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RESEARCH ARTICLE

The spatio-temporal distribution and population structure of green turtles (*Chelonia mydas*) in New Zealand

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ABSTRACT

Despite being endangered internationally and protected nationally, little consideration has been given to the occurrence of green turtles (*Chelonia mydas*) in New Zealand. New Zealand lies on the southern boundary of the distributional range of green turtles in the southwestern Pacific, with individuals found within these waters historically considered to be occasional visitors or stragglers incidentally carried by ocean currents. However, the present work shows that green turtles are present year round in New Zealand's northern waters (c. 34°–38° S). A review of sighting, stranding and incidental capture data collected between 1895 and 2013 illustrate New Zealand's green turtle population comprises post-pelagic immature juveniles to large subadults. The female:male sex ratio of 1.7:1 is similar to those reported from warm temperate foraging grounds in eastern Australia. A subsample of new recruits indicates green turtles recruit to neritic habitats at approximately 40.8 cm curved carapace length. This study suggests that New Zealand's neritic habitats constitute a transitional developmental ground for post-pelagic immature green turtles. We observed an exponential increase in the number of documented records over time, though whether this is due to increased numbers of turtles or increased reporting rates, or both, is unclear and warrants further investigation. More broadly, this work provides a baseline understanding of the ecology of green turtles at the edge of their range, providing opportunities to investigate regional niche modelling and connectivity of this highly mobile species, while also monitoring broad-scale effects of climate-induced environmental change.

Introduction

The green turtle (*Chelonia mydas*) has a circum-global distribution, ranging throughout tropical and subtropical seas (Hirth 1997). They exhibit complex life history patterns which are marked by distinct ontogenetic habitat shifts, coupled with long-distance breeding and foraging migrations (Bjorndal 1997; Bolten 2003). Accordingly, a population's total range can be extensive, dispersing widely to encompass coastal nesting areas, neritic foraging grounds, oceanic habitats and migratory pathways (Balazs 1976; Hirth 1997; Bolten 2003; Luschi et al. 2003; Boyle & Limpus 2008). Upon entering the ocean

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for the first time, neonate hatchlings immediately disperse away from shallow predator-rich coastal waters into oceanic habitats where they forage as opportunistic omnivorous macro-planktivores in the epipelagic zone (Bjorndal 1997; Boyle & Limpus 2008). During this life stage, they will remain in the oceanic habitat for a period of 3 to 10 years, before settling into neritic foraging and developmental habitats at approximately 30–45 cm curved carapace length (CCL) (Balazs 1985; Musick & Limpus 1997; Zug et al. 2002; Bolten 2003; Limpus et al. 2005; Arthur et al. 2008). Once juveniles recruit and take up residence in neritic habitats, they may remain geographically localised, possibly for decades, until they reach maturity (Balazs et al. 1987; Limpus & Chaloupka 1997; Seminoff et al. 2002; Koch et al. 2007; Senko et al. 2010). At the onset of maturity, adult green turtles undertake repeated breeding migrations to nesting rookeries, eventually returning to preferred foraging grounds in between breeding episodes (Hirth 1997).

Despite a wide global distribution, the geographic range of green turtles is generally constrained by the subtropical 20 °C surface isotherm (Marquez 1990; Davenport 1997; Hirth 1997). This is because, as with many marine ectotherms, marine turtles rely on the ambient environmental temperature to support digestion rates and ultimately growth and survival (Avery et al. 1993). Therefore, temperature is one of the key environmental factors that regulate the physiological performance and ultimately the spatio-temporal distribution of green turtles (Spotila et al. 1997). If exposed to temperatures below their thermal tolerance for extended periods, adverse effects can lead to pathological and potentially fatal conditions (Schwartz 1978; Witherington & Ehrhart 1989; Spotila et al. 1997; Sadove & Pisciotta 1998; Southwood et al. 2003). Rapid decreases in temperature to below 10 °C can result in 'cold stunning' and potentially stranding, while the lethal temperature for chelonid marine turtles in experimental conditions is c. 8 °C (Schwartz 1978; Ogren & McVea 1995).

Temperate New Zealand is one habitat that falls outside the preferred thermal envelope (at least seasonally) for this species; where the average sea surface temperature (SST) in northern New Zealand ranges between 20–23 °C in summer and 14 °C in winter (Chiswell 1994; Duffy 2002). Early published reports considered green turtles found in New Zealand waters as 'waifs or strays' (McCann 1966a) or occasional visitors (McCann 1966b). The most recent review of green turtle occurrences in New Zealand waters (Gill 1997), reviewed sparse sighting and stranding data spanning 125 years and reported an absence of green turtles in austral winter (July) and a significant bi-modal seasonal peak in abundance (summer and spring). Although this review did acknowledge that a small sample size and seasonal observer bias limited the strength of the results, this work concluded that green turtles were 'stragglers' from Australia or further north (Gill 1997). Green turtles were mostly found during warmer seasonal months within northern New Zealand waters (Northland), with their influx coinciding with El Niño Southern Oscillation (ENSO) La Niña periods when SSTs were higher than the average for this region of New Zealand.

In temperate regions where SST gradually decreases to around 15 °C during winter, populations can persist year round. For example, at Moreton Bay, Australia (an important warm temperate foraging ground), green turtles actively feed at 15 °C (Read et al. 1996), while further south in New South Wales, green turtles remain active in water as low as 12 °C (C.J. Limpus, pers. obs). These winter temperatures are similar to those experienced in northern New Zealand (Chiswell 1994), with the SST regime characterised by the 20 °C

isotherm seasonally expanding and retracting across the North Island. To our knowledge there are no recent reviews that have examined the distribution and occurrence of green turtles throughout New Zealand waters. The aim of this study, therefore, was to revisit the straggler or occasional visitor hypothesis by compiling 118 years of sighting and stranding data to determine the spatio-temporal distribution and population structure of green turtles in New Zealand. More specifically, we evaluated evidence for: 1. an increase in records of turtles over recent decades; 2. persistent, year-round presence of turtles; 3. variation in turtle records with seasons, coasts (west vs. east coast of northern New Zealand) and anomalies in SST.

Methods

Sighting, stranding and incidental capture data

Sighting, stranding and incidental capture data from New Zealand between 1895 and 2013 were compiled to form the New Zealand Marine Turtle Sightings and Stranding Database (NZMTSSD) for this study. Compiled data included date, location, record type (sighting, stranding or incidental capture) and biometric data (CCL). All records from Gill (1997) were combined with validated records of sightings or strandings collected between 1997 and 2013. Sources included published and unpublished (grey) literature, validated reports from individuals of the public, and records from government and non-government organisations. In this work, 'New Zealand' refers to both North and South Islands, encompassing those outlying islands on the continental shelf within the 200 m isobath and the seas out to the 200 nm Economic Exclusion Zone (EEZ). Records from New Zealand's territorial Kermadec Islands (c. 900 km northeast of New Zealand at c. 30° S) were omitted from this study because this subtropical island group is biogeographically distinct from mainland New Zealand.

Records were initially categorised into three 'types': 'Sighting' (sightings of live, free-ranging green turtles); 'Stranding' (green turtles found alive or dead, either as beach cast or floating at sea); or 'Incidental' capture (by-caught green turtles in recreational or commercial fishery activities). For the present analysis, Incidental captures were included with all Sightings data, as both record types were considered to represent live, free-ranging turtles at the time of capture.

To determine variation in the mean number of records through time (within each quarter [season]-year) R software (R Development Core Team 2014) was used to fit a generalised linear model (McCullagh & Nelder 1989), assuming a log-link function and a Poisson error distribution. Counts of records were modelled using the predictors T: Type (factor with two levels: Sighting/Incidental capture and Stranding), C: Coast (factor with two levels: East and West), Y: Year (continuous), Q: Quarter (factor with four levels: Jan–Mar, Apr–Jun, Jul–Sep, Oct–Dec), QTA: Quarterly Temperature Anomaly (continuous), and ENSO: El Niño Southern Oscillation Multivariate Index (continuous). The most complex model involved fitting three-way interactions between Type, Coast and each of the other four predictors (i.e. Y×T×C, Q×T×C, ENSO×T×C and QTA×T×C). A backwards stepwise procedure based on the AIC criterion was subsequently applied to remove extraneous predictors. Consequently, all terms involving ENSO were removed from the model. Many two-way interactions and two three-way

interactions (i.e. C×T×Y and C×T×Q) were retained in the model. Eight records from prior to 1983 were removed from this analysis because they were too temporally sparse to be informative.

Some specific hypotheses regarding interaction terms were tested in post-hoc analyses using the *phia* package in R (De Rosario-Martinez 2015). Where Year interacted with other terms in the model, a significant effect of Year within and across the levels of the interacting term was tested. Specifically, a significant effect of Year was tested within each combination of Coast and Type, while a difference in the Year-slope between Coasts within each Type was also tested. Interactions between Quarter (season) and Type and Coast were also investigated.

QTA was calculated using a 47 year time series of the SST taken at University of Auckland's Leigh Marine Laboratory (c. 36.3° S, 174.8° E) on the east coast north of Auckland. Averages were calculated for each quarter in each year and then the anomaly was taken by subtracting the respective mean for each quarter across all years, giving the deviation from the expected long-term average for that quarter. Although the Leigh coastal SST dataset was collected from a single location, the data is accordant with the range, amplitude and variability described for northern New Zealand by Chiswell (1994) and Duffy (2002). Therefore the Leigh coastal SST dataset was chosen as a suitable broad-scale regional proxy for the average long-term inshore SST regime for both coasts of northern North Island.

To investigate seasonal variations in Sighting and Stranding patterns between the west and east coasts of New Zealand, we applied a two-dimensional Pearson's χ^2 test. A one-way analysis of variance (ANOVA) was used to compare season (Jan–Mar, Apr–Jun, Jul–Sep, Oct–Dec) and the size of stranded turtles (CCL) to investigate the influence of SST (season) upon the stranding of different size classes. Distribution maps were created using ESRI ArcMap v10.1.

Size-class, sex ratio and maturity

Standard CCL measurements (± 0.1 cm) were recorded for all turtles recovered during the course of this study (Limpus et al. 1994; Bolten 1999). Biometric data was then augmented with CCL data obtained from the New Zealand Department of Conservation Herpetofauna Database, marine turtle rehabilitation records from Kelly Tarlton's Sea Life Aquarium (Auckland) and Gill (1997). To examine the green turtle population structure CCL measurements were grouped into 5 cm size class categories and the frequency distribution described (Limpus et al. 1994; Seminoff et al. 2002; Arthur & Balazs 2008). In addition, 'new' and 'recent' recruits were identified following the descriptions of Limpus et al. (2005).

Where dead stranded turtles were recovered during the course of the study gross examinations were undertaken, with sex and maturity status determined by in situ examination of the gonads and associated ducts, following the criteria of Rainey (1981) and Limpus & Reed (1985). Maturity status was categorised as immature or mature (Limpus et al. 2005; Meylan et al. 2011). Sex ratio was calculated as the proportion of identifiable females in the sample. To test the null hypothesis that there was no significant departure from a sex ratio of 2:1 within the samples—the demonstrated sex ratio for green turtles within eastern

Australia (Limpus et al. 2005; Limpus 2008)—a χ^2 test with Yates correction factor was applied.

Results

Green turtle spatial distribution in New Zealand

In total, 194 green turtle records were obtained, comprising 36 previously published records (Gill 1997, encompassing records from 1895 to 1996) and 158 unpublished records (encompassing records from 1997 to 2013). Records were mostly from the North Island (north of c. 41° S); only three records were reported from the South Island, with the most southerly record from Birdlings Flat, Canterbury (c. 43.8° S). Ninety-two percent ($n = 178$) of all records were from Auckland northward (c. 37° S) (Figure 1). Stranded turtles comprised 65% ($n = 126$) of records, while sightings and incidentally captured turtles comprised 25% ($n = 49$) and 10% ($n = 20$), respectively. A large proportion of records (69% of those between 1895 and 2013) were from the east coast of the North Island. More specifically, nearly all sightings of free-ranging turtles (98%, $n = 48$) and almost two thirds of all strandings (66%, $n = 83$) occurred on the east coast of the North Island. There was only one reported sighting of a free-ranging turtle from the west coast. Of the 20 documented incidental captures, seven occurred on the west coast and 13 occurred on the east coast. All records (except two) were recorded within New Zealand's inshore waters (0–200 m). The two records of green turtles offshore were from northeast of New Zealand; a sighting approximately 24 km west of North Cape (at c. 570 m water depth) and an incidental capture by a commercial shallow long-line fishing vessel approximately 300 km west of Whangarei (at c. 35° S and c. 2000 m water depth). The incidentally captured turtle was a juvenile estimated at < 45 cm CCL and clearly exhibited pronounced plastron ridges, white ventral surface and sharp carapace edges characteristic of an oceanic phase individual.

Size-class, sex ratio and maturity

The size-class frequency distribution of all measured turtles (CCL) encompassed a range of 17.6–94.6 cm ($\mu = 51.9$ cm, SD = 11.6, $n = 86$) (Figure 2). The smallest turtle recorded was considered an oceanic-phase turtle based on size (17.6 cm CCL) and morphological characteristics. The next smallest turtle had a CCL of 37.3 cm. No green turtles in the hatchling size range were observed. Of 64 turtles examined externally, 8% ($n = 5$) of turtles exhibited morphological characteristics of 'new' recruits ($\mu = 40.8$ cm CCL, SD = 3.3, range 37.3–44.8 cm), while a further 39% ($n = 25$) turtles were defined as 'recent' recruits ($\mu = 45.6$ cm CCL, SD = 2.5, range 41.9–52.5 cm); new and recent recruits comprised 47% ($\mu = 44.8$ cm CCL, SD = 3.2, range 37.3–52.5 cm, $n = 30$) of all turtles examined externally. New or recent recruits were encountered every month of the year, suggesting no temporal pattern of settlement.

Of 41 green turtles examined, 15 were males, 25 were females and one was undetermined. All turtles examined were immature juveniles. In all males the testes were undeveloped and inactive, while in all females the ovaries were inactive, with unexpanded stroma with no sign of vitellogenesis. Expressed as a F:M sex ratio (1.7:1), there was no significant
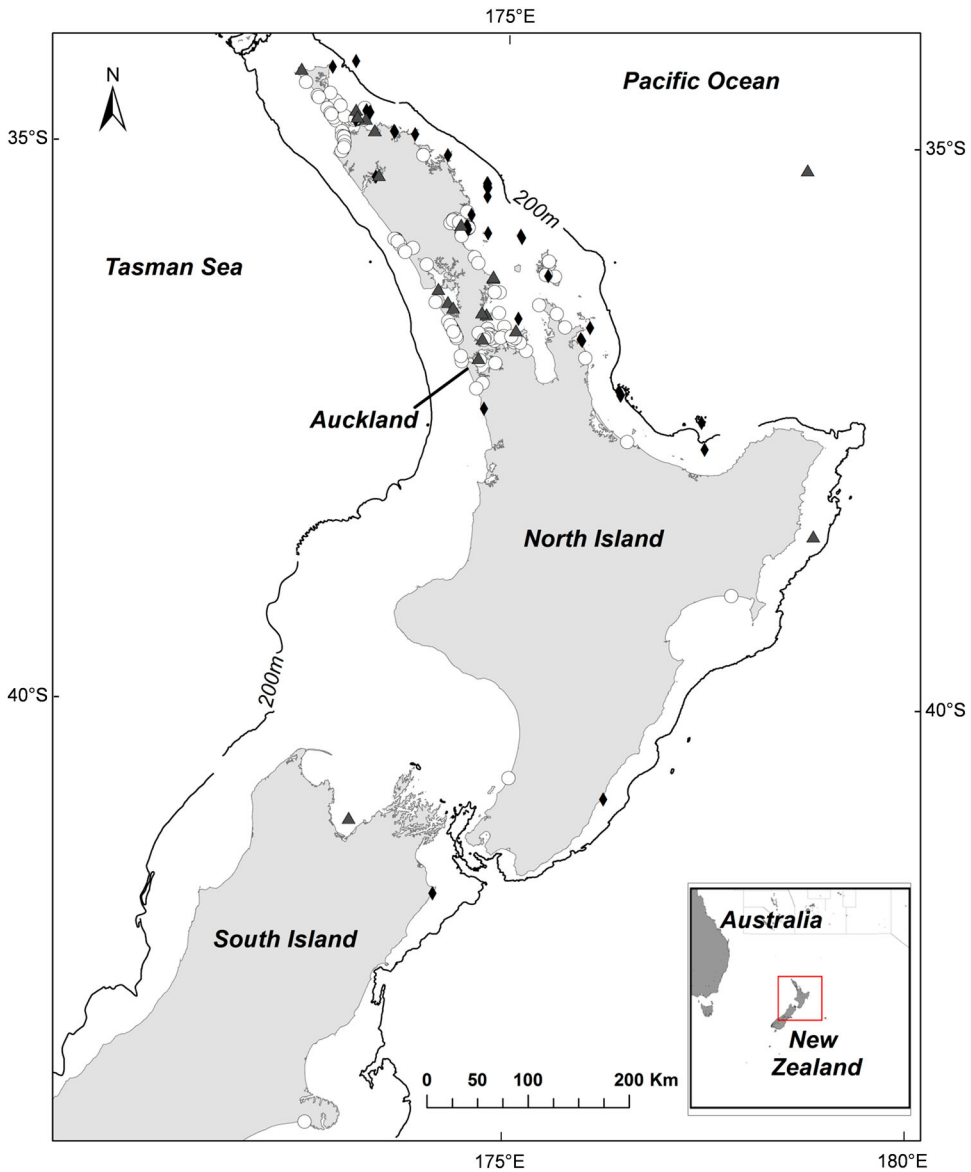
Figure 1. Distribution of green turtle records from New Zealand from 1895 to July 2013 ($n = 194$). Stranded turtles (○); Sightings (◆); Incidental captures (▲).

difference from 2:1 ($\chi^2 = 0.3$, $P = 0.58$, d.f. $= 1$ with Yates correction factor). A t-test revealed no significant difference in the size (CCL) between male and female turtles ($t = 0.97$, $P = 0.34$).

Seasonal patterns

The generalised linear model (GLM) selected by the AIC contained the predictors Type, Coast, Year, Quarter, QTA and a number of interactions (Table 1). Quarter (season)
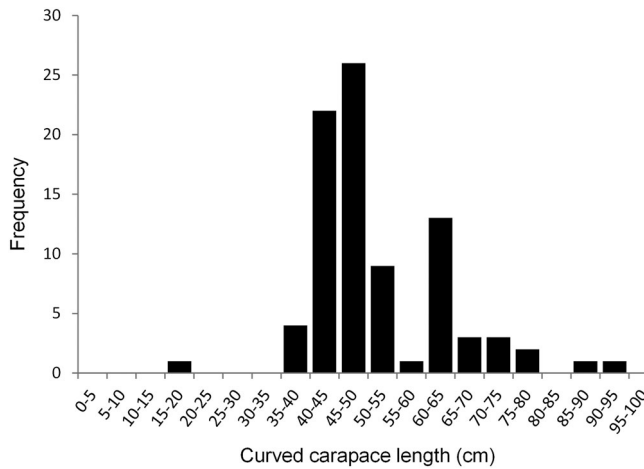
Figure 2. Size-class frequency distribution of green turtles in New Zealand recorded from 1895 to 2013. Mean curved carapace length (CCL) = 51.9 cm (SD ± 11.6 cm, n = 86).

effects were different among combinations of Type and Coast (Table 1). This three-way interaction was not significant at the 5% level; however, the AIC model selection process favoured retaining it in the model. Quarter had a significant effect on east coast sightings (x^2 = 12.00, P = 0.0296; Figure 3C) with July–September (winter) being significantly more likely to have low sightings. However, there was no significant effect of Quarter on strandings on the west coast (x^2 = 8.58, P = 0.1064; Figure 3A) and east coast (x^2 = 3.32, P = 0.6899; Figure 3B), and sightings on the west coast (x^2 = 0.90, P = 0.8255), though it is likely that these tests were low powered. Two-way interactions showed that, overall (across coasts), quarterly effects were not significant for either Sightings (x^2 = 5.78, P = 0.2457) or Strandings (x^2 = 5.25, P = 0.2457). However, Quarter did show a strongly significant effect on the east coast overall (x^2 = 14.07, P = 0.0056), with records significantly less likely to occur during July–September (winter). This effect corresponds to the pattern of sightings described above. Quarter did not significantly affect west coast records (x^2 = 2.03, P= 0.5654). The one-way ANOVA showed no significant

Table 1. Analysis of deviance table for a Poisson generalised linear model of the number of green turtle records.

Predictor	Likelihood ratio x^2	d.f.	P-value
QTA[a]	4.265	1	0.0389
Coast	46.221	1	0.0000
Type	16.418	1	0.0001
Year	106.986	1	0.0000
Qtr[b]	5.646	3	0.1302
QTA×Coast	5.852	1	0.0156
Coast×Type	7.079	1	0.0078
Coast×Year	0.01	1	0.9214
Type×Year	0.329	1	0.5665
Coast×Qtr	12.881	3	0.0049

[a]QTA: Quarterly Temperature Anomaly.
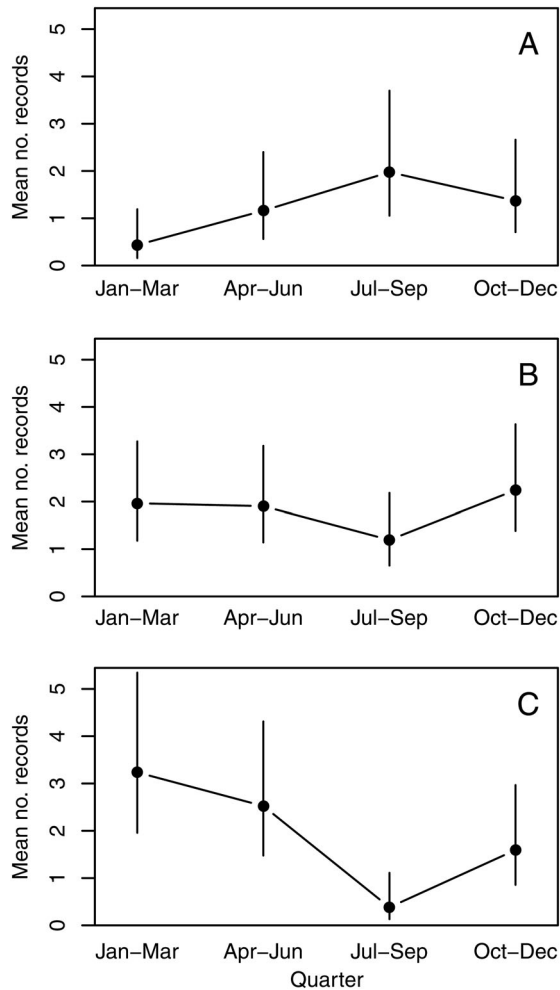[b]QTR: Quarter (season).

Figure 3. Predicted means from a Poisson generalised linear model of the number of sightings and strandings per quarter for 2014, assuming typical temperatures. Error bars represent 95% confidence intervals around the means. **A,** West coast strandings; **B,** east coast strandings; **C,** east coast sightings and captures.

differences in the CCL of stranded turtles and season within which they stranded ($F_{3,72} = 1.141$, $P = 0.338$; Table 2).

Sea surface temperature

The coastal SST regime for northern North Island calculated from the Leigh dataset had a range average of 14 °C (August) to 20.6 °C (February), giving an amplitude of 6.6 °C for the North Island's northeast. The lowest recorded temperature at Leigh was 12.3 °C and the highest was 23.9 °C, with an average annual long-term mean of 17.2 °C. There was a significant negative effect of QTA ($\chi^2 = 4.27$, $P = 0.0389$; Table 1) on the number of records overall, suggesting there were fewer records when it was unusually warm. The QTA effect interacted with the predictor Coast ($\chi^2 = 5.85$,

Table 2. One-way ANOVA comparing curved carapace length (CCL) of stranded turtles and the seasons in which they were recorded (Jan–Mar, Apr–Jun, Jul–Sep, Oct–Dec; $n = 76$).

Source of variation	SS	d.f.	MS	F	P-value	F crit
Between groups	465.708	3	155.236	1.141	0.3384	2.7318
Within groups	9796.206	72	136.058			
Total	10261.910	75				

Note: SS, sum of squares; MS, mean squares.

$P = 0.0156$) and, when tested within Coasts, the result was significant for the west ($\chi^2 = 9.42$, $P = 0.0043$) but not the east coast ($\chi^2 = 0.40$, $P = 0.5271$). This suggests that there were more strandings on the west coast when there were unusually low temperatures recorded at Leigh. There was no evidence of more strandings on the east coast during unusually low SSTs; however, strandings were predicted to be more consistent throughout the year (Figure 3B). In addition, there was no evidence of a difference in the effect of QTA between strandings and sightings; therefore, the QTA:Type interaction was excluded by the model. There was also no detectable relationship between the ENSO Multivariate Index and records of turtles.

Annual trends

The number of green turtle reports has increased each decade since records began, with 98% of all records reported since 1983. From 1983, green turtles were reported every year, with the greatest number recorded during 2011 (18) and 2012 (25). Overall, there were more strandings than sightings (Likelihood ratio $\chi^2 = 16.4$, $P = 0.0001$; Table 1). There was a significant overall linear increase in the log-mean number of records over the 30 years of this study ($\chi^2 = 107.0$, $P < 0.0001$; Table 1). This corresponds to an exponential increase on the untransformed scale (Figure 4). Overall, there was no significant difference between the Year-slopes of the east and west coasts for strandings ($\chi^2 = 1.49$, $P = 0.2223$). However, the rates of increase in sightings over time were marginally different between the east and west coasts ($\chi^2 = 5.06$, $P = 0.0496$).

Discussion

Distribution

Sighting, stranding and incidental capture data reveal a concentration of green turtle occurrence across northern New Zealand; a region of New Zealand's landmass that dissects the western boundary of the South Pacific subtropical gyre system (SPSG). The SPSG and its associated currents in the southwest Pacific (Southern Equatorial Current [SEC], East Australian Current [EAC] and Tasman Front [TF]) have been described as the key transport mechanism for post-hatchling marine turtles dispersing from southwest Pacific rookeries (Boyle 2006; Boyle et al. 2009). Therefore, it seems likely that oceanic-phase juvenile green turtles passively entrained in the SPSG would eventually arrive in New Zealand via the TF and the subtropical East Auckland Current (EAUC)—a natural extension of the TF within the SPSG system. The influence of the TF and EAUC upon the influx of marine reptiles was initially suggested by Gill (1997). Data presented herein support this, with 69% of the total records of green
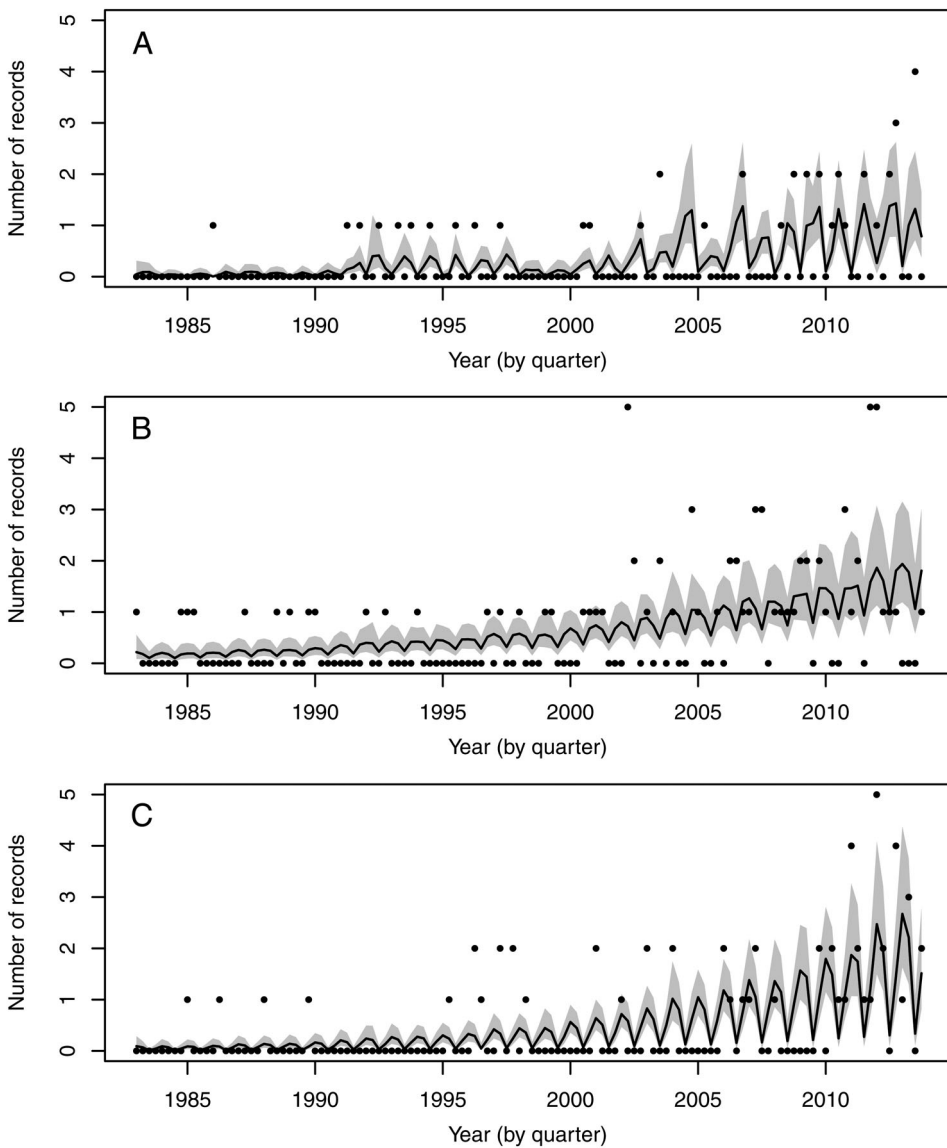
Figure 4. Predictions from a Poisson generalised linear model of the mean of the quarterly counts of turtle records between 1983 and 2013. Circles represent the number of counts recorded, the black lines are the predicted means, and the grey areas show the 95% confidence bounds for the means. **A**, West coast strandings; **B**, east coast strandings; **C**, east coast sightings and captures.

turtles originating from the northeast inshore region of the North Island. This northeast region of New Zealand is where the EAUC (and associated eddies) are the dominant oceanographic transport system (Roemmich & Sutton 1998; Stanton & Sutton 2003). The TF and EUAC have also been identified as the primary mechanism responsible for the influx of tropical fish species to New Zealand (Francis & Evans 1993; Francis et al. 1999).

Size-class, sex ratio and maturity

Our data support the hypothesis that oceanic-phase juvenile green turtles are settling into nearshore neritic habitats following a natural dispersal and settlement pattern. Size-class frequency and sexual maturity data show the New Zealand population comprises a discrete assemblage of post-settlement immature turtles ranging from small juveniles to large subadults (μ = 51.9 cm CCL, SD = 11.6, range 17.6–94.6 cm, n = 86). Size at recruitment and a female-biased proportional sex ratio of 0.63 (F:M sex ratio of 1.7:1) within this study are similar to the expected sex ratio for eastern Australian foraging populations (Limpus & Walter 1980; Limpus & Reed 1985; Limpus et al. 1994). The identification of five new recruits in the range of 37.3–44.8 cm CCL indicates settlement occurs at c. 40.8 cm CCL.

Only 35% of examined turtles were new or recent recruits, with the remaining 65% (n = 34) comprised of older age classes up to large subadults (μ = 63 cm CCL, SD = 9.9, range 46.5–94.6 cm). If turtles settle at c. 40.8 cm CCL as shown, this suggests these older age classes have occupied coastal neritic habitats for some time, hence exhibiting a degree of residency. However, if residency does occur, the absence of mature adult turtles does suggest that turtles are departing from New Zealand coastal areas prior to the onset of puberty. Similarly, discrete assemblages of immature age classes at neritic foraging grounds and puberty related migrations have been observed in other regions (Koch et al. 2007; Meylan et al. 2011). Immature-dominated cohorts occupying neritic foraging areas were initially identified by Carr & Caldwell (1956) and later defined by the term 'developmental migrations' (Carr et al. 1978). This concept denotes the post-settlement progression of juveniles transitioning through a series of developmental habitats as they change in size and ecological requirements prior to ultimately settling at an adult foraging ground (Carr 1980; Musick & Limpus 1997; Bolten 2003; Moncada et al. 2006; Meylan et al. 2011). In these studies, size-class partitioning was influenced by differing habitat requirements between age classes (e.g. food availability, predation risk, and dispersal and migratory behaviour; Moncada et al. 2006; Koch et al. 2007; Bresette et al. 2010; Meylan et al. 2011). Such patterns in size-class partitioning may then be occurring in New Zealand waters, where northern neritic habitats constitute a temporary developmental habitat, with juvenile green turtles dispersing across the southwestern Pacific transitioning through this habitat for a period of time.

Seasonality

Further evidence supporting a temporary developmental habitat in northern New Zealand was the consistent year round occurrence of green turtles shown in the present work. Contrasting with the previous review by Gill (1997) this work found no correlation between ENSO (La Niña periods) and the influx of green turtles, and, despite an average winter SST of 14 °C, sightings of live free-ranging turtles were recorded in all seasons. This contradicts the currently accepted view that green turtles appear incidentally as stragglers or occasional visitors (McCann 1966b, 1966a; Gill 1997). Nevertheless, data presented here detected a significant decrease in sightings on the east coast during winter, despite stranding rates remaining relatively stable throughout the year. Several possibilities may lead to lower detection probability during colder seasons: 1. a seasonal reduction in marine

observers (e.g. recreational fishers and divers) during winter (Gill 1997); 2. a compensatory response to cooler water by temporarily migrating to warmer water (offshore) during winter (Mendonca 1983; Epperly et al. 1995; Ogren & McVea 1995); and 3. turtles employing a 'sit and wait' behaviour during winter, where turtles undergo long quiescent dives of up to several hours with very short surface intervals (Hochscheid et al. 2005). Despite this, the present work does indicate a more permanent occurrence of green turtles in New Zealand's neritic habitats than previously concluded (Gill 1997). The temperature regime described by the Leigh dataset does suggest overwintering turtles would experience some degree of temperature related stress; however, their occurrence in similarly cool winter temperatures has been observed in Australia. For example, at Moreton Bay, Australia (a permanent warm temperate foraging ground), green turtles have been shown to actively feed at 15 °C (Read et al. 1996), while in New South Wales, green turtles remain active in water as cool as 12 °C (C.J. Limpus, pers. obs).

Although season did not affect the occurrence of green turtles overall, strandings on the west coast were significantly affected by QTA. On the west coast there was an increase in strandings during winter, and this was found to be significantly higher during unusually cold winters (reflected by the QTA at Leigh). A correlation between westerlies and southerlies, and colder SST at Leigh has been observed in other studies (Greig et al. 1988). Therefore, we suggest the prevalence of stronger westerly winds and higher storm frequency during winter may substantially impact green turtle populations within the west coast, resulting in higher incidence of stranded turtles within this region. Correspondingly, a marginal decrease in stranded turtles on the east coast during winter may reflect an inverse effect, where stronger offshore westerly winds reduce the probability of stranding incidence. Similarly, a correlation between onshore storm events and turtle strandings has been observed on the east Australian coast (Boyle 2006). One unexpected result was the negative effect of the QTA where fewer records were observed when the SST (based on the QTA) was unusually warm. However, the negative effect of the QTA could be attributed to the fact that the majority of records were of stranded animals; hence, when SST are unusually warm, fewer temperature-related strandings will result in fewer stranding numbers overall during these periods. Also, no relationship between CCL and season was detected; suggesting environmental conditions are exerting equal influence across the population.

Annual trends

The strandings and sightings data show an exponential increase in the number of green turtle records over the time period examined. This increase in records is attributed at least in part to an increase in the number of observers reporting sightings and strandings as a result of public awareness efforts during the course of this study. Similarly, increased observer presence (e.g. SCUBA divers, game fishers and commercial fisheries) over the last 30 years has resulted in increased numbers of newly recorded tropical and subtropical fishes from northeastern North Island (Francis et al. 1999). Nevertheless, other factors that may influence the observed increase should not be discounted. For example, the observed increase may parallel conservation efforts in the region. In the southwestern Pacific, the nearest potential source populations are those at the Southern Great Barrier Reef off Australia's east coast. These populations have recovered over the last several

decades following significant declines due to human over exploitation and other anthropogenic mortality (Limpus 2008). Consequently, if New Zealand green turtles do derive from these populations, we would expect the increase in abundance of oceanic-phase juveniles dispersing through the region as a result would eventually be reflected in the number of observations in New Zealand waters.

Increasing evidence shows that climate change is leading to rapid poleward shifts in the distributional range of marine species (Sorte et al. 2010; Burrows et al. 2011; Feary et al. 2014). These climate-mediated extensions have been observed in a range of tropical fish populations, though most substantially throughout the east coast of Australia, driven by an associated strengthening of the subtropical gyre and poleward penetration of the EAC over the last 60 years (Booth et al. 2007; Ridgway 2007; Last et al. 2011). The strengthening of the EAC has resulted not only in the broadening and extension of this boundary current and its associated eddy system but also led to an increase in the SST of the Tasman Sea (Cai et al. 2005; Neuheimer et al. 2011). Hence, such changes in oceanographic conditions could theoretically transport more juvenile green turtles from eastern Australian rookeries (or farther afield) toward New Zealand waters. Once they disperse to this region of the south Pacific, they would remain in this oceanic developmental habitat until they settle into neritic habitats in northern New Zealand at the size observed here in this study.

Conclusions

Empirical evidence presented here supports the hypothesis that green turtles occurring in New Zealand neritic habitats reflect a natural post-oceanic settlement behaviour rather than oceanic-phase stragglers incidentally blown ashore by storm and other stochastic events. We propose that New Zealand comprises a temperate intermediary habitat where oceanic-phase green turtles dispersing across the southwest Pacific settle and transition through this habitat for a period of time before departing to other regions. This contrasts with the prevailing view that green turtles represent stragglers incidentally blown off course or occasional visitors that seasonally inhabit New Zealand's inshore waters. Although this study has provided some important insights into our understanding of green turtles in New Zealand, several questions still remain. Investigating residency and foraging behaviour would provide further insight into temporal occupancy and habitat use. Furthermore, identifying the genetic origin of the population will assist with establishing region-wide population connectivity. This is particularly important for defining dispersal patterns and migratory pathways. Additionally, for green turtles along the edge of their range, monitoring their response to temperature shifts in relation to rising global temperatures (as noted in Pilcher et al. 2014) will be of fundamental importance for managing this species in the southwest Pacific.

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