

## NEWS AND VIEWS

### PERSPECTIVE

## Swimming in the deep end of the gene pool: global population structure of an oceanic giant

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### Abstract

Despite the impression held by some that few biological mysteries remain, even evocative species such as humpback whales (*Megaptera novaeangliae*), white sharks (*Carcharodon carcharias*) and green turtles (*Chelonia mydas*) have poorly documented movement patterns, reproductive strategies and population dynamics despite years of dedicated research. This is largely due to the difficulty of observing wide-ranging marine species over the majority of their life cycle. The advent of powerful tracking devices has certainly improved our understanding, but it is usually only with molecular tools that the nature of population structure becomes apparent. In this issue of *Molecular Ecology*, Castro and colleagues have provided the first global-scale assessment of population structure for the largest fish — whale sharks (*Rhincodon typus*). Whale sharks can reach lengths > 12 m and are a popular tourist attraction at places where they aggregate, yet for most of their life cycle, we know little indeed of where they go and how they interact with other populations. Previous tracking studies imply a high dispersal capacity, but only now have Castro and colleagues demonstrated high gene flow and haplotype diversity among the major ocean basins where they are found.

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Of the large migratory marine species, sharks represent perhaps some of the more difficult taxa to document in terms of their demography because they are rarely observed in the open ocean where they feed, breed and otherwise interact with conspecifics. Recent work at Ningaloo Reef in Western Australia where whale sharks aggregate yearly from March to June has relied almost exclusively on mark–recapture data from photo-identification to estimate population size, age structure and survival rates (Meekan *et al.* 2006; Bradshaw *et al.* 2007). Some individuals do return semiregularly to the same aggregation site over time, but where they go and

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what they do in-between these times is largely unknown. Information collected via powerful tracking devices (e.g., Hays *et al.* 2004; Bonfil *et al.* 2005) and by satellite telemetry on short-term (< 1 year) movements (Wilson *et al.* 2006) have provided some insights, but the work of Castro *et al.*'s (2007) allows us to infer something about these inter-aggregation movements on the generational scale. Using mitochondrial DNA control regions isolated from 70 individual whale sharks (Fig. 1) collected from five major geographical regions (Gulf of Mexico, Australasia, East Africa, Western and Eastern Pacific), 44 different haplotypes were identified. The corresponding haplotype (*h*) and nucleotide ( $\pi$ ) diversity were relatively high (0.974 and 0.011, respectively) compared with those reported for other sharks (Table 1). Although whale shark nucleotide diversity is approximately an order of magnitude larger than some critically endangered and commercially exploited species, it is lower than that reported for some large pelagic sharks (Table 1). The ecological implications of these measures of nucleotide diversity for sharks, however, are still rather perplexing because so few species have been investigated. With the appropriate caveat that sample sizes were small, there was little structure detected among sampling regions (except perhaps for a differentiation between the Indian/Pacific Ocean and the Gulf of Mexico populations). This is consistent with high maternal gene flow among regions driven by the movement of breeding females. Until Castro *et al.*'s study, nearly nothing was known of female breeding habits in terms of distribution — this latest piece in the puzzle certainly demonstrates that female whale sharks travel extensively between breeding and feeding areas and that populations have a high degree of connectivity only previously speculated (Bradshaw *et al.* 2007). Regardless, reconstructing the population structure from mitochondrial DNA only illuminates one side of the mating coin — the analysis of genomic DNA such as amplified fragment length polymorphisms (e.g. Stow *et al.* 2006) and microsatellites (e.g. Keeney *et al.* 2005) will provide much more insight into the breeding structure and population dynamics of this species.

Castro *et al.* take their data one step further and attempt to estimate current effective female population sizes by assuming various generational mutation rates. Although heuristically useful, the lack of good data describing whale shark generation length (possibly ranging from 15 to 37 years based on assumed age at first breeding of 13–25 years (Bradshaw *et al.* 2007), tertiary (breeding adult) sex ratios, and mutational time scales make any adherence to population size estimates unwise. Indeed, underestimating mutation rates can lead to overestimates of effective population size. Additionally, Castro *et al.* correctly warn that declining populations may in fact retain historical genetic diversity especially if reductions in population size have happened recently and within only a few generations (Bradshaw *et al.* 2007). Nonetheless, the approach at least highlights the remaining big questions that



**Fig. 1** Taking a tissue sample from a whale shark at Ningaloo Reef, Western Australia using a modified sling-spear. Photo credit: C. Speed.

**Table 1** Measured nucleotide diversity ( $\pi$ ) derived from mitochondrial DNA control regions for five shark species; 'status' refers to the species' World Conservation Union (IUCN 2006) Red List classification (in italics) and whether it is exploited by humans commercially, as by-catch or both

Species		$\pi$	Status	Reference
Whale shark	<i>Rhincodon typus</i>	0.011	<i>Vulnerable</i> ; exploited	Castro <i>et al.</i> 2007
Grey nurse shark	<i>Carcharias taurus</i>	0.003	<i>Critically Endangered</i> ; by-catch	Stow <i>et al.</i> (2006)
Blacktip shark	<i>Carcharhinus limbatus</i>	0.002–0.004	<i>Lower Risk</i> ; commercially exploited	Keeney <i>et al.</i> (2005); Keeney & Heist 2006
Scalloped hammerhead	<i>Sphyrna lewini</i>	0.013	<i>Lower Risk</i> ; commercially exploited	Duncan <i>et al.</i> 2006
White shark	<i>Carcharodon carcharias</i>	0.020	<i>Vulnerable</i> ; by-catch	Pardini <i>et al.</i> 2001; Stow <i>et al.</i> (2006)

still need answering for the demography of whale sharks and many other large pelagic shark species: what are: (i) ages at first reproduction, (ii) breeding frequencies, (iii) litter size variation, (iv) tertiary sex ratios, and (v) male-mediated gene flow patterns (Keeney *et al.* 2005; Bradshaw *et al.* 2007)?

The worldwide decline in shark species in recent times (Baum *et al.* 2003; Myers & Worm 2003; Myers *et al.* 2007) underscores the increasing importance of understanding the life histories and behaviour of this taxon. It has been proclaimed many times that despite its large size, the whale shark is one of the least-understood shark species. With Castro *et al.*'s latest contribution and other recent work, I believe it is time we abandon this declaration. The challenge now is to isolate the most elusive demographic parameters to be able to estimate the extinction risk of this and other large shark species. Even though whale sharks appear to have a high dispersal capacity that may offset the risk of local extirpation, their large size and apparently slow reproductive rates suggest a particular vulnerability to overexploitation and rapid environmental change. Further, a high dispersal capacity may be a double-edged sword — over-fishing in one region may affect whale sharks over much broader areas even when some protected areas exist. With such enormous regions over which

large migratory marine organisms realize their life cycles, it is essential that we embrace an ocean-wide approach to understanding and managing these ecologically important species.

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## PERSPECTIVE

### Ever deeper phylogeographies: trees retain the genetic imprint of Tertiary plate tectonics

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#### Abstract

Changes in species distributions after the last glacial maximum (c. 18 000 years BP) are beginning to be understood, but information diminishes quickly as one moves further back in time. In this issue of *Molecular Ecology*, Magri *et al.* (2007) present the fascinating case of a Mediterranean tree species whose populations preserve the genetic imprints of plate tectonic events that took place between 25 million years and 15 million years ago. The study provides a unique insight into the pace of evolution of trees, which, despite interspecific gene flow, can retain a cohesive species identity over timescales long enough to allow the diversification of entire plant and animal genera.

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Phylogeographical studies use molecular markers to trace the historical expansions of species that have led to their current distribution range. The vast majority of these surveys have focused on population dynamics that took place during the Quaternary (spanning the past two million years) and especially after the last glacial maximum (18 000 years BP). However, examples are now accumulating of species that have retained the genetic imprints of much more ancient dynamics (e.g. Dick *et al.* 2003; Petit *et al.* 2005; Grivet *et al.* 2006). A tree species studied by Magri and colleagues in this issue beats all records of stability and population genetic stasis.

The authors investigated the phylogeography of cork oak (*Quercus suber* L., Fig. 1), an emblematic Mediterranean tree exploited since the Antiquity for its bark. They found that its range-wide population structure is consistent with the break-up and separation of several microplates that took place in the Oligocene and Miocene, between 25 million years and 15 million years ago. The current distribution of cork oak spans both sides of the western Mediterranean Basin, including all the major islands. Magri and coworkers collected more than 100 populations throughout the species range to investigate geographical patterns of chloroplast DNA (cpDNA) polymorphism. Using an extensive set of 14 cpDNA microsatellites, they detected just five haplotypes, but with extremely clear-cut distributions. Two haplotypes characterize all stands from Morocco, the Iberian Peninsula, the Balearic Islands and southwestern France, while another two haplotypes occupy the Italian Peninsula. The remaining haplotype shows a striking distribution: it occurs in a narrow belt ranging from Tunisia and Algeria via Sardinia and Corsica to Southeast France. The geographical overlap between the three groups of haplotypes is minimal and population fixation is almost complete ( $G_{ST} = 0.97$ ). Curiously, the authors found that the two Italian haplotypes and one of the two Iberian-Moroccan haplotypes originate from *Quercus cerris* L. and *Quercus ilex* L. through introgression.

These results by themselves were not completely novel. Lumaret *et al.* (2005) had already described very similar patterns of geographical variation, including traces of introgression, based on restriction fragment length polymorphism (RFLP) variation over the whole chloroplast DNA molecule. The innovation of Magri *et al.* (2007) is their new interpretation of the observed haplotype distributions based on the geological history of the region. Rejecting the hypothesis of repeated long-distance colonization events, the authors show that the genetic patterns reflect the geological history of the western Mediterranean Basin. A number of tectonic microplates connected in the early Tertiary broke up in the Oligocene and drifted apart, eventually integrating the Algerian, Spanish, French, and Italian coasts or forming the Balearic Islands, Sardinia and Corsica. Magri and coworkers show that the current geographical distribution of haplotypes can largely be explained by these early land bridges, along with subsequent range expansion across Iberia and Morocco and along the Italian Peninsula. In addition, cork oak populations have introgressed cpDNA haplotypes from two other oak species (*Q. cerris* in Italy and *Q. ilex* in parts of Iberia and Morocco), probably at an early stage of this expansion. Interestingly, cork oak is not the only western Mediterranean tree species that has