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Juvenile recruitment in loggerhead sea turtles linked to decadal changes in ocean circulation

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Abstract

Given the threats of climate change, understanding the relationship of climate with long-term population dynamics is critical for wildlife conservation. Previous studies have linked decadal climate oscillations to indices of juvenile recruitment in loggerhead sea turtles (*Caretta caretta*), but without a clear understanding of mechanisms. Here, we explore the underlying processes that may explain these relationships. Using the eddy-resolving Ocean General Circulation Model for the Earth Simulator, we generate hatch-year trajectories for loggerhead turtles emanating from Japan over six decades (1950–2010). We find that the proximity of the high-velocity Kuroshio Current to the primary nesting areas in southern Japan is remarkably stable and that hatchling dispersal to oceanic habitats itself does not vary on decadal timescales. However, we observe a shift in latitudes of trajectories, consistent with the Pacific Decadal Oscillation (PDO). In a negative PDO phase, the Kuroshio Extension Current (KEC) is strong and acts as a physical barrier to the northward transport of neonates. As a result, hatch-year trajectories remain mostly below 35°N in the warm, unproductive region south of the Transition Zone Chlorophyll Front (TZCF). During a positive PDO phase, however, the KEC weakens facilitating the neonates to swim north of the TZCF into cooler and more productive waters. As a result, annual cohorts from negative PDO years may face a lack of resources, whereas cohorts from positive PDO years may find sufficient resources during their pivotal first year. These model outputs indicate that the ocean circulation dynamics, combined with navigational swimming behavior, may be a key factor in the observed decadal variability of sea turtle populations.

Keywords: climate forcing, decadal oscillations, general circulation models, Lagrangian analysis, physical oceanography, transition zone chlorophyll front

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Introduction

Loggerhead sea turtles are listed as either endangered or threatened under the U.S. Endangered Species Act and are globally considered vulnerable by the International Union for the Conservation of Nature's Red List (Conant *et al.*, 2009; Casale & Tucker, 2015). Their population status is a result of the diverse array of threats loggerhead face on land and in the ocean. Such threats include incidental fishery bycatch, habitat loss and degradation, marine debris ingestion, and pollution – threats that are driven or exacerbated by human actions (Witherington, 2003; Poloczanska *et al.*, 2009; Hamann *et al.*, 2013). To assess the magnitude of these threats and prioritize corresponding management actions, it is essential to maintain long-term monitoring programs and develop a detailed understanding of sea turtle population dynamics (Bjorndal *et al.*, 2010). To this end, recent efforts have focused on understanding the impacts of climate change to sea turtles (Hays *et al.*, 2003; Hawkes *et al.*, 2007) and operationalizing this knowledge for statutory processes and conservation practitioners (McClure *et al.*, 2013; Nye *et al.*, 2014).

As an example, a recent study analyzed 25 time series of index beach counts of loggerhead nests from Japan and Florida (Van Houtan & Halley, 2011). Over a period of several decades, the study documented strong statistical correlations between the observed breeding abundance and key climate indices: the Pacific Decadal Oscillation (PDO) for turtles nesting in Japan and the Atlantic Multidecadal Oscillation (AMO) for those nesting in Florida. In both cases, observed nesting abundance lagged the climate index by 25–30 years. The study noted this lag approximated the time from birth

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to breeding maturity and suggested that the climate indices may reflect that environmental conditions modulate recruitment during the critical survival period of the first year – similar to other marine life (e.g., Hjort, 1914; Pepin, 1991; Chavez *et al.*, 2003).

Here, we test the idea that changes in the ocean environment are the primary cause behind the observed decadal variability in the loggerhead population in the North Pacific. This idea stems from three independent observations. First, ocean currents play a critical role on the long-distance migrations of various sea turtle species toward their foraging hotspots (Gaspar *et al.*, 2006; Polovina *et al.*, 2006; Hays *et al.*, 2010; Scott *et al.*, 2014). Perhaps more fundamentally, ocean currents are a significant factor for the biogeography of nesting populations for various sea turtle species (Putman *et al.*, 2010a, b, 2012a; Okuyama *et al.*, 2011; Shillinger *et al.*, 2012). Second, ocean circulation and the marine environment in the western North Pacific display a well-documented decadal variability that is somewhat paced by PDO (Mantua & Hare, 2002; Chiba *et al.*, 2013; Di Lorenzo *et al.*, 2013; Qiu *et al.*, 2014). Third, for species like sea turtles with high fecundity and low first-year survival, overall population variability is driven primarily by environmental fluctuations that occur during early life stages (J.M. Halley, K.S. Van Houtan, N. Mantua, in review).

To explore this idea, we analyze a 60 year long simulation output from a general ocean circulation model that reproduces the observed decadal variability of the North Pacific Ocean. This enables several analyses. We begin by testing whether the strong current proximate the main nesting region in Japan separates from the coast at a decadal timescale. If neonate loggerheads fail to reach this current, they may not reach their oceanic foraging habitat, which would likely result in recruitment failure. Next, we test whether the oceanic conditions experienced by hatch-year loggerheads are themselves modulated by the PDO – either due to circulation shifts or due to local changes such as sea surface temperature (SST). For this purpose, we release virtual neonates (neonates hereafter) near the main nesting grounds and follow them drifting and swimming with the ocean circulation for one full year. We record the paths and SST experienced by neonates along the trajectories, compare these to known physiological constraints to juvenile sea turtles, and interpret the potential impact to cohort recruitment. As a result, we provide the novel insights into potential oceanographic constrains to neonate survival, and the long-term role of climate in sea turtle population dynamics.

Materials and methods

Region of study

A large fraction (43%) of nesting grounds of loggerhead sea turtles in the North Pacific are found on Yakushima Island (130.5°E, 30.3°N) in southern Japan (Conant *et al.*, 2009; Van Houtan & Halley, 2011). The nesting grounds are located just north of a strong subtropical western boundary current, the Kuroshio Current (KC) that transports warm, saline waters from the tropics to the mid-latitudes of the North Pacific (Fig. 1). At about 35°N, the KC deflects eastward toward the interior of the North Pacific as the Kuroshio Extension Current (KEC), which represents a strong physical barrier between the subtropical and subpolar gyres. On the path of the KEC, between 155°E and 180°, is the Kuroshio Extension Bifurcation Region (KEBR), an important deep-ocean foraging habitat for loggerhead sea turtles (Polovina *et al.*, 2006; Abecassis *et al.*, 2013); hence, the sea turtles use the KC and KEC to migrate from their natal beaches to developmental foraging habitat. As an

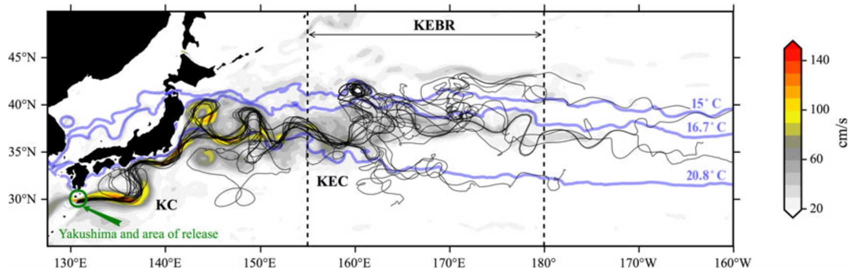

Fig. 1 The North Pacific oceanographic context. The mean amplitude of the surface current (from August 1950 to July 1951) obtained from the OFES simulation is shaded in the background and indicates the position of the Kuroshio Current (KC) and Kuroshio Extension Current (KEC) during that period. Also indicated are the deep-ocean foraging habitat known as the Kuroshio Extension Bifurcation Region (KEBR) and the location of the main nesting grounds of North Pacific loggerhead sea turtles (Yakushima at 130.5°E, 30.3°N) and of the area of release of the neonates. Examples of 16 trajectories of neonates released in August–September 1950 are plotted with black lines. The positions of the 15, 16.6 and 20.7 °C sea surface temperature (SST) contours during July 1951 in the model are also plotted with thick blue lines. The 15 °C isotherm indicates the northernmost latitude before turtle's physiology slows down. The next two isotherms approximately indicate where the Transition Zone Chlorophyll Front (TZCF) lies. OFES, Ocean General Circulation Model for the Earth Simulator.

illustration, Fig. 1 provides examples of trajectories of neonates released off Yakushima obtained from the simulation: The neonates are advected by the currents eastward into the interior of the North Pacific and reach rapidly the KEBR in about 2 weeks.

In the North Pacific transition zone between the highly productive subpolar ocean region and the unproductive subtropical region is a feature called the Transition Zone Chlorophyll Front (TZCF). This is defined as the contour where surface chlorophyll-*a* equals 0.2 mg m^{-3} (Polovina *et al.*, 2001). The TZCF migrates seasonally in the meridional direction, being south of the KEC around 30°N in boreal winter and north of it around 40°N in boreal summer (Fig. S1; Polovina *et al.*, 2001; Ayers & Lozier, 2010; Polovina *et al.*, 2015). The TZCF extends roughly 8000 km zonally across the basin and comprises important foraging habitat and migratory pathways for apex predators, sea turtles, and other marine life (Polovina *et al.*, 2001).

The PDO is the dominant climate mode in SST of the North Pacific Ocean. Over the North Pacific subpolar gyre during a positive phase of the PDO, strong westerly winds and vertical mixing result in a cool SST and (because of light limitation) low spring primary productivity – with the reverse being true during a negative phase (Mantua & Hare, 2002; Miller *et al.*, 2004). The region of the KEC to the west responds to the oscillation 3–6 years later because the anomalies have to first propagate westward via oceanic Rossby waves. As a result, a few years after the start of a positive PDO phase, the KEC tends to be weaker, less stable and located a few degrees south from its average position, with the reverse observed a few years after the start of a negative PDO phase (Qiu, 2003; Qiu & Chen, 2005; Taguchi *et al.*, 2007). The TZCF also responds to the PDO and tends to have a more southerly position (by about 1°) during a positive PDO phase in the central Pacific and a few years after the start of that phase in the KEC region (Chai *et al.*, 2003; Bograd *et al.*, 2004; Lin *et al.*, 2014). The decadal variability of KEC and TZCF is, however, not entirely dictated by the PDO as they are also influenced by secondary climate modes (such as the North Pacific Gyre Oscillation) as well as by the internal variability of the KEC itself (Di Lorenzo *et al.*, 2008, 2013; Ceballos *et al.*, 2009; Qiu & Chen, 2010; Lin *et al.*, 2014; Pierini, 2014; Qiu *et al.*, 2014).

Hypotheses

In the North Atlantic, neonates start to swim from the beach offshore for ~24 h, after which they swim slower for ~1 week until they reach the Gulf Stream (Salmon & Wyneken, 1987; Wyneken *et al.*, 2008). This stage is termed the frenzy period. Assuming that the North Pacific loggerhead sea turtles behave similarly, the distance between the shore and KC may then be critical for the survival of the neonates. Previous studies show that the KC can be unstable and meander up to 50 km from its average path (Qiu & Miao, 2000). If true, this could double the time neonates take to reach the KC. At an average swim speed of 20–40 cm s^{-1}, neonates would need to swim actively for an additional 35–70 h, or 3–6 days if swimming occurs only during daylight (Salmon & Wyneken, 1987; Wyneken *et al.*, 2008). This additional distance is also larger than the largest distance (40 km) that hatchling loggerheads from the Southeastern United States can swim using their residual yolk sac energy (Kraemer & Bennett, 1981). Our first hypothesis is that proximity of the KC to Yakushima Island varies on a decadal scale and dictates whether neonates reach the KC, which is an important factor for juvenile recruitment.

Additionally, neonate survival could be affected by the ocean conditions met during their first year of life, while they are transported into the North Pacific. Young sea turtles stop feeding for temperature lower than 20 °C, swim less actively for temperature lower than 15 °C, and fall into a coma and die for temperatures lower than 10 °C (Davenport, 1997). Hence, low survival rates are expected if the neonate cohort is transported in too cold (<15 °C) water. Furthermore, neonates need to eat and their survival depends also on the concentration of secondary and (indirectly) primary productivity of the region (Polovina *et al.*, 2006). Observations of tracks of juvenile loggerheads indicate that as long as the turtles are situated north of the TZCF, they tend to stay along the KEC where primary productivity is high; only when the TZCF moves north of the KEC in summer do the turtles leave the KEC and follow the TZCF (Polovina *et al.*, 2006; Fig. S1). For neonates, it might be more difficult to follow the TZCF and they might be dependent on the ocean currents to bring them in the productive area north of the TZCF. Our second hypothesis is thus that, depending on the phase of the PDO, the ocean circulation transports each annual cohort of neonates in environmental conditions that are favorable or not to their survival.

Numerical model

For this study, we analyze a 60 year output of the eddy-resolving Ocean General Circulation Model for the Earth Simulator (OFES) model (Masumoto *et al.*, 2004; Taguchi *et al.*, 2007). This output has been studied extensively and has been shown to reproduce remarkably well the seasonal, interannual, and decadal variability of the ocean circulation, SST, and mixed layer depth of the North Pacific (Nonaka *et al.*, 2006; Taguchi *et al.*, 2007; Nishikawa *et al.*, 2011; Qiu *et al.*, 2014). OFES outputs have been used to study (i) the effects of environmental conditions to Japanese sardine survival (Nishikawa & Yasuda, 2011; Nishikawa *et al.*, 2011, 2013), (ii) the trans-Pacific migration of loggerhead sea turtle neonates (Okuyama *et al.*, 2011), and (iii) the decadal variability in zooplankton transport and distribution over the KEC region (Chiba *et al.*, 2013). Further details of the model and of the simulation are in Appendix S1.

The model does not have a biological component but, because SST and surface chlorophyll are controlled to a large extent by the same physical processes (Bograd *et al.*, 2004; Ayers & Lozier, 2010), the position of the TZCF can be approximated from SST (Bograd *et al.*, 2004). By comparing satellite surface chlorophyll data to the model's SST, we thus approximate the position of the TZCF in the model over 155°E–160°W to be within the SST range 16.6–20.7 °C (Fig. S1). A snapshot of these two isotherms in the model for July 1951 is shown in Fig. 1.

Calculation of trajectories and SST records

Each year, we release four parcel groups covering the main period (August 1, August 15, September 1, and September 15) when neonates first swim into the ocean (Matsuzawa *et al.*, 2002; Matsuzawa, 2010). For each of these dates, a cohort is released from a small (0.2° in longitude by 0.3° in latitude) area centered on 130.75°E and 29.85°N south of Yakushima (Fig. 1); the neonates are initially distributed uniformly every 0.01° in longitude and latitude, resulting in a total of 651 neonates. Every year, 2604 parcels are hence released for a total of 156 240 parcels for the 60 year long period. The trajectory of each parcel is computed for 1 year using a velocity field composed of the surface ocean velocity field and a swimming velocity. Latitudes, longitudes, and SST along these trajectories are then recorded and archived every day. Given that swimming has an impact on the ecology of neonates (Putman *et al.*, 2015), we assume, based on the observed migratory paths of juvenile loggerhead sea turtles in the North Pacific (Polovina *et al.*, 2006), that neonates have evolved to swim toward the northeast, in order to be in the productive region north of the TZCF toward their first year of life. The amplitude of the swimming velocity is chosen to be on average about 1.8 km day^{-1}, a value that falls in the range of swimming velocities used in previous models (Putman *et al.*, 2012b; Scott *et al.*, 2012). Details of the computation are given in Appendix S2.

Statistical analyses

We perform several analyses to assess the influence of the PDO phases on the trajectory outcomes. First, we calculate the *P*-value using a bootstrap technique for the null hypothesis that there is no difference between the two groups of years. Second, we apply the BEST Bayesian estimation (Kruschke, 2012), which enables us to calculate the 95% credible interval (CI) of that difference. If that interval does not include zero, then zero is not a credible value for the difference. The Python package used for this analysis is available here: www.indiana.edu/~kruschke/BEST/.

Results

Figure S2 plots the amplitude of the surface ocean current velocity around Yakushima, over a meridional section centered on 130.75°E and between 27°N and 31°N. Over most of the period, the position of the northern edge of KC (that we define as the 100 cm s^{-1} contour) oscillates at the intra-annual timescale (weeks to months) over <10 km. In seven isolated occasions is that edge located more than 10 km south of its average position due to eddy shedding. We observed no decadal variability in the KC position. This is consistent with the path of KC observed from hydrography that varies little from year to year just south of Yakushima (Nishikawa *et al.*, 2011; their Fig. 2). Hence, although this allows the possibility that a few annual cohort over 60 years may undergo extreme mortality, it does not support the hypothesis that the meridional shift of KC south of Yakushima is the cause for the decadal variability of the turtle population.

Next, we explore the hypothesis that the environmental conditions encountered by the neonates may cause a decadal variability in their recruitment. For this, we first analyze the median SST for each annual cohort of neonates over their first year of life (Fig. 2a). SST starts in the 26–29 °C range, then decreases to 11–18 °C before increasing back to 14–27 °C 1 year later. Interestingly, once SST starts to be relatively high or low (compared to other years), it stays relatively high or low over the whole record. For instance, if we group each SST record depending on their final median SST (1 year after release), we see that all records with a relatively warm or cold final median SST group together. Indeed, the histogram of median SST shows a dip around 22.5 °C, suggesting that their distribution is bimodal (Fig. S2, panel a). Consequently, we chose this final median SST as an indicator for the relative warmth of a certain record. Using the overall median SST at the end of the first year of 21.6 °C as a threshold (dashed line, Fig. 2a), we consider that a cohort has been released during a warm year if at least 70% of that cohort has a SST greater than 21.6 °C at the end of the first year. Similarly, we consider that a cohort has been released during a cold year if at least 70% of that cohort has a SST lower than 21.6 °C at the end of the first year. All other years are considered uncertain in term of their relative warmth.

Because of the relationship between SST and surface chlorophyll (Fig. S1), the relative warmth of a year is a proxy for relative productivity. With the estimated position of the TZCF plotted in Fig. 2a, we conclude that during warm years, the cohort spends a significant portion of its first year south of the TZCF, especially toward the end of the year. Conversely, during cold years, the cohort is on average always within or north of TZCF after day 100, and remaining so to the end of its first year. This suggests that cohorts released during warm years may have more difficulty accessing food than cohorts released during cold years. This may be especially true toward the end of their first year.

Figure 3 compares the time series of median SST 1 year after release to the annual averaged PDO index (PDOi). The 1944–1975 period of mostly negative PDOi appears to be associated with the 1951–1980 period of mostly warm years, while the 1977–2006 period of mostly positive PDOi appears to be associated with the

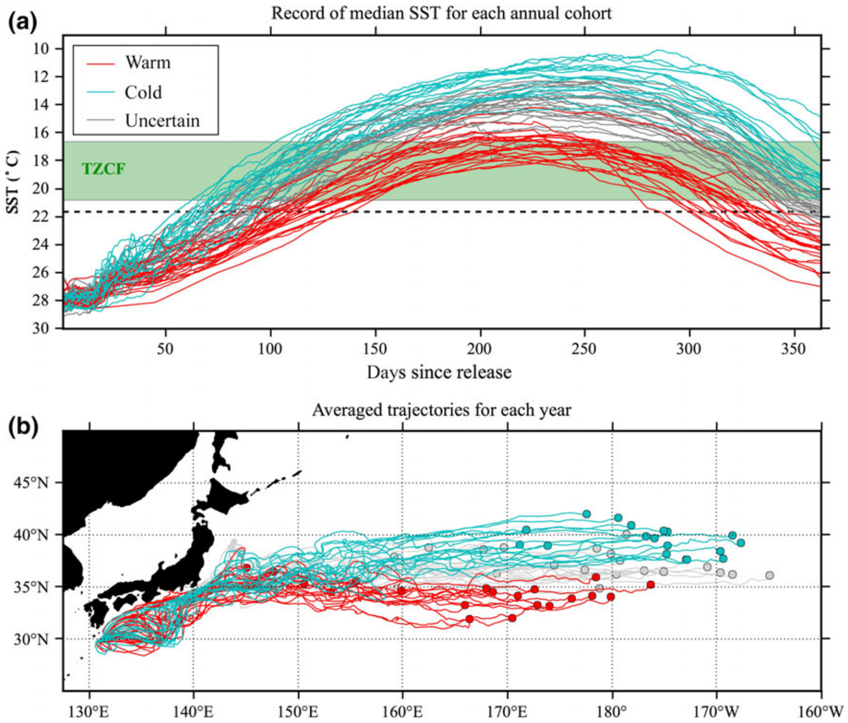

Fig. 2 (a) The 61 records of median SST for each annual cohort of neonates between 1950 and 2010. Red lines correspond to warm years (70% of neonates released that year are within a SST greater than 21.6 °C 1 year later), blue lines to cold years (70% of neonates released that year are within a SST lower than 21.6 °C 1 year later), and grey lines to uncertain years (all other years). The green shading shows the approximate location of the TZCF based on model's SST (see Fig. S1) so that warm years also correspond to years where the cohort spends most of its year in an unproductive area (south of the TZCF). The dashed line indicates the 21.6 °C isotherm. Notice that SST increases down the *y*-axis so that the *y*-axis is roughly equivalent to latitude (with going up the figure corresponding to going north). (b) The 61 records of the mean trajectory of neonates for each year. Color code is the same as in (a). The mean position 1 year after release is shown with a dot. Notice how trajectories from cold years (blue) are located more north and extend further east than trajectories from warm years (red). SST, sea surface temperature; TZCF, transition zone chlorophyll front.

1981–2009 period of mostly cold years. The approximate 5 year delay makes sense as it matches the time it takes for PDO anomalies to reach the KEC region (see Materials and methods). To confirm this conclusion, we calculate the difference in PDOi between warm and cold years for a delay varying from −2 years (the SST time series leads PDOi by 2 years) to +11 years (PDOi leads the SST time series by 11 years) (Fig. 3c). For each delay, we calculate the *P*-value of that difference using a Monte Carlo analysis (for the null hypothesis that there is no relationship between PDOi and the SST time series) as well as its Bayesian 95% CI. We find that the maximum difference in PDOi is obtained for a delay of 5 and 6 years, which matches our visual inspection; the difference is 0.63, which represents about 0.8 times the standard deviation of PDOi. It is found to be statistically significant at the 95% level for both delays. Finally, it is only for these two delays that the 95% CI of the difference is found to exclude zero. Hence, two different statistical tests confirm that, when the SST time series lags PDOi by about 5 years, there is a statistically significant difference in PDOi between warm and cold years.

The last objective of the study is to understand what causes this difference: ‘Is it because of PDO-induced changes in SST over the whole North Pacific or because the ocean currents transport the neonates to different latitudes depending on the phase of the PDO?’ The answer is both but with a larger difference caused by changes in the ocean circulation. To see this, we first recall that the PDO generates a basin-wide surface cooling in the western and central North Pacific during a positive PDO phase (see Methods); this cooling could indeed explain why neonates tend to encounter cold SST in the KEC region a few years after the start of a positive PDO phase. Yet, the cooling is only about 0.5–1 °C on average (e.g., Mantua & Hare, 2002) and that is insufficient to explain the several degree difference observed between cold and warm years of Fig. 2a – nor would that also explains the 5 year delay. Changes in the ocean circulation may then be influential. Figure 2b plots the average trajectory for each year with the color

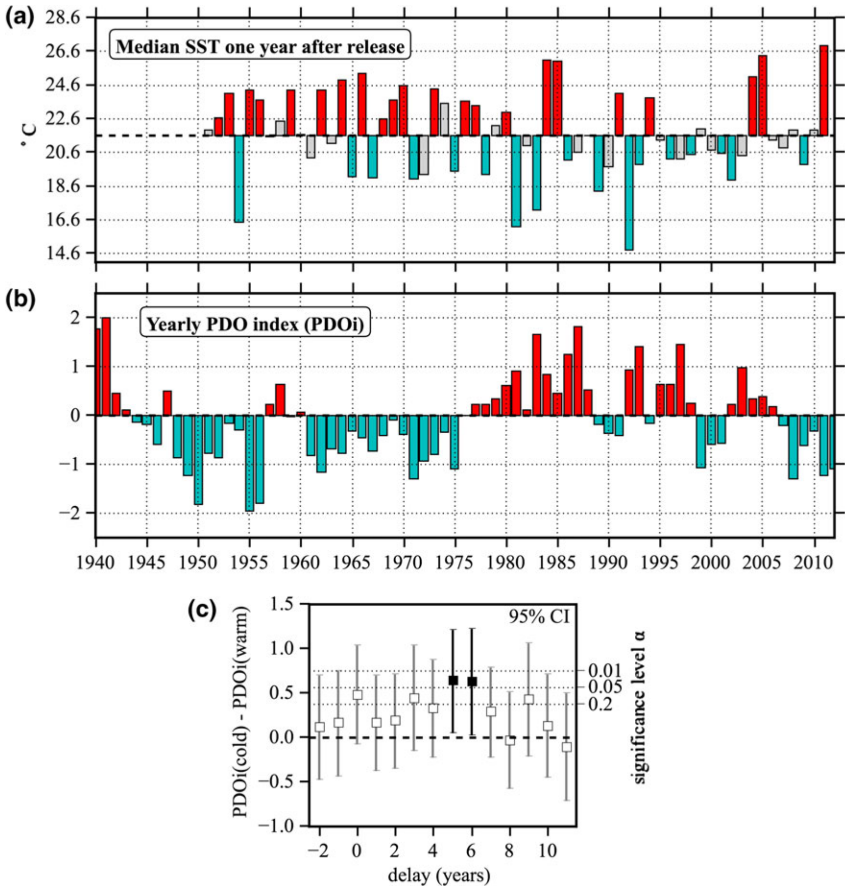

Fig. 3 (a) Median SST 1 year after release. Color code is the same as in Fig. 2. (b) Yearly averaged PDO index (PDOi). The plot for the PDO index starts 10 years before the SST time series in (a) in order to consider any delay between the PDO and the KEC region. (c) Difference between PDOi averaged over cold years and PDOi averaged over warm years. The difference is plotted against a delay in years between the PDOi of (b) and the SST time series of (a); if the delay is positive, the PDOi leads the SST time series. The results of two statistical tests are also shown in (c). First, the locations of three significance levels α (1%, 5% and 20%) are indicated; any difference above a certain α level indicates that this difference is statistically significant at that α level. The vertical bars indicate the 95% credible interval (CI) obtained from the BEST Bayesian test; if zero is not among the CI, we are 95% confident that the difference is real. Filled markers indicate differences that are statistically significant according to both tests. SST, sea surface temperature; KEC, Kuroshio Extension Current.

code, indicating whether the trajectory corresponds to a warm, cold, or uncertain year. Trajectories from cold years are located about 2–7° in latitude more north than the trajectories of warm years. This result itself can explain the SST difference between cold and warm years (Fig. 2a). The ocean currents are thus greatly exacerbating the effect of the PDO-induced SST changes on the neonates by transporting the neonates in more northern and southern latitudes during surface cooling and warming phases of the PDO, respectively.

The pattern of Fig. 2b, however, is intriguing because, during positive PDO (cold) years, the KEC is located more south and is weaker than during negative PDO (warm) years – apparently inconsistent with the obtained trajectories. By looking at the mean meridional ocean velocity averaged zonally over the KEC region (145°E–180°E), we find that it is on average directed southward, but is weaker during positive PDO years than during negative PDO years (Fig. S3, panel a). The difference is mostly associated with the difference in the geostrophic flow, not in the wind-driven Ekman flow: During positive PDO years, the KEC is weaker, and because the KEC is not perfectly zonal, that is associated with a weaker zonal pressure gradient resulting in a weaker meridional geostrophic flow. Here, navigational swimming may be significant. The mean meridional ocean flow also has a magnitude similar to that of the mean swimming velocity (1.8 km day^{-1} or about 2.1 cm s^{-1}), suggesting that it might be easier for neonates to reach the northernmost latitudes during positive PDO years than during negative PDO years. To test this idea, we calculate trajectories of neonates in the meridional direction using the annual cycle of the surface ocean current constructed either on negative PDO years (1950–1980) or on positive PDO years (1986–2010) (see Appendix S3 for details). For the average swimming speed used in the full calculation (about 1.8 km day^{-1}), we find that the difference in the meridional flow between positive and negative PDO years is enough to explain the different groupings in latitudes of the neonates' trajectories. Other process, such as mesoscale eddy activity, may need further investigations for explaining the magnitude of these differences. The KEC thus appears to act as a physical barrier preventing the neonates to reach north of the TZCF. We anticipate this barrier is worse during negative PDO years when the KEC is strong than in positive PDO years when the KEC is relatively weak.

Summary & discussion

Our analysis of the ocean circulation and its environment in the numerical model suggests that the PDO-related variations in loggerhead sea turtle population are not a priori due to a failure of neonates to reach the KC. It suggests, instead, that the population variations may be due to a change in the ocean circulation combined with a change in SST and productivity, all being modulated to some degree by the PDO. More specifically, the KEC appears as a physical barrier that naturally prevents neonates from reaching northern latitudes and remaining in the productive area within and north of the TZCF. During a positive PDO phase, that barrier is weak and the ocean circulation is more favorable for neonates to reach northern latitudes and stay within or north of the TZCF. Contrarily, during a negative PDO phase, the KEC barrier is strong and the ocean circulation appears to direct neonates south of the TZCF. This scenario of neonates swimming against the prevailing southward component of the current in order to reach productive area to the north would likely result in lower-than-normal recruitment during negative PDO years; this, then, would explain the documented relationship between the PDO and loggerhead nesting in Japan (Van Houtan & Halley, 2011).

Given the importance of the meridional ocean component of the KEC and the fact that it has a magnitude similar to the swimming velocity, we might wonder how sensitive our results are to the model swimming velocity. Figure S3 shows the distribution in latitudes of the neonates at the end of their first year for either positive or negative PDO years. This was performed for four different average swimming speeds (0, 1, 1.8, and 3.1 km day^{-1}) in the simplified case where the trajectories are calculated with the annual cycle of the surface ocean velocity (see Appendix S3). Unsurprisingly, faster swimming speeds enable neonates to reach more northern latitudes. Perhaps more interestingly, we find that the difference in latitude between the two PDO phases tends to increase with the swimming velocity and that, if the neonates do not swim, they arrive at the same southerly latitude (31°N), independent of the PDO phase. This suggests that the act of navigational swimming alone may be critical for the neonates to stay within or north of the TZCF habitat and that, in combination with differences in ocean circulation, is critical for triggering the differences in latitudes between the two PDO phases.

To confirm these suggestions, we have also performed the calculation of the trajectories using the full ocean velocity field but with the directed swimming component replaced by a random walk of similar magnitude. In this case, most of the neonates finish south of the TZCF at the end of the first year (Fig. S4) with the final median SST distribution being narrower than in the case with directed swimming and with no apparent bimodality (Fig. S2, panel b) – consistent with the results of Fig. S3. Using the same procedure to define cold and warm years (with the overall median SST 1 year after release now being 24.8 °C), we find that the difference in PDOi between cold and warm years is now statistically significant for the case of no delay between the PDOi and the time series of final median SST (Fig. S5). This suggests that the differences in SST between warm and cold years are mostly due to the basin-wide changes in SST that are synchronized with the PDO. Yet, these differences are smaller than in the case of directed swimming (Fig. S2) and, most importantly, most of the neonates fail to be within or north of the TZCF at the end of their first year. Given that tracking studies show juvenile and adult loggerheads maintain positions within or north of the TZCF (Polovina *et al.*, 2006), these results suggest that northerly navigational swimming appears to be necessary for the survival of the neonates. Moreover, navigational swimming coupled with PDO-driven changes in the ocean circulation may trigger a decadal variability in the recruitment of neonates. Future studies on the natal swimming behaviors of loggerheads in the North Pacific may help refine our results.

Another conclusion that may be drawn from our results is concerned with the actual location of the nesting grounds in Yakushima, which is the only location south of Japan where the KC path is relatively stable at the decadal time scale. This is reminiscent of the findings by Putman *et al.* (2010a) that the main loggerhead nesting grounds in Southeastern United States are nearest to the position of the Gulf Stream. We hence conclude that, in addition to the distance between the current and shore, the stability of the current position itself may factor in the selection and biogeography of sea turtle nesting grounds.

Beyond juvenile loggerhead sea turtles, the KEC is an important nursery habitat for many fishes including sardines, anchovies, albacore and skipjack tunas and a key forage habitat for many adult species including bluefin tuna, sperm whales, swordfish, and squids. It is the combination of the seasonal input of high productivity from the southward Ekman transport of nutrient-rich waters together with the persistent eddies and meanders of the KEC that concentrate planktonic organisms in sufficient densities to allow food webs going to high trophic levels to develop (Polovina *et al*., 2006). Pelagic animals respond to this seasonal physical and biological dynamics. For example, electronic tagging and satellite remotely sensed data showed that juvenile loggerhead sea turtles forage in the KEC during winter, spring, and fall when surface chlorophyll is high but in summer when the KEC become oligotrophic, the foraging loggerheads leave the KEC and travel north to more productive waters (Polovina *et al*., 2006). Our current results illustrate how this linkage between the biology and physics operates on a decadal scale with impacts for hatchling loggerhead survival, but there are most likely impacts to other species using the KEC. For example, species including sardine and anchovy (and perhaps even bluefin tuna) that spawn in coastal waters off Japan and then are advected to the KEC may experience similar decadal dynamics in productivity as our loggerhead hatchlings. Further, mobile species that forage specifically in the eddies and meanders of the KEC may find that the number and longevity of these mesoscale features vary decadally (Nishikawa *et al*., 2011; Okuyama *et al*., 2011; Chiba *et al*., 2013; Lin *et al*., 2014) with impacts to forage habitat, populations, and trophic cascades.

Looking into the future, the TZCF is expected to migrate north by about 5–10° over the next century due to global warming (Polovina *et al*., 2011, 2015). Future projections for the KEC suggest that its velocity may increase without any meridional migration (Sakamoto *et al*., 2005). The combined influence of these projections indicates that neonate loggerheads would need to travel significantly greater distances under stronger barriers to reach productive oceanic habitat. Such future conditions are considerably ominous for loggerhead juvenile recruitment as neonates in the future are far more likely to remain south of the TZCF. A study that repeats the present analysis with a numerical model that reproduces the future state of the ocean would be needed to quantify this probability.

Finally, we have not attempted in this study to quantify the effect of the differences in SST history and food availability on the actual recruitment rate. In a future study, we hope to combine the present results with a dynamic model of neonate metabolism. Such interdisciplinary analyses that link circulation models and ecosystem resources to organism physiological constraints will be critical in understanding the long-term population impacts of climate change to sea turtle populations and other marine species.

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Supporting Information

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

Figure S1. (a) October 1997–October 2008 mean surface chlorophyll profile averaged zonally over 155°E–160°W. The dashed vertical line shows the position of the TZCF defined as the 0.2 mg m^{-3} contour. (b) Probability distribution of the latitude of the TZCF with respect to model SST over 155°E–160°W; SST is defined as the temperature in the top layer (0–5 m depth) of the model. The vertical dashed lines show the 15%, 50% and 85% percentiles, which correspond to the 16.6, 18.7 and 20.8 °C isotherms, respectively. (c) Latitude of the TZCF zonally averaged over 155°E–160°W. The green band shows the range of TZCF's latitude estimated from the model SST using the 15% and 85% percentiles. The horizontal dashed line indicates the averaged mean position of the KEC.
Figure S2. Amplitude of the surface horizontal ocean velocity at the longitude of Yakushima (130.5°E, 30.3°N) from 1950 to 2010 in the OFES model.
Figure S3. Histogram of median SST 1 year after release: (a) case with directed swimming toward the northeast and (b) case where directed swimming is replaced by a random walk. Color code is the same as in Fig. 2. The dashed line shows the overall median in each case.
Figure S4. (a) Model meridional surface ocean velocity averaged between 145°E and the dateline and over 1950–1980 (negative PDO/warm years; red) or 1986–2010 (positive PDO/cold years; blue). The dashed line indicates the averaged position of KEC. (b) Trajectories in the meridional direction of a thousand neonates swimming on average at 1.8 km day^{-1} toward the northeast and embedded in the meridional current shown in (a). Color code as in (a). (c) The 2.5th, 50th and 97.5th percentiles of the latitude distribution of neonates on July 31 of the following year for four different averaged swimming speed (0, 1, 1.8 and 3.1 km day^{-1}). Color code as in (a).
Figure S5. Same as Fig. 2a except for the case where directed swimming is replaced by a random walk. The dashed line indicates the 24.8 °C isotherm.
Figure S6. Same as Fig. 3 but for the case where directed swimming is replaced by a random walk.
Appendix S1. Details of the Ocean General Circulation Model for the Earth Simulator (OFES).
Appendix S2. Details of the numerical methods used for computing trajectories and recording position and SST.
Appendix S3. On the calculation of the trajectories of neonates using the annual cycle of the surface ocean velocity constructed either on positive or negative PDO years.