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The Implications of Philopatry in Sharks for the Management of Shark Fisheries

(Elasmobranch Fisheries – Oral)

by

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Abstract

Evidence of philopatric behavior in sharks is accumulating through various sources of data, including studies of shark behavior, genetics and fisheries. If sharks display some 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 profoundly affected. We review the accumulating evidence for philopatry in sharks and discuss its ramifications for the fisheries management and conservation of shark species.

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 most 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 not only in many of these recent cases but also in the further resolution of the degree of philopatry in salmonids (Wenburg 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 at least examine the emerging trends and consider the implications of this trait on 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 focused on patterns of long-distance migration but some have examined their data for evidence of philopatric behavior or designed studies to specifically address the issue. Sims *et al*. (2001) reported strong sex-specific philopatry in the small-spotted catshark (*Scyliorhinus canicula*) resulting in sexual segregation of the species in a small bay in southwest Ireland. Sundström *et al*. (2001) described tagging studies designed to determine if adult female lemon sharks (*Negaprion brevirostris*) are philopatric for their natal nursery to mate or give birth in the Bahamas, 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 nursery. 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 were also 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*., unpub. data; Pratt *et al*., unpub. data).

The Center for Shark Research (CSR) has been tagging coastal sharks along the Florida Gulf of Mexico coast for ten years. Over 11,000 sharks of 16 species have been tagged and overall recapture rate has been 3.5%. Tag returns have shown 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, Florida, have demonstrated strong 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 in the Gulf by late summer. Of 23 recaptures of blacknose sharks tagged in the lower bay (3% recapture rate), 16 were long-term returns (1+ year) of which 12 (75%) returned to the same vicinity in the bay on a one-year (4), two-year (1), three-year (4), or four-year (3) cycle. Another blacknose shark tagged with a CSR tag by the National Marine Fisheries Service (NMFS) in Panama City, Florida, was recaptured five days short of exactly five years later within 14 nm of the tagging site. Like Tampa Bay, this more northern location off the Florida panhandle region is a summer feeding and mating area for the blacknose, and the sharks leave the area for distant warmer waters in the winter.

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 juvenile animals in nursery areas along the Florida Gulf coast. Over 3,000 juvenile blacktips have been tagged in this area and 127 recaptures (4%) have been reported. From these recaptures a pattern of natal philopatry has emerged for at least the first three years of life (Fig. 1). When juveniles tagged in the months of May, June, July are recaptured in the same months one year, two years, or three years from tagging, they tend to be back in the vicinity of the natal nursery. Winter recaptures of blacktip juveniles, on the other hand, show the animals to have migrated typically over one hundred miles south to winter feeding grounds along the coast (Fig. 2). This suggests that the juveniles are philopatric for their natal nursery 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 nm 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 U.S. coast can migrate at least as far as 1,159 nm (Kohler *et al*., 1998).

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 a natal nursery (Terra Ceia Bay, Florida) have been tracked for the entire time that the pups are in the nursery. As a small (5 km x 1.5 km), semi-enclosed (one opening 0.5 nm wide) bay inside a larger estuary (Tampa Bay), and with an entrance that is approx. 8 nm 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. Natural and fishing mortality of the YOY pups inside this nursery is high, estimated to be 61-91% (Heupel and Simpfendorfer, 2002), but of the pups that survived their first summer and successfully migrated out of Terra Ceia Bay in the fall, 30% of 2000-tagged pups returned to their natal nursery the following year in 2001, and 50% of 1999-tagged pups returned two years later in 2001 (Heupel, unpub. data). Given the natural and fishing mortality that the juveniles must be exposed to during their winter migrations, these return rates 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 fully determine 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 nursery areas and 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 gene frequencies to diverge such that following a sufficient number of generations each group exhibits its own characteristic gene frequency. Migration among reproductive groups eliminates the effects of genetic drift by maintaining similar gene 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 nursery–will thus determine the genetic separability of 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 migrants per generation among reproductive groups can be estimated. Typically an estimate of greater than ten 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 gene frequency approach 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 nursery areas as a single reproductive group. Furthermore, the asymptotic relationship between low F_{ST} values and the number of migrants mean that a small error in the measurement of F_{ST} value accompanies 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 to reproductive locations in females than males. For example, such an effect is seen in female sea turtles that 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).

Current genetic data from blacktip sharks (Keeney *et al*., unpub. data) indicate that females exhibit a greater degree of reproductive philopatry than males. However, 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 (microsatellite) gene frequencies were measured among four widely spaced nurseries along the Atlantic and Gulf coasts of North America (South Carolina, Gulf coast of Florida, Texas, and Mexican Yucatan). F_{ST} values for mitochondrial markers were highly significant and were approximately 50 times as large as the mostly nonsignificant F_{ST} values for microsatellites. The strong signal in the mtDNA data indicate that females return to the same region for parturition while the lack of signal in nuclear markers indicate a greater degree of malemediated gene flow among regions. Comparisons among three nurseries separated by to 100 to 250 km along the Florida Gulf coast failed to detect significant F_{ST} values for either mtDNA or nuclear markers. 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 detection 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 of the southwest Pacific Ocean and southwest Indian Ocean are more philopatric than males. The non-roaming female vs. roaming male pattern also has been detected for another pelagic lamnid, the shortfin mako shark *Isurus oxyrinchus* (Heist *et al*., unpub. data) as well as for the blacktip shark as mentioned above. This could very well prove to be the rule for shark species in general, but much 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, 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 for sharks comes from a variety of sources including shark meshing programs in South Africa and commercial fisheries in Australia (Walker, 1998).

Data from recreational shark tournaments in Florida in the 1970's and 1980's indicate 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-1980's, 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 in these species could explain the asynchronous, localized declines in recreational catch rate that were observed.

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).

Ramifications for Fisheries Management and Conservation

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 to give birth would have high fitness and pass on their genes. That nursery would, in effect, be "selected for" because it was successful in producing animals that reproduced, and thus the 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 ramifications of this behavior for the management and conservation of shark species.

Shark Nursery Areas: For sharks with natal philopatry, the individual nursery area, however that is geographically defined, has a special value for the population beyond the usual definitions of essential fish habitat. If sharks are not natally 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 takes a very long time, even if the habitat can be recovered. 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 reproduction 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 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 would have 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. And 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 based on the degree of species philopatry. This concept should not be overlooked for sharks just 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 purview 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 animals and fleets that fish for them. But from the standpoint of *fish* management, this could be a challenge 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 is now required by federal law to protect essential fish habitat for managed species, and in the case of philopatric species, this mandate takes on added meaning. The concern with large-scale management of highly migratory species, however, is that the effective protection of these essential areas can be difficult unless there is a dynamic linkage between 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. With the emerging evidence of philopatry in various shark species, however, 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.

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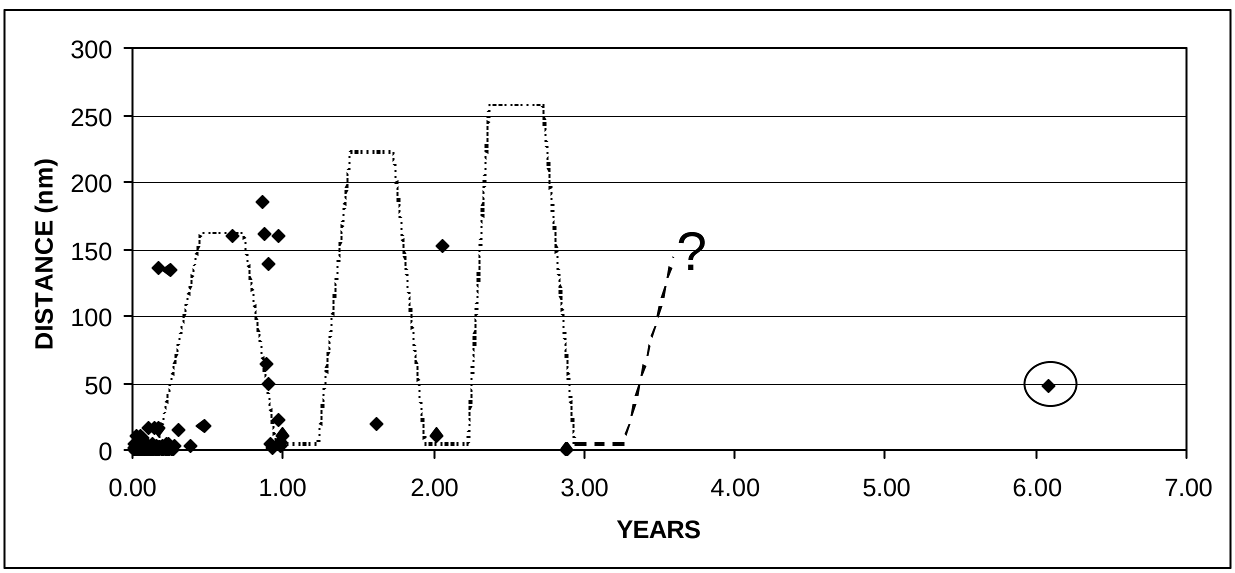

Fig. 1. Recaptures of blacktip sharks (*Carcharhinus limbatus*) tagged in the months of May/June/July (time 0.00 years) along the Florida Gulf coast (n = 94 recaptures). All sharks were juveniles when tagged. YEARS is time at liberty between tagging and recapture; DISTANCE is shortest by-sea distance between tag and recapture sites. Dotted line is hypothetical 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 nm 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.

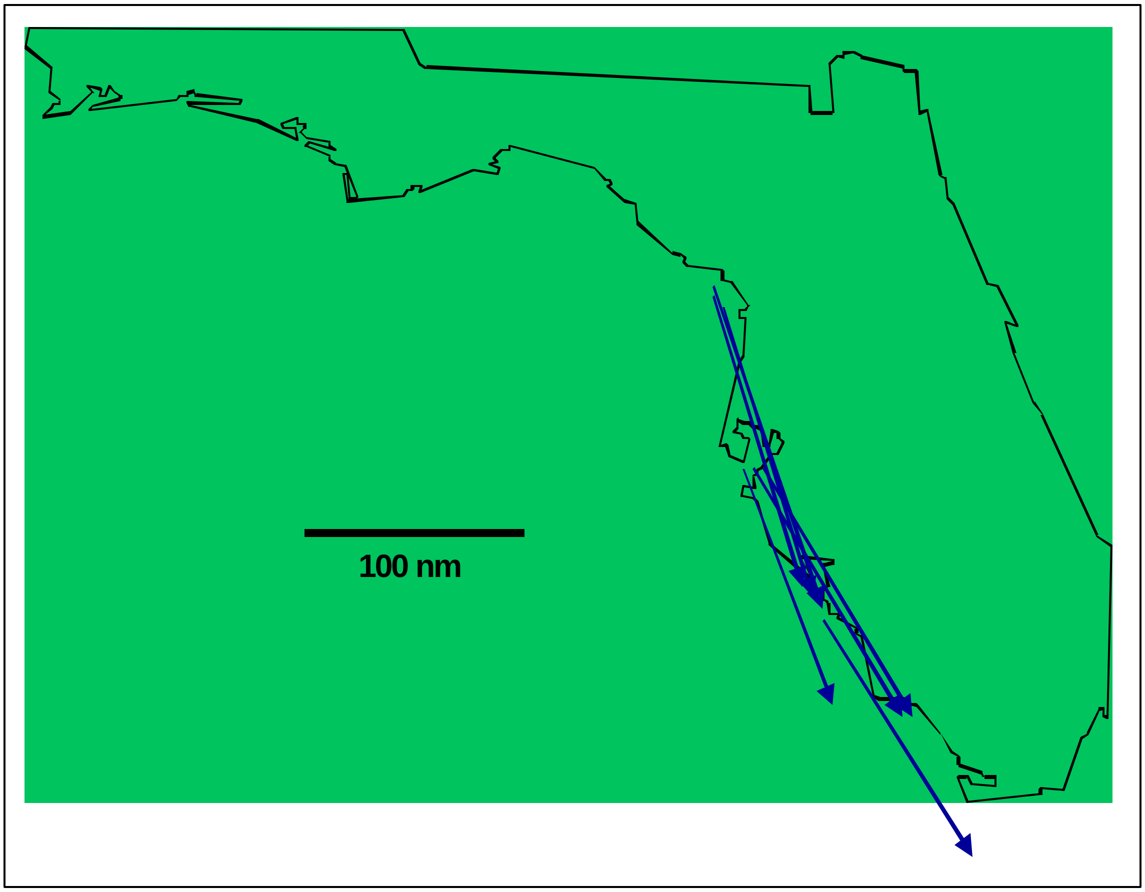

Fig. 2. Recaptures of young blacktip sharks tagged in summer nursery areas and recaptured in winter months. All sharks migrated south over 100 by-sea nm from their natal nursery.