

Evidence of Philopatry in Sharks and Implications for the Management of Shark Fisheries

R. E. Hueter and M. R. Heupel

Center for Shark Research, Mote Marine Laboratory
Sarasota, Florida 34236, USA

and

E. J. Heist and D. B. Keeney

Fisheries and Illinois Aquaculture Center, Southern Illinois University
Carbondale, Illinois 62901, USA

Hueter, R. E., M. R. Heupel, E. J. Heist, and D. B. Keeney. 2005. Evidence of Philopatry in Sharks and Implications for the Management of Shark Fisheries. *J. Northw. Atl. Fish. Sci.*, 35: 239-247. doi:10.2960/J.v35.m493

Abstract

Evidence of philopatric behavior in diverse species of sharks is accumulating through various sources of data, including studies of shark behavior, genetics and fisheries. If sharks display natural tendencies to return to a home area, birthplace or another adopted locality during portions of their life cycles, as opposed to roaming and dispersing throughout their overall ranges, the impact of fisheries removals and habitat alterations on shark populations and stocks could be profound, and the use of shark catch data to assess stocks could be complicated. We review the accumulating evidence for philopatry in sharks and discuss its implications for fisheries management and conservation of shark species.

Key words: elasmobranch, fisheries management, genetics, migration, nursery, philopatry, shark, tagging

Introduction

Philopatry, derived from the Greek for "home-loving," is the tendency of an individual to return to, or stay in, its home area, natal site, or another adopted locality (Mayr, 1963), as opposed to nonreturning roaming behavior or simple dispersal away from home areas. Although most research on philopatry has concentrated on the homing behavior of migratory birds, it now appears that many animal species display some degree of philopatric behavior. Philopatric tendencies can be strong or weak for a given species, and special patterns of this behavior can include natal philopatry (returning to the natal nursery area) and sex-specific philopatry (where one sex is more philopatric than the other, as in many male birds and female mammals). Recent studies of terrestrial animals have examined philopatric trends in a diversity of mammals including bats (Kurta and Murray, 2002), deer (Purdue *et al.*, 2000), and even ancestral hominids (O'Connell *et al.*, 1999).

The number of published reports of philopatry in marine animals has increased in recent years, building upon the long-accepted findings of strong philopatric behavior in anadromous salmon (Wisby and Hasler, 1954) and sea turtles (Carr, 1967). The literature now contains

many examples of philopatry in taxa as divergent as corals (Hellberg, 1994), marine teleosts (Gold *et al.*, 1999; Robichaud and Rose, 2001), sea birds (James, 1995; Weimerskirch and Wilson, 2000) and marine mammals (Goodman, 1998; Gladden *et al.*, 1999; Lyrholm *et al.*, 1999). New genetic techniques are being applied in much of this research, including studies to further resolve the degree of philopatry in salmonids (Wenburger and Bentzen, 2001) and sea turtles (Meylan *et al.*, 1990; FitzSimmons *et al.*, 1997).

Researchers investigating the population genetics, migratory behavior and fisheries ecology of chondrichthyan fishes have been challenged to find evidence of philopatry in sharks (Hueter, 1998). Evidence has been accumulating, albeit slowly, as this group of marine animals poses special problems in this research. As large, highly mobile fishes, sharks are not the easiest group to study with conventional tagging or tracking methodology, and their intrinsically low levels of genetic variation are difficult to resolve by population geneticists (Heist, 1999). Nevertheless, enough data on shark philopatry now exist to examine the emerging trends and consider the implications of this trait for shark fisheries management and conservation.

Evidence of Philopatry

Tagging/Tracking Studies of Shark Migration

Numerous research programs in shark tagging and tracking exist around the world. Most conventional tag-recapture programs have been focused on patterns of long-distance migration, but some researchers have examined their data for evidence of philopatric behavior or have designed studies to specifically address the issue (Table 1). Sims *et al.* (2001) reported strong sex-specific philopatry in *Scyliorhinus canicula* resulting in sexual segregation of this small shark species in a southwest Ireland bay. Sundström *et al.* (2001) described tagging studies designed to determine if adult female lemon sharks (*Negaprion brevirostris*) are philopatric for their natal nursery in the Bahamas to mate or give birth, and Feldheim *et al.* (2002), reporting on the results of the Bahamas studies using both tagging and genotyping, concluded that reproductive females showed strong philopatry to the natal nursery area. Pratt and Carrier (2001) found sex-specific philopatry in adult nurse sharks (*Ginglymostoma cirratum*) using tagging methods to identify reproductive males and females at a mating site in the Dry Tortugas, Florida. Individual males were found to return to the specific area each year during the mating season whereas females returned on a biennial cycle. Juveniles also were recaptured in the same vicinity on an annual cycle but the extent of their migrations away from the site are not known. Several studies of young sandbar sharks (*Carcharhinus plumbeus*) in nursery areas along the northeast U.S. coast have provided some evidence of natal philopatry in the juveniles (Musick *et al.*, pers. comm.; Pratt *et al.*, pers. comm.).

Mote Marine Laboratory's Center for Shark Research (CSR) has been collecting and tagging coastal sharks along the Florida Gulf of Mexico coast from north Florida to the Florida Keys for over ten years. More than 11 500 sharks of 16 species have been tagged

in this region and overall recapture rate has been 4.0%. CSR tag recaptures have been reported from a broad geographic range including U.S. and Mexican waters of the Gulf of Mexico, U.S. waters of the Atlantic Ocean, and other areas, and these tag returns have indicated varying degrees of philopatric behavior in a number of shark species. Juvenile and adult blacknose sharks (*Carcharhinus acronotus*) tagged in the summer in Tampa Bay, a large (approx. 400 naut. miles²) estuary on the Florida Gulf coast, have demonstrated philopatry for the bay on annual cycles. These sharks enter the lower bay from the Gulf of Mexico in late spring and early summer for mating and feeding, and they leave the bay for offshore waters of the Gulf by late summer (Hueter and Manire, 1994; Hueter, unpubl. data). Of 13 total recaptures of all blacknose sharks tagged in the lower bay and recaptured 1+ year later in any location, 12 (92%) were found to have returned to the same vicinity inside the bay (0–9 naut. miles away from the tagging site) on a one-year (4 sharks), two-year (1), three-year (4), or four-year (3) cycle. (The 13th shark was recaptured 3.6 years after tagging approx. 23 naut. miles from the tagging site in a coastal area just south of the bay entrance.) Two other long-term recaptures of blacknose sharks tagged with CSR tags by the National Marine Fisheries Service (NMFS) in Panama City, Florida, have been reported, and both showed a similar pattern to the Tampa Bay sharks: one was recaptured 19 days short of exactly four years later within 7 naut. miles of the tagging site, and the other was recaptured five days short of exactly five years later within 14 naut. miles of the tagging site. Like Tampa Bay to the south, the coastal waters and estuaries near Panama City in the north Florida panhandle region serve as summer feeding and mating areas for the blacknose, and the sharks leave these areas for distant warmer waters in the winter. These tag return data provide a strong indication that blacknose sharks inhabiting the eastern Gulf of Mexico return to discrete inshore areas on annual cycles.

TABLE 1. Recent examples of studies revealing philopatry in sharks.

Order	Species	Evidence	Reference
Orectolobiformes	<i>Ginglymostoma cirratum</i>	Tagging	Pratt and Carrier, 2001
Lamniformes	<i>Carcharodon carcharias</i>	Genetic	Pardini <i>et al.</i> , 2001
Lamniformes	<i>Isurus oxyrinchus</i>	Genetic	Schrey and Heist, 2003
Carcharhiniformes	<i>Scyliorhinus canicula</i>	Tagging, tracking	Sims <i>et al.</i> , 2001
Carcharhiniformes	<i>Negaprion brevirostris</i>	Genetic, tagging	Feldheim <i>et al.</i> , 2002
Carcharhiniformes	<i>Carcharhinus plumbeus</i>	Tagging, tracking	Musick <i>et al.</i> (pers. comm.) Pratt <i>et al.</i> (pers. comm.)
Carcharhiniformes	<i>Carcharhinus limbatus</i>	Tagging, tracking, Genetic	Keeney <i>et al.</i> , 2003 This study

Conventional tagging studies of the blacktip shark (*Carcharhinus limbatus*) by the CSR have concentrated on the movements of neonate, young-of-the-year (YOY) and older juveniles in nursery areas along the Florida Gulf coast. This coastal region contains many pupping and nursery areas for blacktips from north Florida to the Florida Keys (Castro, 1996; Hueter and Tyminski, 2002). Over 3 200 juvenile blacktips have been tagged in this region and 154 total recaptures (4.8%) have been reported year-round. From these recaptures a pattern consistent with some degree of natal philopatry has emerged for at least the first three years of life. When juveniles tagged in the months of May, June or July of any year are recaptured in the same months one year, two years or three years after tagging, they tend to be back in the vicinity of the nursery (Fig. 1). Winter recaptures of blacktip juveniles, on the other hand, show the animals to have migrated typically over 100 naut. miles south to winter feeding grounds along the coast (Fig. 2). This suggests that the juveniles may be philopatric for their natal nurs-

ery on annual cycles, returning each spring/summer for at least the first three years. The longest time-at-liberty of a blacktip shark in the CSR database is for an animal tagged in June 1994 as a three year-old in a nursery area and recaptured six years and one month later in July 2000 within 48 naut. miles of the tagging site (Fig. 1). As this was a mature, nonpregnant female at the time of recapture, it is possible this was a postpartum shark that had visited its natal nursery the month before to give birth to her pups. It is equally possible that this was a female in a resting reproductive year. In either case, it is interesting that this animal was recaptured relatively close to the tagging site, which was probably its natal nursery (although that cannot be known for sure), almost exactly six years from when it was tagged, given that adult blacktip sharks off the southeast US coast can migrate at least as far as 1 159 naut. miles away from the tagging site (Kohler *et al.*, 1998).

These conventional tagging results with blacktip sharks are at best suggestive of a pattern of philopatry that calls for further tag-and-recapture studies and electronic tracking of individual shark movements. To that end, recent tracking studies using passive acoustic telemetry (Heupel and Hueter, 2001) have revealed new insights into the natal philopatry of blacktip sharks. In studies conducted since 1999, the movement patterns of neonate blacktips in their natal nursery (Terra Ceia Bay, Florida) have been monitored for long periods of time while the sharks are in the nursery. As a small (5 km × 1.5 km), semi-enclosed (one opening 0.5 naut. miles wide) bay inside a larger estuary (Tampa Bay), and with an entrance that is approx. 8 naut. miles from the open waters of the Gulf of Mexico, Terra Ceia Bay represents a small target for juvenile blacktips returning from winter areas. It is unlikely that roaming sharks simply following the coastline north during spring migrations would find their way back into this small bay by chance. Natural and fishing mortality of the YOY pups inside this natal nursery is high, estimated to be 61–91% (Heupel and Simpfendorfer, 2002). Of the pups that survive their first summer and successfully migrate out of Terra Ceia Bay in the autumn, 30% of 2000-tagged pups were reacquired by acoustic monitors inside the natal nursery area the following year in 2001, and 50% of 1999-tagged pups were reacquired inside the nursery two years later in 2001. The appearance of these animals in 2001 (two from 1999 and three from 2000) indicate up to half of the pups surviving their first summer in the natal nursery area are returning to that same nursery in subsequent years. All five of these individuals were long-term residents of the nursery area as YOY pups and were resident for variable periods of time upon their return in 2001 (Fig. 3). Given the natural and fishing mortality that the juveniles must

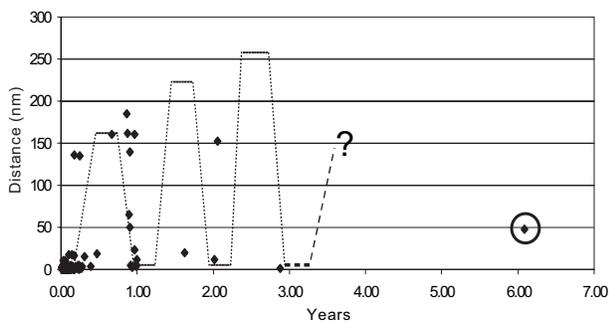


Fig. 1. Recaptures of blacktip sharks (*Carcharhinus limbatus*) tagged in the months of May/June/July of multiple years (standardized time 0.00 years) along the Florida Gulf coast and recaptured at any time of year thereafter ($n = 94$ recaptures). All sharks were juveniles when tagged. Years is time at liberty between tagging and recapture; Distance is shortest by-sea distance between tag and recapture sites. Dotted line is a theoretical pattern for a shark that is philopatric for its natal nursery in its first three years, in which troughs represent time in the nursery, ascending limbs are fall migrations, plateaus are time in winter feeding grounds, and descending limbs are return migrations back to the natal nursery in the spring. Dashed line indicates uncertainty of the pattern as sharks become older, but mature females philopatric for their own natal nursery would be expected to be found near the nursery during pupping season. Circled point is a mature female tagged in early June of 1994 and recaptured in early July of 2000 approx. 48 naut. miles away from where it was tagged as a three year-old juvenile. This shark was not pregnant at the time of recapture, thus it could have been either postpartum or in a resting reproductive year.

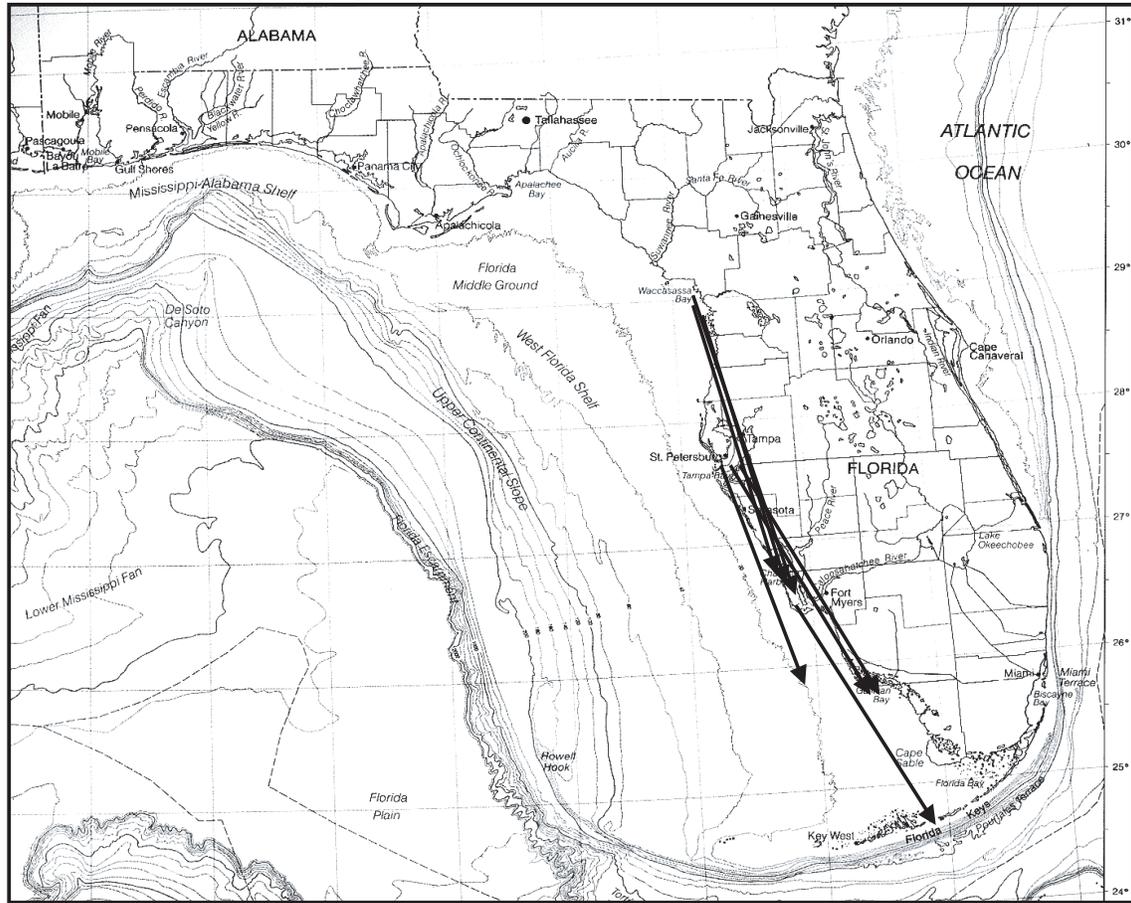


Fig. 2. Recaptures of young blacktip sharks (*C. limbatus*) tagged in summer nursery areas and recaptured in winter months. All sharks migrated south over 100 by-sea nm from their natal nursery. (Map template courtesy of NOAA/National Ocean Service.)

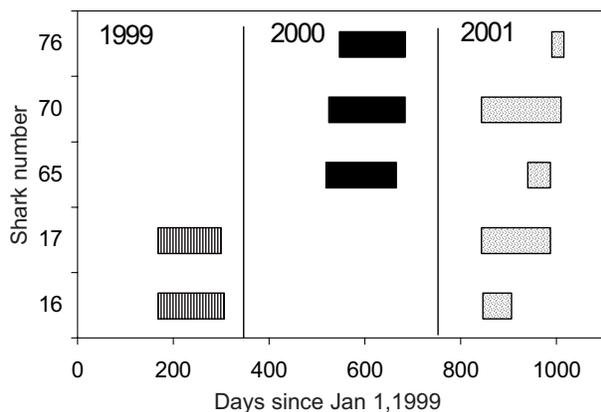


Fig. 3. Monitoring periods for five passively tracked juvenile *C. limbatus* in a Florida natal nursery during 1999–2001. Bars in 1999 and 2000 indicate monitoring periods for the neonate/YOY animals within the natal nursery. Bars in 2001 indicate the timing and duration of return of the 1–2 year-olds to the nursery.

be exposed to during their winter migrations, as well as the limitations of acoustic transmitter battery life and other technical considerations, these rates of return and reacquisition in the natal nursery are significant.

These and other examples of shark philopatry as indicated by tagging and tracking studies are intriguing, but ultimately long-term tracking of the complete life cycle of shark species using archival or satellite tags is needed to determine fully the degree and nature of philopatry. Because conventional tagging programs tend to focus on long-distance tag returns, those recaptures with short tag-recapture distances but long tag-recapture times may be overlooked as uninteresting, but they may be the result of philopatric behavior. By looking deeper into temporal patterns, especially annual cycles, and bringing in other evidence from related studies of shark migration, the hypothesis that many, if not most, shark species are philopatric for their natal or post-natal nursery areas or

other critical parts of their ranges (Hueter, 1998) may gain support.

Genetic Evidence

Molecular genetics has been used to detect natal philopatry against a background of large-scale seasonal movement in such vertebrate taxa as salmonids, sea turtles, marine mammals, and birds. When animals segregate geographically for mating or parturition, even if their distributions overlap at other times, they can still be genetically separable into discrete reproductive groups. Genetic drift causes allele frequencies of genes to diverge such that following a sufficient number of generations of reproductive isolation, separate groups exhibit their own characteristic genetic profile. Migration and mating (gene exchange) among reproductive groups eliminates the effects of genetic drift by maintaining similar allele frequencies across groups. The degree of site fidelity in natal philopatric behavior – or looking at it the other way, the degree of straying from the natal or post-natal nursery areas – will thus determine the likelihood of genetic divergence among animals from different nursery areas.

By measuring the variance in allele frequencies among reproductive groups (F_{ST}) and by assuming a specific model of gene flow and population structure, the number of interbreeding migrants per generation among reproductive groups can be estimated. Typically an estimate of greater than ten interbreeding migrants per generation is taken as evidence of a single reproductive group, while fewer than one migrant per generation indicates discrete groups (Mills and Allendorf, 1996). One limitation of the genetic approach to estimating movement and sources of recruitment is that the number of migrants that reduce the magnitude of F_{ST} to undetectable levels (e.g. several individuals per generation) may not be sufficient in terms of recruitment to define a collection of natal or post-natal nursery areas as a single reproductive group. Furthermore, the asymptotic relationship between low F_{ST} values and the number of migrants means that a small error in the measurement of F_{ST} values is accompanied by a large error in estimating the number of migrants (Waples, 1998).

Nuclear and mitochondrial (mt) DNA markers differ in inheritance pattern and can produce vastly different F_{ST} values in some circumstances. Nuclear markers are equally inherited from both male and female parents while mtDNA is passed directly from females to offspring of both sexes without any transmission from the male parent. Large F_{ST} values in mitochondrial but not nuclear markers are often taken to indicate higher

fidelity in females than males to particular groupings or reproductive locations. For example, such an effect is seen in female sea turtles, which faithfully return to their natal beach for nesting yet mate with males from different natal beaches (FitzSimmons *et al.*, 1997), and in some whales that are socially structured into maternal groups with males mating outside the group (Lyrholm *et al.*, 1999).

Preliminary genetic data (mtDNA and microsatellites) from 146 neonate and YOY blacktip sharks collected in 2000 (Keeney *et al.*, unpubl. data) indicate that females exhibit a greater degree of reproductive philopatry than males. However, sharks from nursery areas separated by hundreds of kilometers do not exhibit significant differences in gene frequencies, indicating some degree of female straying. Mitochondrial DNA and nuclear (four microsatellite loci) allele frequencies were measured in juvenile blacktip sharks from four widely spaced nurseries along the Atlantic and Gulf coasts of North America (South Carolina, Gulf coast of Florida, Texas, and Mexican Yucatan). The overall F_{ST} value for the mitochondrial marker was highly significant ($F_{ST} = 0.111$, $P < 0.001$) and several orders of magnitude larger than the nonsignificant overall F_{ST} value for microsatellites ($F_{ST} < 0.001$, $P = 0.316$). Pairwise regional comparisons are listed in Table 2. The strong signal in the mtDNA data indicates that females return to the same region for parturition while the lack of signal in nuclear markers indicates a greater degree of male-mediated gene flow among regions. At a finer scale, comparisons among three nurseries separated by 100 to 250 km along the Florida Gulf coast failed to detect significant F_{ST} values for either mtDNA ($F_{ST} = 0.022$, $P = 0.117$) or nuclear markers ($F_{ST} = 0.001$, $P = 0.308$). Mitochondrial data incorporating a second year of sampling from South Carolina and the Gulf coast of Florida were consistent with female philopatry in these two regions ($F_{ST} = 0.090$, $P < 0.001$) (Keeney *et al.*, 2003). Thus, while female blacktip sharks exhibit regional philopatry, there appears to be considerable straying among specific, adjacent nursery areas and female blacktip sharks may not be as philopatric as some other vertebrate taxa (e.g. sea turtles and salmon).

These results are perhaps not surprising given the limitations of gene frequency data and the more or less continuous distribution of blacktip shark nursery areas along the Gulf coast of Florida. If the majority of females return to the precise location of their own parturition but a small percentage of females stray to nearby nurseries, the resultant F_{ST} value will be too small to detect. Other techniques, such as telemetry or fine-scale determination of genetic relatedness among year classes (i.e. the detec-

TABLE 2. Pairwise F_{ST} values for mitochondrial markers (above the diagonal) and four nuclear microsatellite loci (below the diagonal) from juvenile blacktip sharks (*Carcharhinus limbatus*) collected in four nursery areas along the U.S. and Mexican coasts of the Atlantic Ocean and Gulf of Mexico.

	South Carolina	Florida Gulf	Texas Gulf	Yucatan
South Carolina	—	0.101	0.277	0.149
Florida Gulf	0.006	—	0.050	0.134
Texas Gulf	0.004	<0.001	—	0.080
Yucatan	0.010	<0.001	<0.001	—

tion of the offspring of individual females over multiple years), will be necessary to determine the actual degree of philopatry in this species.

In other shark species, genetics has indicated strong to moderate signals of philopatry. Feldheim *et al.* (2002) provided compelling genetic evidence that adult female lemon sharks, which are biennially reproductive, are strongly philopatric for the same pupping area in Bimini, Bahamas for parturition every other year. Whether or not these females are returning to their own natal nursery to give birth is not yet clear, nor is the range of options of alternate pupping sites available to these females in the insular environment of Bimini. Pardini *et al.* (2001), comparing the results of mtDNA analyses with microsatellite analyses, concluded that female white sharks (*Carcharodon carcharias*) of the southwest Pacific Ocean and southwest Indian Ocean are more philopatric than males. The non-roaming or returning female *vs* roaming male pattern also has been detected for another pelagic lamnid, the shortfin mako shark *Isurus oxyrinchus* (Schrey and Heist, 2003) as well as for the blacktip shark as mentioned above. This may prove to be a common pattern for shark species in general, but further research needs to be done on a broader phylogenetic and ecological spectrum of sharks.

Fisheries Evidence

If sharks are philopatric for specific parts of their ranges, be they nursery areas, feeding grounds, mating areas or other locations, fishing within those areas can remove individual animals that depend on and, in a sense, "belong to" those localities rather than are part of a larger, fully mixed stock. This would be true regardless of the highly migratory nature of shark species. In this case, fishery removals can have a more dramatic effect on the relative abundance of species in localized areas, with the appearance that species density has been "hole-punched" in a specific part of its range. This phenomenon, known as localized stock depletion, has been reviewed for sharks by Walker (1998). Although not well

documented, evidence of localized stock depletion of sharks comes from a variety of sources including shark meshing programs in South Africa (Dudley, MS 2002) and commercial fisheries in Australia (Walker, 1998).

Data from recreational shark tournaments in Florida in the 1970s and 1980s suggest localized depletion of large coastal sharks through overfishing, as shark abundance and size in the recreational fishery declined dramatically in one Florida coastal site after another, but not all at the same time (Hueter, 1991). This occurred well before the region's commercial directed longline fishery developed in the mid-1980s, indicating that concentrated overfishing by the recreational fishery led to localized depletions. This fishery targeted large species such as sandbar, dusky (*Carcharhinus obscurus*), hammerhead (*Sphyrna* spp.) and bull sharks (*Carcharhinus leucas*), all migratory sharks with large ranges. Philopatric tendencies for feeding, mating or other activities in adults of these species could explain the asynchronous, localized declines in recreational catch rate that were observed in the Florida shark fishery.

Some highly migratory shark species with large home ranges, roaming behavior, and weak or no philopatry may not be susceptible to localized stock depletion. The tiger shark (*Galeocerdo cuvier*) could be one such species, and Simpfendorfer (1992) reported no localized trends in tiger shark catch rates over time in a shark meshing program in Australia. In addition, other highly migratory species may give the appearance of localized depletion but other phenomena may be responsible, as in the case of ecological changes affecting the distribution of basking sharks off Ireland (Sims and Reid, 2002).

Discussion

The search for evidence of philopatry in sharks is still in its early stages, but there exist enough behavioral, genetic and fisheries data to conclude that at least some sharks are strongly philopatric for portions of their

ranges, especially nursery areas, and many other sharks may be at least moderately philopatric for nurseries, mating areas, feeding areas or other localities. The development of natal philopatry, in particular, would be evolutionarily favored in K-selected species like sharks, for by definition females that successfully survive, mature, mate and return to their natal nursery areas to give birth would have high fitness and pass on their genes. Those specific pupping grounds would, in effect, be "selected for" because they were successful in producing animals that reproduced, and thus the natal nursery as a site-specific component of species life history is favored. This is truer for animals that live in structured habitats rather than open environments (Wilson, 1975), so selection for philopatry theoretically would be greater in coastal and benthic species than in roaming, dispersing, pelagic species, but that remains to be seen. In any case, given the likelihood that philopatry in sharks exists in some form, it is wise to consider the implications of this behavior for the management and conservation of shark species.

Shark Nursery Areas. For sharks with reproductive philopatry, that is, a pattern of returning to natal or post-natal nursery areas, those discrete nurseries would have special value for the population beyond the usual definitions of essential fish habitat. If sharks are not reproductively philopatric, all nursery areas in a species range combine to form a more or less homogeneous habitat for juvenile production, and the impacts of overfishing or habitat loss in specific nursery areas may be buffered by production in other nurseries. Nursery areas for strongly philopatric sharks, on the other hand, would constitute truly essential locations for components of the population, like natal streams for salmon or nesting beaches for sea turtles. Once the population components using those areas are depleted or the habitat is lost, re-establishment of reproduction by straying animals may take a very long time, even if the habitat can be recovered. As a case in point, Robichaud and Rose (2001) concluded that the natal philopatry of Atlantic cod (*Gadus morhua*), a prolific spawner, has impeded recolonization of depopulated spawning grounds and has led to a slower rate of stock recovery in the North Atlantic. Overfishing or environmental perturbations, either natural or human-induced, in shark nursery areas could have a dramatic, long-lasting effect, particularly since sharks have extremely low reproductive rates and long generation times (Musick, 1999). This effect would depend on the amount of straying of juveniles or pregnant females among nursery areas.

Stock Structure and Genetic Biodiversity. Depending on the degree and nature of philopatry, a shark stock that may otherwise be viewed as a single population

because of overlapping ranges and congruent migratory routes may in fact constitute a metapopulation of genetically heterogeneous components. In this case, genetic biodiversity could be lost when localized depletion occurs. However, as pointed out above, the number of straying animals required to dampen genetic heterogeneity between areas is exceedingly small, so this concern should not be overstated.

Stock Assessment, Depletion and Recovery. Increased mortality (natural or fishing) in specific nurseries, feeding grounds, mating grounds, or other essential portions of a shark's range can lead to localized stock depletions if the species is philopatric for those areas. This could produce a number of effects. First, it could explain inconsistencies in catch rates between seemingly similar, adjacent areas for otherwise wide-ranging stocks of sharks – the "hole-punch" effect – which underscores the risk of using CPUE data from spatially or temporally inappropriate areas of a philopatric species' range to determine overall stock abundance. Second, depending on the degree of philopatry, stock recovery in those depleted areas could take much longer than projected by a production model that is based on the premise of a uniform stock utilizing all available habitat equally.

Spatial Management of Shark Fisheries. For philopatric sharks, the conservation and management of shark fisheries would need to take into consideration the spatial distribution of catch on a different level than is traditionally done. Gold *et al.* (1999) addressed this concern for the management of red drum (*Sciaenops ocellatus*), a teleost with genetic indications of female natal philopatry. They proposed that management of this species be based on a concept of "geographic neighborhood" in which management actions are spatially structured according to the degree of species philopatry. This approach should not be rejected for sharks simply because they are more migratory than red drum. Along the U.S. east coast, the management of coastal shark fisheries outside of state waters is under the jurisdiction of the National Marine Fisheries Service (NMFS), not the regional fishery management councils, because sharks are classified as highly migratory species that cross regional geographic boundaries, like tunas and billfishes. From the standpoint of fisheries management, this large-scale approach is probably the only logistically feasible one for these wide-ranging stocks and the fleets that fish for them. But from the standpoint of fish management, this could present challenges for the conservation of philopatric sharks. The nursery areas of most coastal sharks are typically in state waters where state jurisdiction applies, but feeding grounds, mating areas, and the migratory paths in between can often be in federal waters. NMFS

also is required by federal law to protect essential fish habitat for managed species, and in the case of philopatric species, this requirement takes on added meaning. The concern with large-scale management of highly migratory sharks is that the effective protection of these essential habitats can be difficult unless there are dynamic linkages among federal, regional, state and local bodies charged with management of shark fisheries.

Many shark species are highly migratory, some covering thousands of miles of ocean in a single year. However, with the emerging evidence of philopatry in various shark species, it would be wise from a conservation and management perspective to not view this group of marine fishes as oceanic nomads, but rather as more sophisticated, long-distance travelers with a number of discrete homes in the sea. How precise those homes are will need to be established with further research and analysis.

Acknowledgements

Funding from NMFS, the National Science Foundation, the Florida Department of Natural Resources and Mote Marine Laboratory supported this work. We thank J. Tyminski and C. Manire for help with the CSR shark tagging program and database analyses, J. Carlson at the NMFS Panama City Laboratory for tag return data, and C. Simpfendorfer for many helpful discussions.

References

- CARR, A. 1967. So Excellent a Fish: A Natural History of Sea Turtles. Scribner, New York, NY, 280 p.
- CASTRO, J. I. 1996. Biology of the blacktip shark, *Carcharhinus limbatus*, off the southeastern United States. *Bull. Mar. Sci.*, **59**: 508–522.
- DUDLEY, S. F. J. MS 2002. Shark catch trends and effort reduction in the beach protection program, KwaZulu-Natal, South Africa. *NAFO SCR Doc.*, No. 124: 1–21.
- FELDHEIM, K. A., S. H. GRUBER, and M. V. ASHLEY. 2002. The breeding biology of lemon sharks at a tropical nursery lagoon. *Proc. R. Soc. Biol. Sci., Lond., Ser. B*, **269**: 1655–1661.
- FITZSIMMONS, N. N., C. J. LIMPUS, J. A. NORMAN, A. R. GOLDIZEN, J. D. MILLER, and C. MORITZ. 1997. Philopatry of male marine turtles inferred from mitochondrial DNA markers. *Proc. Natl. Acad. Sci. USA*, **94**: 8912–8917.
- GLADDEN, J. G. B., M. M. FERGUSON, M. K. FRIESEN, and J. W. CLAYTON. 1999. Population structure of North American beluga whales (*Delphinapterus leucas*) based on nuclear DNA microsatellite variation and contrasted with the population structure revealed by mitochondrial DNA variation. *Mol. Ecol.*, **8**: 347–363.
- GOLD, J. R., L. R. RICHARDSON, and T. F. TURNER. 1999. Temporal stability and spatial divergence of mitochondrial DNA haplotype frequencies in red drum (*Sciaenops ocellatus*) from coastal regions of the western Atlantic Ocean and Gulf of Mexico. *Mar. Biol.*, **133**: 593–602.
- GOODMAN, S. J. 1998. Patterns of extensive genetic differentiation and variation among European harbor seals (*Phoca vitulina vitulina*) revealed using microsatellite DNA polymorphisms. *Mol. Biol. Evol.*, **15**: 104–118.
- HEIST, E. J. 1999. A review of population genetics in sharks. *In: Life in the Slow Lane: Ecology and Conservation of Long-Lived Marine Animals*, Bethesda, Maryland USA. J. A. Musick, (ed.). *Am. Fish. Soc. Symp.*, **23**: 161–168.
- HELLBERG, M. E. 1994. Relationships between inferred levels of gene flow and geographic distance in a philopatric coral, *Balanophyllia elegans*. *Evolution*, **48**: 1829–1854.
- HUPEL, M. R. and R. E. HUETER. 2001. Use of an automated acoustic telemetry system to passively track juvenile blacktip shark movements. *In: Electronic Tagging and Tracking in Marine Fisheries*. J. R. Sibert and J. L. Nielsen, (eds.). Kluwer Academic Publishers, Netherlands, p. 217–236.
- HUPEL, M.R. and C.A. SIMPFENDORFER. 2002. Estimation of mortality of juvenile blacktip sharks, *Carcharhinus limbatus*, within a nursery area using telemetry data. *Can. J. Fish. Aquat. Sci.*, **59**: 624–632.
- HUETER, R.E. 1991. Survey of the Florida recreational shark fishery utilizing shark tournament and selected longline data. *Mote Mar. Lab. Tech. Rpt.*, **232A**: 1–94.
1998. Philopatry, natal homing and localised stock depletion of sharks. *Shark News* (Newsletter of the IUCN Shark Specialist Group) **12**: 1–2.
- HUETER, R. E. and C. A. MANIRE. 1994. Bycatch and catch-release mortality of small sharks in the Gulf coast nursery grounds of Tampa Bay and Charlotte Harbor. *Mote Mar. Lab. Tech. Rpt.*, **368**: 1–183.
- HUETER, R. E. and J. P. TYMINSKI. 2002. U.S. shark nursery research overview, Center for Shark Research, Mote Marine Laboratory 1991–2001. *Mote Mar. Lab. Tech. Rpt.*, **816**: 1–15.
- JAMES, R.A. Jr. 1995. Natal philopatry, site tenacity, and age of first breeding of the black-necked stilt. *J. Field Ornithol.*, **66**: 107–111.
- KEENEY, D. B., M. HUPEL, R. E. HUETER, and E. J. HEIST. 2003. Genetic heterogeneity among blacktip shark, *Carcharhinus limbatus*, continental nurseries along the U.S. Atlantic and Gulf of Mexico. *Mar. Biol.*, **143**: 1039–1046.
- KOHLER, N. E., J. G. CASEY, and P. A. TURNER. 1998. NMFS Cooperative Shark Tagging Program, 1962–93: an atlas of shark tag and recapture data. *Mar. Fish. Rev.*, **60**(2): 1–87.
- KURTA, A. and S. W. MURRAY. 2002. Philopatry and migration of banded Indiana bats (*Myotis sodalis*) and effects of radio transmitters. *J. Mammal.*, **83**: 585–589.
- LYRHOLM, T., O. LEIMAR, B. JOHANNESON, and U. GYLLENSTEN. 1999. Sex-biased dispersal in sperm whales: contrasting mitochondrial and nuclear genetic structure of global populations. *Proc. R. Soc., Lond., Ser. B*, **266**: 347–354.
- MAYR, E. 1963. *Animal Species and Evolution*. Belknap Press of Harvard University Press, Cambridge, Mass. 797 p.

- MEYLAN, A. B., B. W. BOWEN, and J. C. AVISE. 1990. A genetic test of the natal homing *versus* social facilitation models for green turtle migration. *Science*, **248**: 724–727.
- MILLS, L. S. and F. W. ALLENDORF. 1996. The one-migrant-per-generation rule in conservation and management. *Cons. Biol.*, **10**: 1509–1518.
- MUSICK, J. A. (ed.). 1999. *In: Life in the Slow Lane: Ecology and Conservation of Long-Lived Marine Animals*, Bethesda, Maryland. *Am. Fish. Soc. Symp.*, **23**: 265 p.
- O'CONNELL, J. F., K. HAWKES, and N. G. BLURTON JONES. 1999. Grandmothering and the evolution of *Homo erectus*. *J. Human Evol.*, **36**: 461–485.
- PARDINI, A. T., C. S. JONES, L. R. NOBLE, B. KREISER, H. MALCOLM, B. D. BRUCE, J. D. STEVENS, G. CLIFF, M. C. SCHOLL, M. FRANCIS, C. A. J. DUFFY, and A. P. MARTIN. 2001. Sex-biased dispersal of great white sharks. *Nature*, **412**: 139–140.
- PRATT, H. L., Jr. and J. C. CARRIER. 2001. A review of elasmobranch reproductive behavior with a case study on the nurse shark, *Ginglymostoma cirratum*. *Env. Biol. Fish.*, **60**: 157–188.
- PURDUE, J. R., M. H. SMITH, and J. C. PATTON. 2000. Female philopatry and extreme spatial genetic heterogeneity in white-tailed deer. *J. Mammal.*, **81**: 179–185.
- ROBICHAUD, D. and G. A. ROSE. 2001. Multiyear homing of Atlantic cod to a spawning ground. *Can. J. Fish. Aquat. Sci.*, **58**: 2325–2329.
- SCHREY, A. W., and E. J. HEIST. 2003. Microsatellite analysis of population structure in the shortfin mako (*Isurus oxyrinchus*). *Can. J. Fish. Aquat. Sci.*, **60**: 670–675.
- SIMPFENDORFER, C. A. 1992. Biology of tiger sharks (*Galeocerdo cuvier*) caught by the Queensland shark meshing program off Townsville, Australia. *Aust. J. Mar. Freshwater Res.*, **43**: 33–43.
- SIMS, D.W., J. P. NASH, and D. MORRITT. 2001. Movements and activity of male and female dogfish in a tidal sea lough: alternative behavioural strategies and apparent sexual segregation. *Mar. Biol.*, **139**: 1165–1175.
- SIMS, D.W. and P. C. REID. 2002. Congruent trends in long-term zooplankton decline in the north-east Atlantic and basking shark (*Cetorhinus maximus*) fishery catches off west Ireland. *Fish. Oceanogr.*, **11**: 59–63.
- SUNDSTRÖM, L. F., S. H. GRUBER, S. M. CLERMONT, J. P. S. CORREIA, J. R. C. DE MARIGNAC, J. F. MORRISSEY, C. L. LOWRANCE, L. THOMASSEN, and M.T. OLIVEIRA. 2001. Review of elasmobranch behavioral studies using ultrasonic telemetry with special reference to the lemon shark, *Negaprion brevirostris*, around Bimini Islands, Bahamas. *Env. Biol. Fish.*, **60**: 225–250.
- WALKER, T. I. 1998. Can shark resources be harvested sustainably? A question revisited with a review of shark fisheries. *Mar. Freshwater Res.*, **49**: 553–572.
- WAPLES, R. S. 1998. Separating the wheat from the chaff: patterns of genetic differentiation in high gene flow species. *J. Hered.*, **89**: 438–450.
- WEIMERSKIRCH, H. and R. P. WILSON. 2000. Oceanic respite for wandering albatrosses. *Nature*, **406**: 955–956.
- WENBURG, J. K. and P. BENTZEN. 2001. Genetic and behavioral evidence for restricted gene flow among coastal cutthroat trout populations. *Trans. Am. Fish. Soc.*, **130**: 1049–1069.
- WILSON, E. O. 1975. *Sociobiology: The New Synthesis*. Belknap Press of Harvard University Press, Cambridge, Mass. 697 p.
- WISBY, W. J. and A. D. HASLER. 1954. Effect of occlusion on migrating silver salmon (*Oncorhynchus kisutch*). *J. Fish. Res. Bd. Can.*, **11**: 472–478.
-

