

Philopatry and migration of Pacific white sharks

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Advances in electronic tagging and genetic research are making it possible to discern population structure for pelagic marine predators once thought to be panmictic. However, reconciling migration patterns and gene flow to define the resolution of discrete population management units remains a major challenge, and a vital conservation priority for threatened species such as oceanic sharks. Many such species have been flagged for international protection, yet effective population assessments and management actions are hindered by lack of knowledge about the geographical extent and size of distinct populations. Combining satellite tagging, passive acoustic monitoring and genetics, we reveal how eastern Pacific white sharks (*Carcharodon carcharias*) adhere to a highly predictable migratory cycle. Individuals persistently return to the same network of coastal hotspots following distant oceanic migrations and comprise a population genetically distinct from previously identified phylogenetic clades. We hypothesize that this strong homing behaviour has maintained the separation of a northeastern Pacific population following a historical introduction from Australia/New Zealand migrants during the Late Pleistocene. Concordance between contemporary movement and genetic divergence based on mitochondrial DNA demonstrates a demographically independent management unit not previously recognized. This population's fidelity to discrete and predictable locations offers clear population assessment, monitoring and management options.

Keywords: site fidelity; animal movement; habitat utilization; migration; gene flow; white shark

1. INTRODUCTION

The movement behaviour of individual organisms can have profound implications for the ecology and dynamics of populations (Dingle & Holyoak 2001). The open ocean is an environment where movement behaviour is particularly relevant because there are few apparent barriers obstructing active swimming species. Among large oceanic sharks with long-distance movement capacity, broad dispersal and mixing can swamp population structure within or even between ocean basins (Hoelzel *et al.* 2006; Castro *et al.* 2007). However, many animals restrict their movement to areas much smaller than one might expect from observed levels of mobility. Site fidelity, the return to, and reuse of, a previously occupied location (Switzer 1993), has been noted in a number of oceanic and migratory sharks including white sharks (*Carcharodon carcharias*) (Klimley & Nelson 1984; Domeier & Nasby-Lucas 2007; Weng *et al.* 2008) and is likely to have important impacts on the spatial dynamics of their populations. The causes and consequences of individual movement behaviour in the open ocean remain poorly understood.

Depletion of top oceanic predators is a pressing global concern, particularly among sharks because they are slow reproducers (Baum *et al.* 2003; Myers & Worm 2003; Dulvy *et al.* 2008). White sharks have been listed for international protection under the Convention on International Trade in Endangered Species (CITES) and the World Conservation Union (IUCN, Category VU A1cd+2cd) (Dulvy *et al.* 2008). Despite these precautionary listings, trade in white shark products, primarily fins, persists (Shivji *et al.* 2005). Information on population structure and distribution of oceanic sharks is critical for implementing effective management efforts and the absence of such data impedes protection at all scales (Palsboll *et al.* 2007). Combining electronic tagging and genetic technologies to elucidate the movement and population structure of high-seas predators can accelerate our capacity to protect these important components of oceanic ecosystems.

White sharks have a circumglobal distribution with primary concentrations in South Africa (SA) (Pardini *et al.* 2001; Bonfil *et al.* 2005), Australia/New Zealand (ANZ) (Pardini *et al.* 2001; Bruce *et al.* 2006) and the northeastern Pacific (NEP) (Boustany *et al.* 2002; Weng *et al.* 2007; Domeier & Nasby-Lucas 2008). Precipitous declines in *C. carcharias* observations have been reported in the north Atlantic (Baum *et al.* 2003) and in the

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Mediterranean (Compagno 1984; Cavanagh & Gibson 2007). To date, two white shark clades have been identified globally; mitochondrial DNA (mtDNA) analyses indicate SA and ANZ form genetically distinct populations (Pardini *et al.* 2001). Tagging and genetics studies have led researchers to hypothesize that some spatial overlap occurs among these distant populations via *trans*-oceanic migrations by both sexes (Pardini *et al.* 2001; Bonfil *et al.* 2005). In the NEP, data from satellite pop-up archival transmitting (PAT) tags have demonstrated that white sharks tagged in California (Boustany *et al.* 2002; Weng *et al.* 2007) and at Guadalupe Island off northern Mexico (Domeier & Nasby-Lucas 2008) share common oceanic habitats. However, the origin and relationship of NEP white sharks relative to SA and ANZ populations are unknown.

To determine the spatial dynamics and demographic scope of white sharks in the NEP and their relationship to Southern Hemisphere populations, we used a combination of satellite tagging, passive acoustic monitoring and mtDNA analysis. Our goal was to genetically characterize individuals for whom explicit broad scale (PAT tags) and finer coastal movements (acoustic tags) were tracked for periods of up to 2 years. This approach enabled us to investigate contemporary movement patterns of an oceanic apex predator in the context of evolutionary scale gene flow in order to (i) evaluate the causes for onshore/offshore seasonal migration patterns, (ii) explore potential consequences of individual movement behaviour at the population level, and (iii) determine the implications of site fidelity patterns for future population assessment and management.

2. MATERIAL AND METHODS

We deployed 97 satellite PAT tags (PAT 2.0, 3.0, 4.0 and Mk10-PAT; Wildlife Computers, Redmond, Washington, USA) on white sharks. Data from 68 satellite tags (of 97 deployments) were retrieved (electronic supplementary material, table S1) including 14 recovered satellite tags with archival records, and 54 satellite-transmitted datasets. Satellite deployments rendered 6850 light-based longitude and 6016 latitude estimates based on light and sea surface temperature (SST) (Teo *et al.* 2004) as well as 68 global positioning system deployment locations, and 60 Argos endpoint positions from post-release satellite tag transmissions. Additionally, we deployed 78 individually coded acoustic transmitter tags (V16-4H; Vemco, Halifax, Nova Scotia) on white sharks in 2006 ($n = 20$), 2007 ($n = 31$) and 2008 ($n = 27$). The tags were placed on free-swimming white sharks using a 59 mm titanium dart with an 18–20 cm monofilament leader and inserted into the dorsal musculature with a tagging pole (Boustany *et al.* 2002; Weng *et al.* 2007). The 136 kg test monofilament was protected by shrink-wrap (after 2007 hollow braided Dacron was added under the shrink-wrap to protect from abrasion). Total length was estimated as each shark swam alongside a research vessel of known length (4.5–6 m). Video and photography were used to help determine sex and individual identification.

Latitude and longitude estimates from satellite tags were determined using previously described methods (Teo *et al.* 2004; Weng *et al.* 2007) with updated software versions (Wildlife Computers, WC-GPE v.1.02; sstlats v.0.9.5). Diving behaviour was quantified from high resolution

archival datasets from recovered PAT tags. For each time step (30 s) the change in depth (m) was used to determine rate of vertical movement (m s^{-1}). To determine the horizontal area used by males in the Café during high intensity diving, the area of an ellipse described by the longitudinal and latitudinal inter-quartile range of all male geolocations occurring during the identified period was used.

White shark DNA was extracted using the DNeasy® Tissue Kit (Qiagen). Mitochondrial control region sequences were obtained from the polymerase chain reaction using primers (ProL2 and PHeCacaH2) and conditions described in Pardini *et al.* (2001). Control region fragments were sequenced by Genaway Research, LLC (Hayward, CA, USA) and aligned using Clustal W option in Bioedit (Hall 1999). Modeltest v.3.7 (Posada & Crandall 1998) determined the best-fit evolutionary model (AIC criterion) to be TVM + I + G with a gamma shape parameter equal to 0.9066 and proportion of invariable sites equal to 0.7604. This information was used to construct likelihood trees in PAUP v.4.0.2 (Swofford n.d.) from which a heuristic search with 100 bootstrap replicates produced a consensus 50 per cent majority ruled tree. A Bayesian tree was drawn using MrBayes v.3.1.2 (Huelsenbeck & Ronquist 2001) (starting parameters: GTR + I + G model, lset = 6, nchains = 4, Revmatpr = Dirichlet (1,1,1,1), 5 million generations). Burn-in was arbitrarily set at 10 000. Estimates of alpha (0.06873) and proportion of invariable sites (0.8118) converged to 1. F_{ST} statistics were estimated using Arlequin v.3.11 from genetic distances derived from the TVM + I + G model (as determined by Modeltest v.3.7) and calculated in TreeFinder (Jobb 2008).

3. RESULTS AND DISCUSSION

(a) Migratory cycle and evidence of site fidelity

A total of 179 *C. carcharias* were tagged from 2000 to 2008 using satellite, acoustic and/or mtDNA tags (electronic supplementary material, tables S1 and S2; $n = 47$ individuals both sequenced and electronically tagged). Acoustic and satellite tagging data collected during tracking periods of up to 766 days (mean = 199 days \pm 97 s.d.) revealed site fidelity and repeated homing in a highly structured seasonal migratory cycle with fixed destinations, schedule and routes. There were 68 successfully transmitting or recovered satellite tags rendering 6978 longitude and 6144 latitude estimates (see §2). Additionally, 68 338 acoustic transmissions from 78 tagged sharks have been recorded to date on acoustic receivers (Vemco, VR-3; see electronic supplementary material, methods S1) at four central California locations including Año Nuevo Island (ANI), South Farallon Island (SEFI), Point Reyes (REY) and Tomales Point (TOM). Further detections have occurred on receivers placed along the California coast between 33.5 and 41.5° N as well near the islands of Oahu and Hawaii. The distribution of geolocation estimates and acoustic detection locations ($n = 74\,354$) across the northeastern and central Pacific demonstrate that white sharks were consistently focused on three core areas: (i) the North America shelf waters, (ii) the slope and offshore waters of the Hawaiian archipelago, and (iii) the offshore white shark 'Café' (figure 1; Weng *et al.* 2007).

Each winter, white sharks left coastal aggregation sites off central California and migrated 2000–5000 km offshore to sub-tropical and tropical pelagic habitats

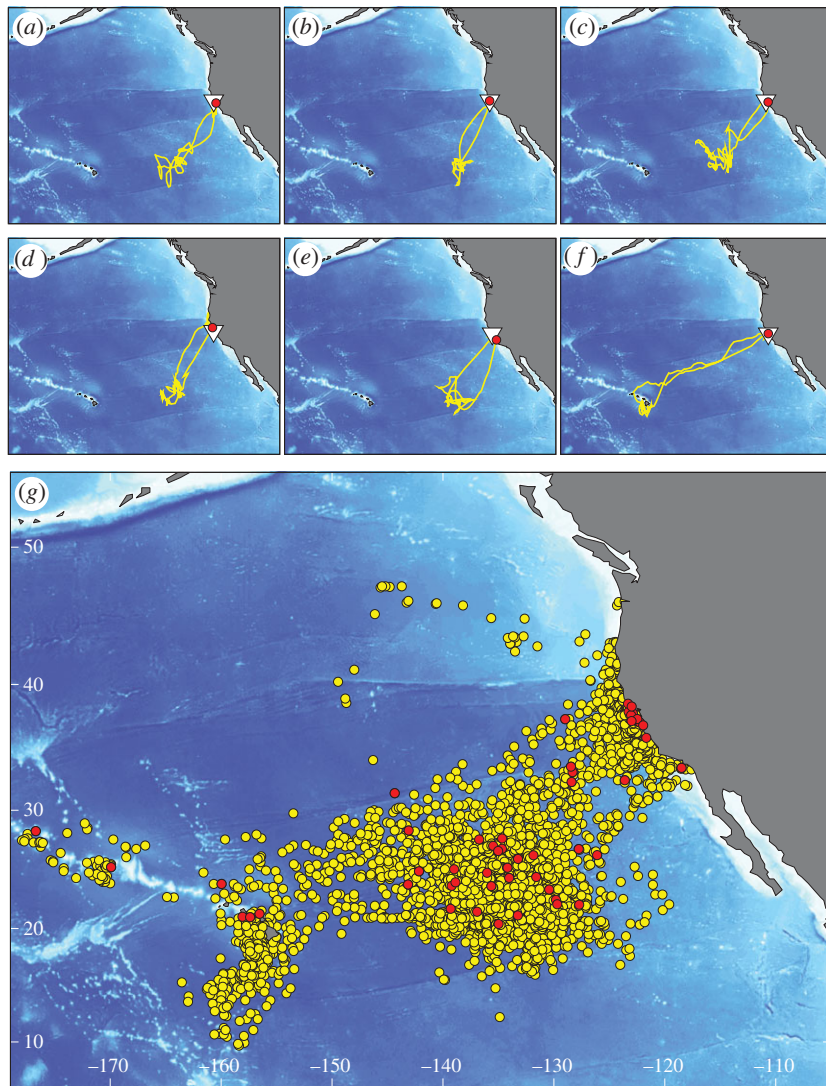


Figure 1. Site fidelity and homing of white sharks (*Carcharodon carcharias*) tagged along the central California coast during 2000–2007 revealed by PAT records. (a–f) Site fidelity demonstrated by six individual tracks (yellow lines; based on five-point moving average of geolocations). Triangles indicate tag deployment locations and red circles indicate satellite tag pop-up endpoints (Argos transmissions) for white sharks returning back to central California shelf waters after offshore migrations. (g) Site fidelity of all satellite tagged white sharks ($n = 68$) to three core areas in the NEP included the North American continental shelf waters, the waters surrounding the Hawaiian Island Archipelago and the white shark ‘Café’. Yellow circles represent position estimates from light- and SST-based geolocations (Teo *et al.* 2004), and red circles indicate satellite tag endpoint positions (Argos transmissions), respectively.

(figure 1). Their return in late summer to the original tagging location was evident from long-term tag deployments ($n = 23$ acoustic and $n = 11$ PAT deployments; see electronic supplementary material, figure S1) describing a recurring ‘to and fro’ migratory pattern (Dingle 1996) (figure 2). Acoustic tags revealed a regular presence/absence pattern in North American coastal habitats with presence peaking during the months of August through February followed by near-complete absence during spring between mid-April and mid-July (figure 2a). This precise and repeatable site fidelity over the scale of years, coupled with long-term photo-identification studies (Klimley & Anderson 1996; Anderson & Pyle 2003; Domeier & Nasby-Lucas 2007), suggests that North American coastal foraging hotspots are composed of a limited number of seasonally returning individuals.

Understanding the causes and consequences of movement at the individual level can provide important insight as to how the behaviour of individuals influences the spatial

dynamics of populations. Migration is an energetically costly endeavour. Long-distance ‘to and fro’ seasonal migrations typically connect foraging and reproductive grounds (Dingle 1996). For white sharks, both mating and oceanic foraging are hypothesized functions explaining potential trade-offs for undertaking such extensive migrations to offshore areas (time offshore = $234 \text{ days} \pm 45.2 \text{ s.d.}$ measured from $n = 10$ returning satellite tags, and $231.1 \text{ days} \pm 48 \text{ s.d.}$ from $n = 19$ acoustic records) away from year-round coastal pinniped prey concentrations (Le Beouf & Laws 1994; Long *et al.* 1996). Additionally, white shark movement to warmer oceanic waters coincides with the peak period of cold upwelling in the California Current (Pennington & Chavez 2000) suggesting a potential environmental influence on the migration pattern.

(b) *The white shark Café*

Both foraging and mating are cogent explanations for spatial utilization patterns in the Café. The name ‘Café’

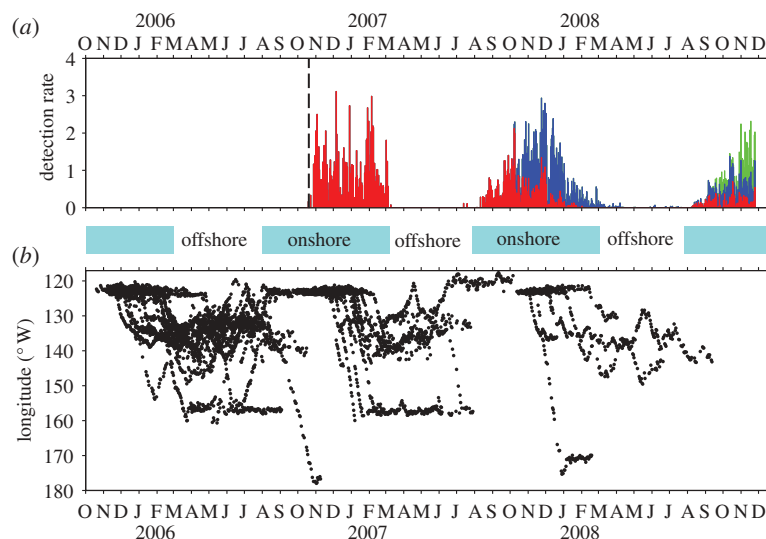


Figure 2. White shark migratory cycle and site fidelity revealed by a combination of acoustic and satellite tagging. (a) Detections of tagged white sharks by an array of acoustic receivers (see figure 5b for map) along the central California coast show seasonal presence and absence pulses. Twenty individuals carried acoustic tags deployed in 2006 (red bars), 31 in 2007 (blue bars) and 27 in 2008 (green bars), respectively. The number of detections per day was normalized by the number of sharks tagged and the number of active receivers. Dashed line indicates when acoustic tagging began. (b) Longitude geolocation estimates from PAT tag records between October 2005 and June 2008 show a corresponding seasonal onshore–offshore migration pattern. Shading indicates peak onshore periods.

implies a location where either of these activities might be initiated. The Café has also previously been referred to as an ‘offshore focal area’ (Weng *et al.* 2007), and a ‘shared offshore foraging area’ (Domeier & Nasby-Lucas 2008). The Café lies within the eastern boundary of the North Pacific Gyre and was visited by 47 PAT-tagged white sharks (21 males, 14 females and 12 unsexed individuals) (figure 3). Rapid oscillatory diving, revealed by four archival records from recovered tags ($n = 4$ males), is a characteristic behaviour of white sharks visiting the Café (Weng *et al.* 2007; Domeier & Nasby-Lucas 2008). But while white sharks began arriving around the Café as early as December this signature diving behaviour, resulting in an order of magnitude increase in vertical displacement rate (from a mean of $0.02 \text{ m s}^{-1} \pm 0.022 \text{ s.d.}$ to $0.21 \pm 0.074 \text{ m s}^{-1}$, respectively; t -test, $p = 0.003$), began only at the peak offshore period between the mid-April and mid-July (figure 4). During this ‘high energy’ diving period, male white sharks converged within an approximately 250 km radius centred around $23.37 \pm 2.88^\circ \text{ N s.d.}$ and $132.71 \pm 2.16^\circ \text{ W s.d.}$ ($n = 16$ males totalling 323 latitude and 363 longitude estimates, respectively, during 5 separate years). The described area was surprisingly small (inter-quartile elliptical area smaller than Panama) considering geolocation error (Teo *et al.* 2004), potential variation from year to year and the regionally homogeneous pelagic environment. During the same time period, 13 females (out of 15 still carrying satellite tags) visited the Café area, but in contrast with males, were dispersed over a broader spatial domain, moving in and out of where males converged, rather than remaining there (figures 3 and 4). In many organisms sexual segregation may result from sexual dimorphism in body size (Wearmouth & Sims 2008). Interestingly, there was no significant size difference among the tagged male and female white sharks visiting the Café ($p = 0.984$, Mann-Whitney rank sum test; $n = 15$ males, median = 453.5 cm; $n = 16$ females,

median = 457.0 cm). This suggests that differential habitat use by gender is likely to be related to some aspect of reproduction rather than morphological dissimilarity that could, for example, result in differences in the swimming capabilities of the sexes (Wearmouth & Sims 2008).

Some foraging almost certainly must occur in the Café region since fasting seems unlikely over such an extended period. Oscillatory diving could reflect searching behaviour for prey. Vertical movement rates were greatest from about 100 to 200 m depth, relatively shallower than the average maximum depth of approximately 400 m (figure 4). Shoaling of the oxygen minimum layer in the tropical eastern Pacific is thought to compress the vertical habitat of predators such as billfish and tunas (Prince & Goodyear 2006). The Café occurs near this shoaling hypoxic area; a boundary where these potential prey species could become concentrated and targeted by white sharks. If foraging is a primary function of the Café then the observed sexual segregation may reflect differential nutritional demands or energetic budgets related to gestation (Wearmouth & Sims 2008).

Alternatively, the Café may function primarily as a mating area. Mating is likely to occur where males and females overlap consistently. Observed overlap was minimal near Hawaii but occurred at coastal sites and at the Café (figures 3 and 4). No direct or indirect evidence of copulation at North American coastal sites has ever been reported, despite decades of observation (Anderson & Pyle 2003; Domeier & Nasby-Lucas 2008). Reported incidental captures of neonates in the Southern California Bight peak between July and October (mean recorded TL during those months was 1.41, 1.65, 1.69 and 1.73 m respectively) (Klimley 1985) suggesting that parturition occurs there during spring and summer (Francis 1996). If *C. carcharias* gestation period is greater than 12 months and likely around 18 months as has been proposed (Francis 1996; Mollet *et al.* 2000), copulation would have to occur sometime between March and August. This coincides

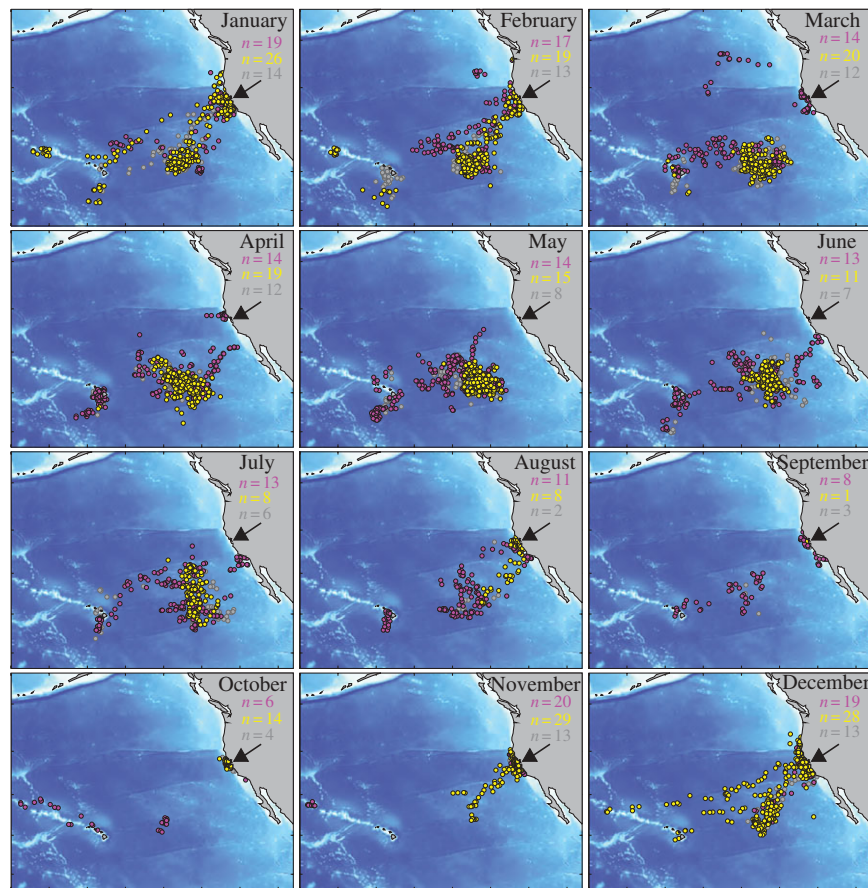


Figure 3. Seasonal migratory pattern and distribution of male ($n = 32$), female ($n = 23$) and unsexed ($n = 14$) white sharks tagged in central California (arrow) with PAT tags. Yellow (male), magenta (female) and grey (unsexed) circles represent position estimates from light- and SST-based geolocation. The peak offshore period was between April and July and the peak onshore period between September and November, respectively. Male positions are plotted over female, then unsexed positions, respectively, showing a higher aggregation of males in the Café between April and July, while females moved in and out of the same area.

with the peak period of activity in the Café, when virtually all males still bearing PAT tags occurred there (figures 3 and 4). If mating occurs in the Café, periodic segregation could reflect refuging by females from costly mating activities (Wearmouth & Sims 2008). Additionally, some tagged females remained offshore (four out of eight) or in the Southern California Bight nursery habitat (one out of eight) through August and as late as November (figures 3 and 4) consistent with previous observations that females may only return to coastal aggregation sites every second year owing to an extended reproductive cycle (Anderson & Pyle 2003; Domeier & Nasby-Lucas 2007).

(c) The Hawaiian archipelago

Hawaii is likely to be an important foraging area for white sharks. Extensive use of waters surrounding the Hawaiian island archipelago in winter and spring was evident from 13 satellite tag records (22% of tags with offshore tracks) and five acoustic tags (10% of 2006 and 2007 deployments) detected opportunistically by receivers stationed near the islands of Oahu and Hawaii (together comprising six males, six females and six unsexed individuals) (figure 1). The most precise geopositions and acoustic records from Hawaii included Argos endpoint transmissions ($n = 8$) with location errors of 150 m s.d. (Teo *et al.* 2004) and acoustic tags detected at fixed locations ($n = 5$). These occurred in slope and near shore waters

along the entire 3000 km archipelago from the big island of Hawaii extending through the Papahānaumokuākea Marine National Monument to Laysan Island and Midway Atoll (electronic supplementary material, figure S2). While this distribution includes areas with colonies of endangered monk seals (Baker *et al.* 2007), detailed dive records from four recovered satellite tags (three females and one unsexed; three separate years) indicated that the dominant behaviour, when not transiting (Weng *et al.* 2007), was a precise diel vertical migration, between the surface and 600 m, consistent with foraging within the deep scattering layer community (Shepard *et al.* 2006) (electronic supplementary material, figure S3).

(d) Fine-scale coastal spatial dynamics

White shark coastal habitat utilization comprises a network of high residence 'primary' and more transitory 'hub' focal points with direct travel between them. Upon their return to the coast, acoustically tagged white sharks were routinely detected by receivers at a number of central California locations. Four of these listening stations accounted for a disproportionately high number of detections during the coastal aggregation phase, revealing a preference for a limited number of key hotspots (figure 5). Frequent and persistent detections (mean = 17.93 detections per individual per day, maximum = 207, s.d. = 19.373) within the limited acoustic range (approx. 250 m; see electronic

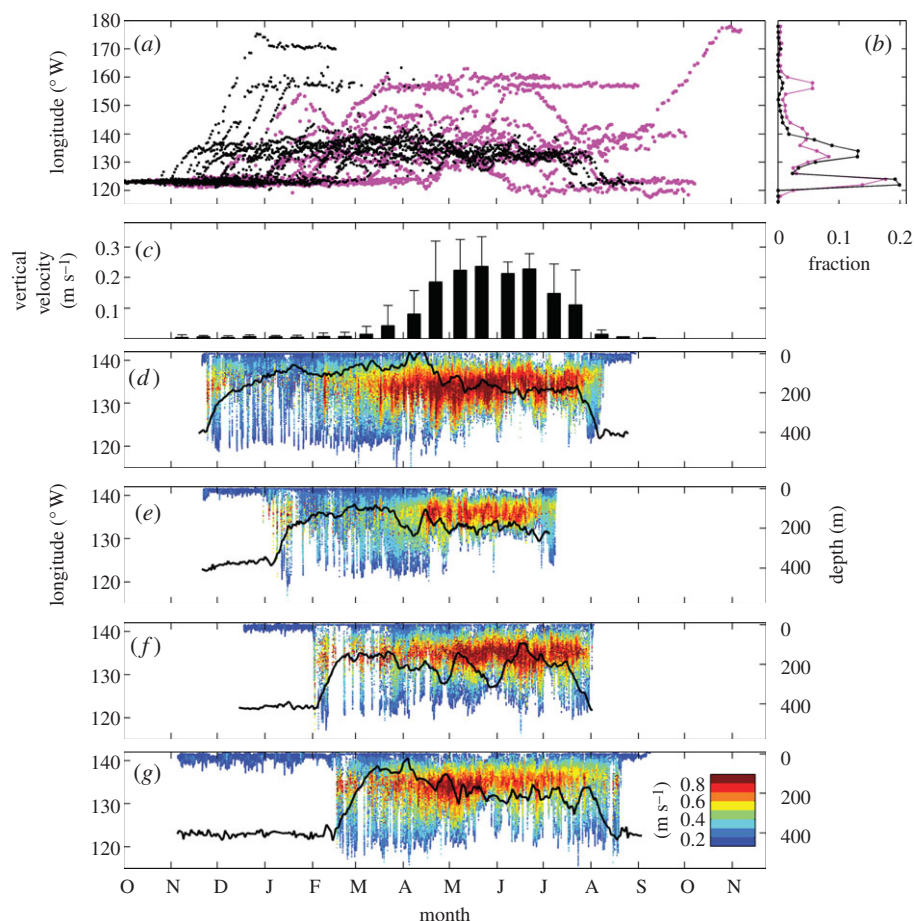


Figure 4. Male and female *C. carcharias* movement and habitat use at the white shark 'Café'. (a) Longitude geolocations of 32 males (black) and 23 females (magenta) tagged with satellite tags during 7 separate years plotted over one seasonal cycle revealed the consistent converging of males near 133° W (Café) between April and July. (b) The frequency of geolocations over longitude demonstrates that while offshore, males (black) are more focused in the Café while females (magenta) are more dispersed between the Café and Hawaii. (c) Rapid oscillatory diving behaviour in the Café identified (from archival recovery tags) by an order of magnitude increase in median vertical displacement rate occurring between 15 April and 15 July ($n = 4$ sharks; $p = 0.003$; t -test). Bars indicate the average median displacement rate among individuals ($n = 4$; \pm s.d.). (d–g) Four individual archival records (all male; PAT #s 45, 49, 54 and 22; electronic supplementary material, table S1) recovered from white sharks visiting the Café showing longitude (left axis), depth (right axis) and vertical displacement rate (colour scale) over time. Oscillatory diving occurs primarily between 15 April and 15 July, during the same period when males are most aggregated, despite earlier arrival.

supplementary material, methods S1) of the stationary receivers suggested near-constant patrolling (Goldman & Anderson 1999; Klimley *et al.* 2001) at these key locations over residence periods extending from days to months (maximum = 107 days and minimum = 1; figure 5 and electronic supplementary material, figure S4). These residency periods were punctuated at times by relatively rapid transits to the other monitored sites, away from the original tagging location (mean transit rate = $38.16 \text{ km d}^{-1} \pm 24.97 \text{ s.d.}$), where sharks once again remained resident and frequently detected by receivers. Residence was longest at SEFI (mean = $35 \pm 27.8 \text{ s.d.}$; maximum = 107 days) and ANI (mean = $23 \pm 22.5 \text{ s.d.}$; maximum = 101 days), the two primary island elephant seal rookeries in central California (Le Beouf & Laws 1994). Relatively little movement was detected directly between SEFI and ANI (five of 160 between-site transits), whereas transits were frequent to and from sites with briefer residence (figure 5b,c), for example there were 92 transits between REY (mean = 4 ± 2.7 , maximum = 14 days residence) and TOM (mean = 9 ± 11.9 , maximum = 91 days residence). The periods when tagged sharks were not detected within this network

were remarkably few and short in duration except when satellite tag results showed sharks migrated to offshore waters (figure 5a and electronic supplementary material, figure S4). The brief lapses during the coastal phase probably represented visits to additional focal sites outside of the instrumented network. One location that was recently noted includes the entrance to the San Francisco Bay. Five individuals were briefly detected by acoustic receivers (installed to detect salmon smolt) spanning the entrance just inside the Bay (electronic supplementary material, figure S5).

(e) Population divergence

The electronic tracking data presented here overlap remarkably with a second population of NEP white sharks tagged off Mexico near Guadalupe Island (Domeier & Nasby-Lucas 2008). Together both datasets reveal the adherence of satellite ($n = 123$) and acoustic ($n = 78$) tagged white sharks to a fixed geographical range with no evidence of straying or spatial overlap with ANZ. This result has implications for a white shark population unique to North American shores.

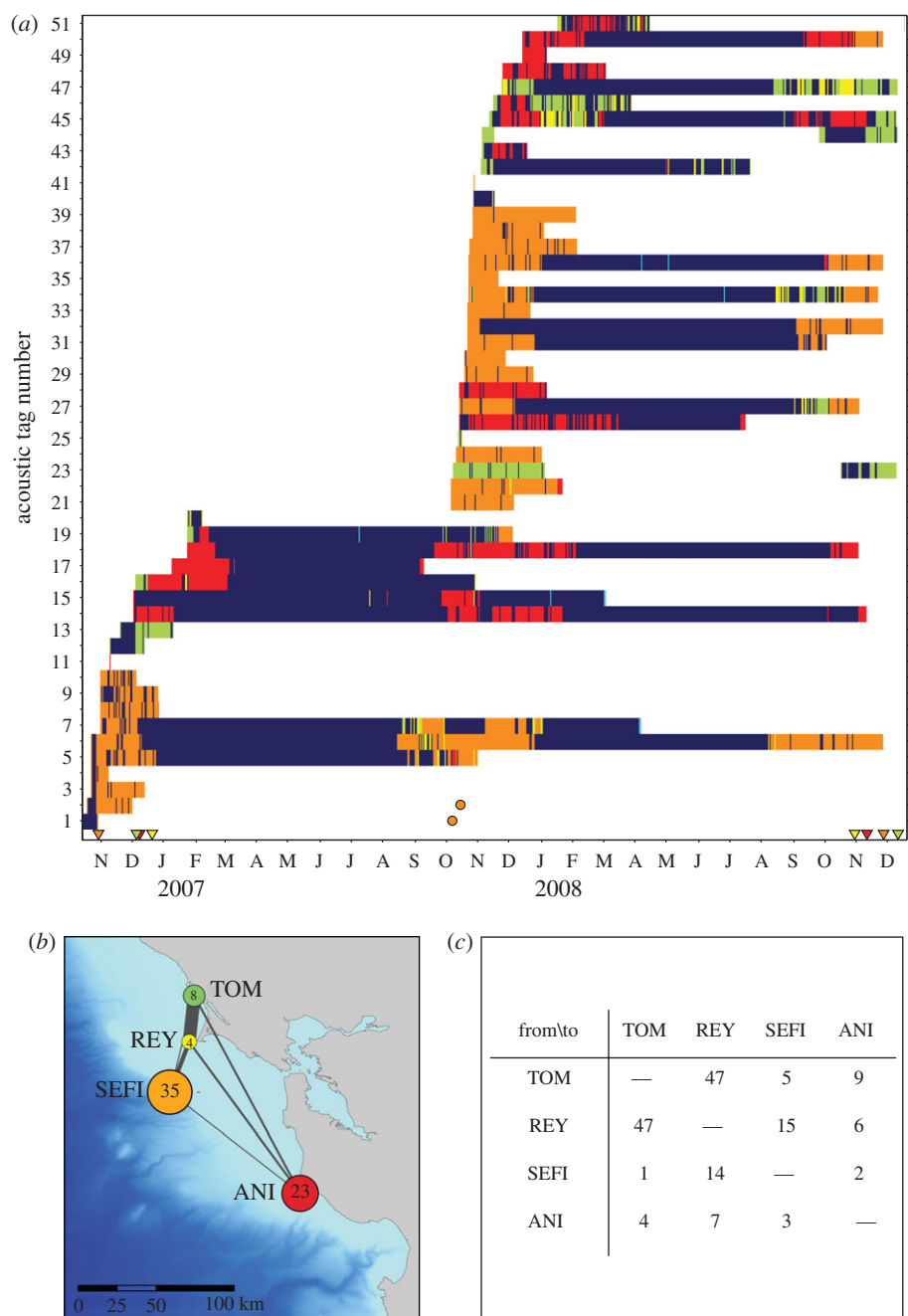


Figure 5. White sharks tagged with acoustic transmitters along the central California coast (2006 and 2007 deployments) detected by acoustic receivers reveal periods of presence and absence. (a) Acoustic detections over time revealed the presence (1-day vertical bands coloured by location; see panel (b) for colour key; Hawaii indicated by cyan) and absence (dark blue; between first and last detections) of individuals near receivers (250 m detection range). Circles, coloured by location, represent the presence of individuals (photographed) with failed tags (electronic supplementary material, figure S1). Triangles indicate start and end times for data collection, coloured by location, respectively. (b) Receiver locations scaled in size by mean residence time (days in text) from north to south include TOM (green), REY (yellow), SEFI (orange) and ANI (red). Lines connecting locations are scaled in thickness relative to the number of transits between adjoining sites. (c) The number of transits by white sharks between receiver sites determined from acoustic detection at one site followed by a subsequent detection at another.

To examine if site fidelity observed from electronic tagging was associated with a genetically discrete population, we compared mitochondrial control region sequences (1109 base pairs) from biopsies of 47 tagged and 12 untagged (electronic supplementary material, tables S1 and S2) NEP white sharks sampled in California to published sequences (GenBank) from SA and ANZ (Pardini *et al.* 2001). Strong clustering of these NEP sharks with those from ANZ was evident (figure 4), yet NEP sharks formed a unique monophyletic clade (bootstrap = 58%, Bayesian posterior probability = 60%) of relatively recently derived lineages.

The relative degree of divergence within this NEP clade was quite low. Nucleotide diversity for the NEP ($\pi = 0.00131 \pm 0.00089$) was the lowest among all three regions ($\pi = 0.00488 \pm 0.00286$ and $\pi = 0.00395 \pm 0.00231$ for SA and ANZ, respectively). Twenty unique mtDNA haplotypes were detected ($h = 0.79$), but 60 per cent of the samples belonged to just two of these lineages. Shark mtDNA is known to undergo a reduced rate of base

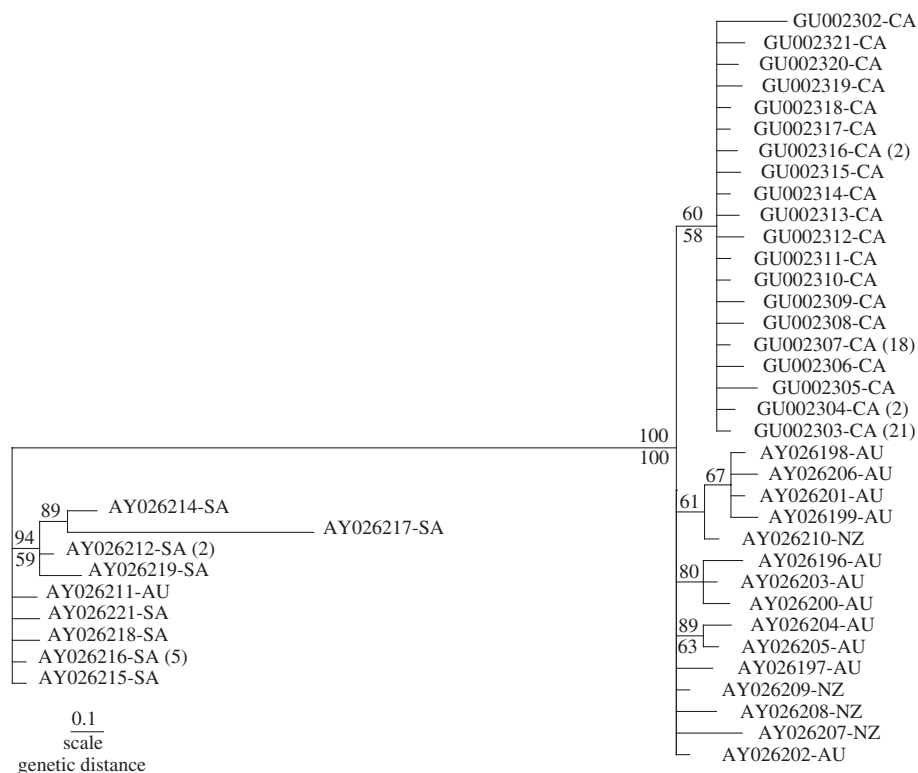


Figure 6. Phylogeny of unique haplotypes found in Indo-Pacific white sharks inferred from comparisons of mitochondrial DNA control region sequences (1109 base pairs) of 59 individuals from the central California coast with previously published sequences from SA and ANZ. Bayesian tree branch lengths reflect substitutions per site. The number of samples comprising each haplotype is given in parentheses if greater than 1. GenBank accession numbers are indicated for each haplotype followed by the location of the sample. Bayesian posterior probabilities are indicated above nodes while likelihood bootstrap values are shown below. NEP sharks from California (CA) form a monophyletic clade (bootstrap = 58%, Bayesian posterior probability = 60%). Individuals from the two dominant lineages within this clade had similar migratory patterns.

substitution compared with other vertebrates (Martin *et al.* 1992). Nonetheless, we believe the small number of substitutions (1.3 mean pairwise differences) among NEP haplotypes along with the short, star-like branching (figure 6) is indicative of a population established from a limited number of founders sometime during the Late Pleistocene. The NEP population is more similar to, and a clear descendent, of the ANZ group. However, highly significant population divergences (pairwise $F_{ST} = 0.68$, $p < 0.0001$, table 1) indicate that since their introduction into the NEP, female white sharks aggregating off California have maintained little gene flow with the southwestern Pacific ANZ population.

Maternally inherited mtDNA clearly divides NEP and ANZ white shark populations in the Pacific; however, it is unknown whether genetic divergence is maintained primarily by females as has been suggested between SA and ANZ populations (Pardini *et al.* 2001). Future analyses of microsatellite and other nuclear loci will help determine whether the ancestral connection between ANZ and NEP populations is explained by the historical translocation of ‘founder’ females along with complex male gene flow (Pardini *et al.* 2001; Bonfil *et al.* 2005), or whether both sexes actually share the same philopatric life history, as tagging strongly suggests.

(f) Site fidelity and population structure

Carcharodon carcharias individuals exhibited site fidelity at multiple scales. At the ocean basin scale, white sharks made predictable long-distance migrations to and from

Table 1. Population comparisons (F_{ST}) among Indo-Pacific white sharks *C. carcharias*.

	1	2	3
1. ANZ	—		
2. SA	0.93302***	—	
3. NEP	0.68217***	0.96995***	—

***Significant F_{ST} ($p < 0.0001$).

defined oceanic core areas. At the regional scale individuals tagged off central California returned to this same coastal region. Likewise, white sharks tagged off Guadalupe Island (1000 km from central California) also returned to their respective region despite extensive overlapping at the Café (Domeier & Nasby-Lucas 2008). At the local scale, within the central California region, individuals exhibited clear preferences for particular coastal sites separated by only kilometres to which they consistently homed following offshore periods or occasional visits to similar adjacent sites (figure 6).

Preference for a small subset of available coastal foraging sites is noteworthy given an extensive capacity for movement. Recurring site fidelity at familiar sites is likely to increase foraging success for white sharks. Theoretical and empirical consensus in diverse vertebrate taxa suggests that spatial familiarity, particularly in topographically complex habitats, can improve foraging efficiency, territorial defence and predator escape, ultimately leading to increased individual fitness (Stamps 1995; Van Moorter *et al.* 2009). Previous

active telemetric tracking at SEFI demonstrated that white sharks patrolled shallow foraging habitat (approx. 30 m) close to and highly correlated with rugose bathymetry, and larger individuals favoured specific discrete areas around the island (Goldman & Anderson 1999). Persistent site fidelity to highly localized coastal sites (e.g. ANI or SEFI; figure 4) despite periodic visits to the equivalent adjacent sites suggests that the cost of relocation may outweigh potential benefits of re-establishing fidelity in less familiar locations (Stamps 1995). Site fidelity across multiple scales in the NEP indicates a low likelihood for individuals of this population reaching ANZ, which is supported by significant genetic divergence from the ANZ population.

(g) Conclusions and management implications

While the ecological purpose of the predictable onshore/offshore seasonal migration pattern is an ongoing topic of investigation (i.e. foraging versus mating), the evolutionary implications of this pattern had not previously been explored. Based on our combined telemetry and genetic dataset, we uncovered new details providing insight into the purpose of these energetically costly movement patterns. Further, we conclude that this tendency towards philopatric migration patterns may serve as a primary mechanism of isolation for the NEP white shark population over evolutionary time scales.

Our findings show that NEP white sharks form a demographically isolated population with clearly defined spatial demarcation. The geographical isolation revealed from electronic tagging coupled with significant genetic (mtDNA) divergence evident from monophyletic clade structure indicates that NEP sharks, particularly females, are isolated from previously studied populations in the South Indo-Pacific, specifically ANZ and SA. The highly predictable seasonal distribution of NEP white sharks including repeated homing to and focus at a network of key coastal hotspots highlights where future population assessment and monitoring can be effectively conducted within US territorial waters. These results further emphasize the need for coordinated ocean management between the USA and Mexico.

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