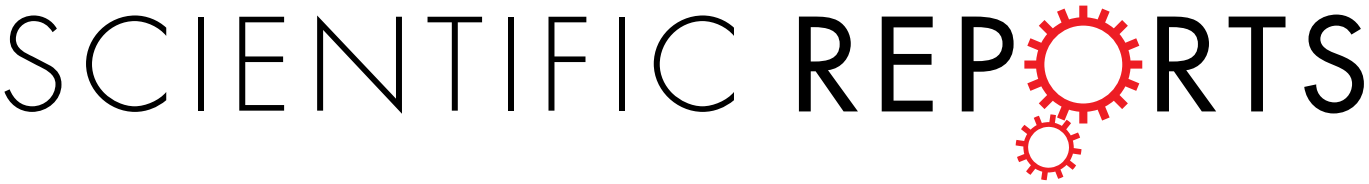

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Seasonal heterogeneity of ocean warming: a mortality sink for ectotherm colonizers

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Distribution shifts are a common adaptive response of marine ectotherms to climate change but the pace of redistribution depends on species-specific traits that may promote or hamper expansion to northern habitats. Here we show that recently, the loggerhead turtle (*Caretta caretta*) has begun to nest steadily beyond the northern edge of the species' range in the Mediterranean basin. This range expansion is associated with a significant warming of spring and summer sea surface temperature (SST) that offers a wider thermal window suitable for nesting. However, we found that post-hatchlings departing from this location experience low winter SST that may affect their survival and thus hamper the stabilization of the site by self-recruitment. The inspection of the Intergovernmental Panel on Climate Change model projections and observational data on SST trends shows that, despite the annual warming for this century, winter SST show little or no trends. Therefore, thermal constraints during the early developmental phase may limit the chance of population growth at this location also in the near future, despite increasingly favourable conditions at the nesting sites. Quantifying and understanding the interplay between dispersal and environmental changes at all life stages is critical for predicting ectotherm range expansion with climate warming.

Anthropogenic induced climate warming is projected to be a major challenge to Earth's biota in the 21st century[1]. Despite slower ocean warming over the last 50 years, the average speed of isotherm migrations at the ocean surface has been as fast as or even faster than the terrestrial counterpart[2]. Shifts in species' distributions have been observed in many different marine taxa and are considered as one of the key adaptive mechanisms to endure changes in ambient temperature[3,4]. In particular, marine ectotherms, being thermal range conformers, are predicted to expand poleward with ongoing warming as new locations that were previously too cold for survival will become suitable for colonists[5]. However, the pace of redistribution depends on the cumulative effects of climate warming on all ontogenetic life stages that may occupy different habitats, differ in behavioural traits and/or thermal sensitivity[6].

In this respect, the endangered loggerhead turtle is an interesting example[7]. This species possesses the widest nesting range among marine reptiles spanning from tropical to temperate latitudes. As all extant sea turtle species, the loggerhead turtle has survived major climate changes in the past by altering the equilibrium between colonization and local extinction, but how and whether it is responding to present day climate warming is still under debate[8–10]. Loggerhead turtles, as well as salmon and many other marine and terrestrial animals, exhibit philopatry, i.e. they return to their natal sites, a strategy that increases reproductive success but sets certain limits to genetic diversity and adaptability of populations[11,12]. Philopatric animals rely on imprinting mechanisms during the early life stage to recognize site specific environmental features of their birth area that guide them home. Poleward expansion of the nesting range must therefore occur through self-recruitment, which means that the occasional nesting of straying turtles at higher latitudes is associated with the production of female offspring that survive to nest decades later at the same location[12–14]. Given the influence of sand temperatures on embryonic development, it is not surprising that the majority of studies on climate induced range shifts have focused on the nesting beaches[10,15,16]. However, other factors might create a barrier towards the colonization of northern habitats.

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