2005) Conserving sea turtles in Canada: successful community-based collaboration between fishers and scientists. *Chelonian Conserv Biol* 4:899–907
- Mazaris AD, Fiksen O, Matsinos YG (2005) Using an individual-based model for assessment of sea turtle population viability. *Popul Ecol* 47:179–191
- Paladino FV, O'Connor MP, Spotila JR (1990) Metabolism of leatherback turtles, gigantothermy, and thermoregulation of dinosaurs. *Nature* 344:858–860
- Reina RD, Mayor PA, Spotila JR, Piedra R, Paladino FV (2002) Nesting ecology of the leatherback turtle, *Dermochelys coriacea*, at Parque Nacional Marino Las Baulas, Costa Rica: 1988–1989 to 1999–2000. *Copeia* 2002:653–664
- Rivalan P, Godfrey MH, Prévot-Julliard AC, Girondot M (2005) Maximum likelihood estimates of tag loss in leatherback sea turtles. *J Wildl Manag* 69:540–548
- Shuter BJ, Jones ML, Korver RM, Lester NP (1998) A general, life history based model for regional management of fish stocks: the inland lake trout (*Salvelinus namaycush*) fisheries of Ontario. *Can J Fish Aquat Sci* 55:2161–2177
- Spotila JR, Dunham AE, Leslie AJ, Steyermark AC, Plotkin PT, Paladino FV (1996) Worldwide population decline of *Dermochelys coriacea*: are leatherback turtles going extinct? *Chelonian Conserv Biol* 2:209–222
- Spotila JR, Reina RD, Steyermark AC, Plotkin PT, Paladino FV (2000) Pacific leatherback turtles face extinction. *Nature* 405:529–530
- Stewart S, Johnson C, Godfrey MH (in press) The minimum size of leatherbacks at reproductive maturity, with a review of sizes for nesting females from the Indian, Atlantic and Pacific Ocean basins. *Herpetol J*
- Threlfall W (1978) First record of the Atlantic leatherback turtle (*Dermochelys coriacea*) from Labrador. *Can Field-Nat* 92:287
- Troëng S, Chacón D, Dick B (2004) Possible decline in leatherback turtle *Dermochelys coriacea* nesting along the coast of Caribbean Central America. *Oryx* 38:395–403
- Tucker AD, Frazer NB (1991) Reproductive variation in leatherback turtles, *Dermochelys coriacea*, at Culebra National Wildlife Refuge, Puerto Rico. *Herpetologica* 47:115–124
- Witt MJ, Broderick AC, Johns DJ, Martin C, Penrose P, Hoogmoed MS, Godley BJ (2007) Prey landscapes help identify potential foraging habitats for leatherback turtles in the NE Atlantic. *Mar Ecol Prog Ser* 337:231–244
- Witzell WN (1998) Distribution and relative abundance of sea turtles caught incidentally by the US pelagic longline fleet in the western North Atlantic Ocean, 1992–1995. *Fish Bull* (Wash, DC) 97:200–211

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