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Primary and secondary nursery areas for leopard and brown smoothhound sharks in San Francisco Bay, California

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Both leopard (*Triakis semifasciata*) and brown smoothhound sharks (*Mustelus henlei)* are inshore species endemic to the eastern Pacific ranging from the Gulf of California to Oregon, with brown smoothhound sharks also found off Ecuador and Peru. Leopard sharks are viviparous without a yolk sac placenta, while brown smoothhound sharks are viviparous with a yolk sac placenta. Both species give birth in the spring to early summer with leopard sharks producing 7 to 36 young about 20 centimeters total length (cm TL), while brown smoothhound sharks give birth to up to 10 young from 19 to 30 cm TL in the spring (Ebert 2003).

In U. S. waters, parturition for both species takes place in several California bays including Humboldt, Tomales, San Francisco and several locations south (Smith and Abramson 1990, Ebert 2003, Ebert and Ebert 2005, Smith 2005, Carlisle et al. 2007, Lewallen et al. 2007, Carlisle and Starr 2009, Russo 2015). These bays are generally composed of a variety of habitats including deepwater channels, shallow mudflats, eelgrass meadows and shoreline marsh sloughs and channels. Elkhorn Slough (Monterey Bay) is a long, winding channel surrounded by marsh and smaller drainages where leopard sharks, but not brown smoothhound sharks, are known to give birth (Ackerman 1971).

Primary nurseries have been defined as places where parturition occurs and neonates in the range of length-at-birth for that species are found and spend the earliest parts of their lives (Bass 1978, Merson and Pratt Jr. 2007). Similarly, secondary nurseries are larger areas where slightly older, but not yet mature, sharks forage and grow, following departure from primary nursery grounds. These definitions and concepts were applied to the determination of physical boundaries of nurseries in this study. Though it varies by species and locale, individual sharks may remain in their primary nurseries from one to three years or return to their natal nurseries seasonally up to nine years after parturition (Springer 1967, Talent 1985, Ebert 1989, Rechisky and Wetherbee 2003, Ebert and Ebert 2005, Heithaus 2007, Heupel et al. 2007, McCandless et al. 2007a, b, Nosal et al. 2014).

Identification of specific nursery habitat for elasmobranchs has been defined as a key component for overall species management (McCandless et al. 2007a, Hussey et al. 2009, Hughes et al. 2014). Generally, San Francisco Bay has long been known among scientists as a "nursery" for leopard sharks, brown smoothhound sharks, broadnose sevengill sharks (*Notorhynchus cepedianus*), and bat rays (*Myliobatis californicus*) (Ebert 1989, Ebert 2003, Russo 2015).

Given the variety and extent of habitats within the bay, however, details of specific parturition sites are lacking for most species. The purpose of this phase of the overall study (1970 to 2001) was to determine primary and secondary nursery habitats for leopard and brown smoothhound sharks within South San Francisco Bay, adding new knowledge to the biology of both species.

Fishing trips were conducted monthly, year-round, weather and equipment availability permitting, at pre-chosen locations to spread coverage and to answer specific data gaps, primarily between coordinates 37° 48' N, 122° 22' W (San Francisco Bay Bridge) and 37° 27' N, 122° 01' W at the entrance of Alviso Slough at the south end of San Francisco Bay (Figures 1, 2). Long-lines, rod and reel, and otter trawls were employed from 1970 to 1996; thereafter rod and reel was used exclusively until 2001. On several occasions, catch events (one date, location, and gear type) occurred in the approximate locations as previously fished as determined by detailed nautical charts, depth, and triangulation. Sampling methods for the overall study included 146 catch events using two 6 mm thick, 152 m long nylon long-lines; 36 catch events using rod and reel (3-5 h, 3-4 rods); and 42 events using a 1.3 cm mesh, 4.8 m otter trawl (7-15 min tow time).

Rod and reel and trawl catch events produced neonates and young-of-the-year (YOY) that were not captured by long-lines due to hook and mesh size selectivity. While long-line efforts were scattered throughout the central part of the South Bay as well as south of the Dumbarton Bridge, otter trawl events were generally restricted to the shallows (<5 m) of the East Bay shoreline and the larger Coyote Creek, the Guadalupe and Alviso Sloughs and near the entrances to Newark and Mowry Slough (Figure 2). Eelgrass meadow locations were largely unknown at the time and were discovered only as a result of initial trawling. Trawling in the narrow channels of Newark, Mowry and Mud Sloughs was determined to be too destructive and dangerous and thus avoided. Although some specimens were sacrificed for diet and reproductive data (Russo 1975, Russo 2018), the over-arching paradigm was "catch and release."

Neonate leopard sharks were defined as specimens presumably within a month or so of parturition, as evidenced by unhealed and visible natal scars located ventrally between the pectoral fins and measuring about 4 mm long (Brewster-Geisz and Miller 2000, Lucifora et al. 2005, Duncan and Holland 2006, Hussey et al. 2010, Aca and Schmidt 2011) and measuring 16 to <25 cm TL. Neonates born within ten days of capture appeared gaunt with slightly concave bellies, as they fed on residual yolk and energy reserves stored in their livers (Francis and Stevens 2000, Mollet et al. 2000) prior to feeding on wild prey. YOY leopard sharks measured >25 to 50 cm TL, while juveniles measured from >50 to 80 cm TL and adult males were >86 cm TL with females >105 cm TL in this overall study (R. Russo unpublished data). Neonate brown smoothhound sharks were defined as specimens born within a month or so and showing unhealed natal scars and measuring 17 to <30.4 cm TL (in this study), while YOY were generally <40 cm TL and adults were >51 cm TL (Yudin and Cailliet 1990, Ebert 2003, Perez-Jimenez and Sosa-Nishizaki 2008). As a means

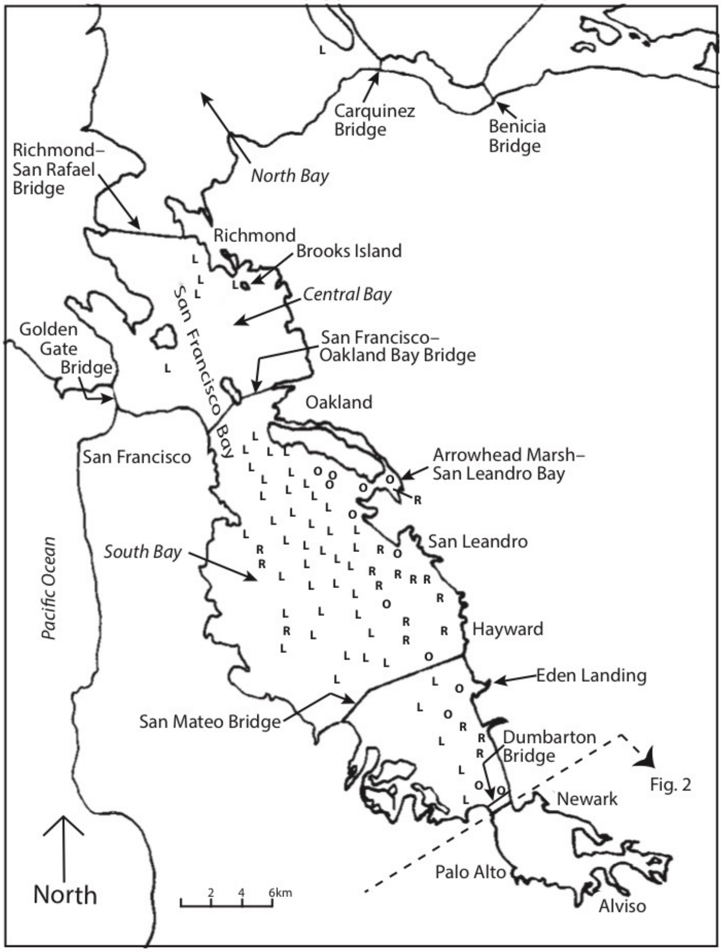

Figure 1.—Map of San Francisco Bay study area showing the locations of 224 sampling events (1970-2001) by gear type with long-lines (L), otter trawl (O), and rod and reel (R). While all otter trawl (n=42) locations are indicated here and in Figure 2, long-line and rod and reel symbols represent one or more catch events of that gear type in that immediate vicinity in many instances. Map courtesy of the East Bay Regional Park District (EBRPD)

of assigning size/life stage categories, size ranges are relative and not finite in that actual individual growth can be influenced by metabolism, food availability, competition, health parasites, and other factors, as we see with most animals.

The mean total length (MTL) was calculated only for the 328 specimens captured in a commercial shrimp trawl. For all specimens captured in this study, careful attention was paid to the size and the condition of each neonate and its natal scar, and YOY such that capture locations could be characterized with regard to their degree of utilization as primary and secondary nursery grounds (Adams and Paperno 2007).

Across the period of the study, 4,121 elasmobranchs were captured, including 2,478 (60.1%) leopard sharks, of which 696 were neonate and YOY specimens from South San Francisco Bay. Additionally, there were 842 (20.4%) brown smoothhound sharks including

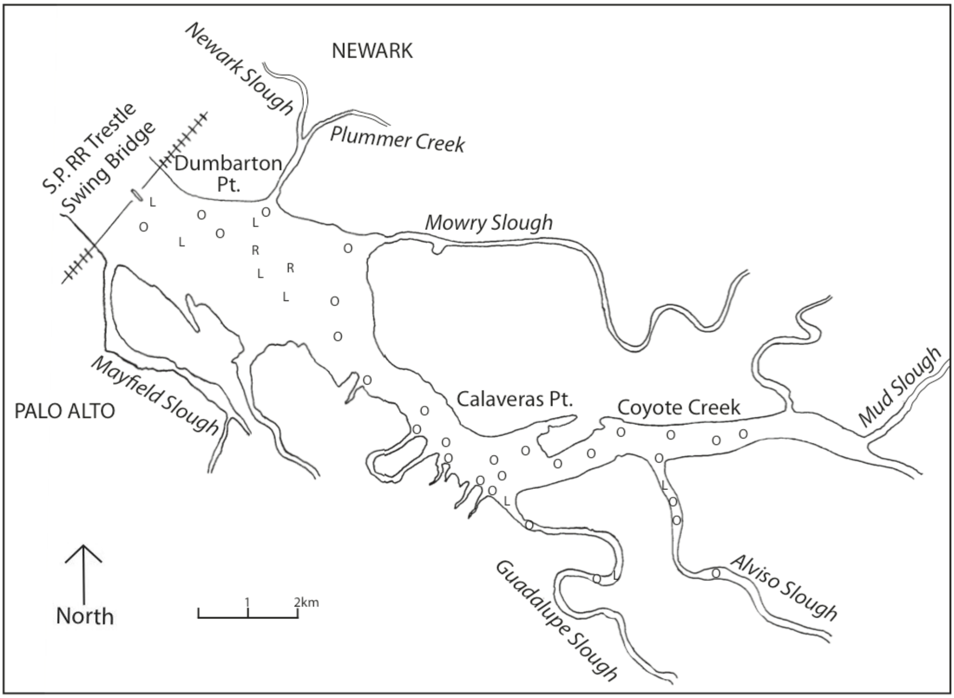

Figure 2.—An expanded view as existed in 1985 of the southern end of South San Francisco Bay, south of the Dumbarton Bridge and the Railroad Trestle where leopard shark neonates and YOY were captured mostly by trawl. Map courtesy of the EBRPD.

234 neonates and YOY; 316 (7.7%) spiny dogfish (*Squalus suckleyi*) adults and juveniles; 107 (2.6%) juvenile tope sharks (*Galeorhinus galeus*); 126 (3.1%) broadnose sevengill sharks of all age classes; 239 (5.8%) bat rays of all age classes; and 13 (0.3%) adult big skate (*Raja binoculata*). On 23 May 1979 while on board a commercial shrimp trawler in the Alviso Slough area (Russo 2015), an additional 328 recently born leopard shark neonates ranging from 17 to 21 cm (19.4 cm MTL) were superficially examined (length, sex, general condition) as bycatch.

Overall, leopard shark neonates ranged in size from 16.5 to 25 cm TL with the 16.5 cm neonate caught by otter trawl on 21 May 1982 being the smallest reported thus far in the literature. Brown smoothhound shark neonates ranged in size from 17.5 to 30.4 cm TL, in contrast to the literature.

The use of otter trawl and rod and reel throughout the South Bay (Table 1) resulted in captures of neonate (*n* = 378) and YOY (*n* = 318) leopard sharks at the entrances to Mowry and Newark Sloughs (Figure 2), within Coyote Creek and Guadalupe and Alviso Sloughs and around the edges of Arrowhead Marsh in the East Bay (Figure 3) and, to a lesser extent, in near-shore eelgrass meadows.

Results of the sampling (Table 1) indicate that brown smoothhound neonates and YOY strongly preferred eelgrass habitat, while leopard shark neonates and YOY primarily utilized marsh sloughs and channels, and to a lesser extent eelgrass meadows. Both tended to move

Table 1.—Catch locations (1970-2001) for 3,320 sharks including 2,478 leopard sharks and 842 brown smoothhound sharks by approximate age classes as related to habitat of capture with the number of sharks (N) and the percentage (%) for that growth phase. Each growth phase per species is also calculated for Total percentage (%) compared to other growth phases. Size/life stage categories are as found in this study and from the literature.

Life Stage	Open Bay >5m to <11 m N / %	Eel Grass Meadows <3m N / %	Marsh Sloughs N / %	Total N / %
		Leopard Shark		
Neonate	-	81 (21.4)	297 (78.6)	378 (15.2)
YOY*	18 (5.6)	94 (29.6)	206 (64.8)	318 (12.8)
Juvenile	983 (94.6)	21 (2.0)	35 (3.4)	1,039 (41.9)
Adult	634 (85.3)	36 (4.9)	73 (9.8)	743 (30.0)
		Brown Smoothhound Shark		
Neonate	1 (0.7)	132 (99.3)	-	133 (15.8)
YOY*	14 (13.9)	87 (86.1)	-	101 (12.0)
Juvenile	188 (87.8)	26 (12.2)	-	214 (25.4)
Adult	367 (93.2)	27 (6.8)	-	394 (46.8)

*YOY = young-of-the-year

out into open Bay as older juveniles. Of the 378 neonates captured by trawl and rod and reel, 297 (78.6%) were captured in sloughs and channels, while 81 (21.4%) were captured in eelgrass (Table 1). Similarly, of the 318 YOY leopard sharks captured, 206 (64.8%) were captured in sloughs and channels, while 94 (29.6%) were captured in eelgrass. A small, size-related aggregation of YOY (n = 18, 5.6%) leopard sharks all within 15.2 cm of each other (R. Russo, unpublished data) were captured by long-line in open water between 5 to 7 m deep. While most of the juvenile leopard sharks (n = 983, 94.6%) were captured in deep water <10 m by long-line, a relatively small number were captured in eelgrass (n = 21, 2.0%) or in marsh sloughs and channels (n = 35, 3.4%) by other methods. Similarly, most adult leopard sharks (n = 634, 85.3%) were captured by long-line in deep water >7 m, while 36 (4.9%) were caught by trawl and rod and reel in eelgrass and 73 (9.8%) were captured by all methods in marsh sloughs and channels primarily south of the Dumbarton Bridge.

The captures of juvenile and adult leopard sharks in eelgrass and marsh sloughs and channels usually coincided with parturition and mating period of April through June. Leopard shark neonates were captured along the East Bay shoreline north of the San Mateo Bridge in April and May, but were not captured south of the Dumbarton Bridge until the first week of June. Sexually mature leopard shark females (n = 19) captured by long-line at the entrance to Mowry Slough were examined 21 June 1971 with 13 (68.4%) recently impregnated having uterine embryos. The remaining six (31.6%) had experienced parturition, but had empty uterine canals and had not yet been re-impregnated by this date.

Over 99% of brown smoothhound shark neonates (n = 132) were captured in near-shore eelgrass meadows (Table 1), with one rare exception of a 30.4 cm TL neonate being

Figure 3.—Aerial view of Arrowhead Marsh (foreground) in 1990, which is part of the Martin Luther King Jr. Memorial Shoreline Regional Park in San Leandro Bay and east of the Oakland Airport with Bay Farm Island at the water's edge, the outer Bay and San Francisco in the background. Photo courtesy of Steve Bobzien.

captured in water 10.7 m deep, which was likely the result of an accidental, premature birth. Of the 101 YOY captured, 87 (86.1%) were found in eelgrass meadows with only 14 (13.9%) found in deeper water (<7 m deep) immediately adjoining eelgrass meadows. All neonate and YOY brown smoothhound sharks were captured by trawl or rod and reel with most neonates captured in May. The majority of juvenile brown smoothhounds (n = 188, 87.8%) and adults (n = 367, 93.2%) were captured by long-line in deep water <11 m, while nearly an equal number of juveniles (n = 26, 12.2%) and adults (n = 27, 6.8%) were captured by trawl or rod and reel in eelgrass meadows generally in May and June. No brown smoothhound sharks were captured south of the Dumbarton Bridge nor in marsh sloughs or channels. Thus eelgrass meadows north of the bridge were found to be the most important primary nursery habitat for neonate and YOY brown smoothhounds.

Trawling helped define eelgrass meadows along the East Bay shoreline that occupy a relatively narrow zone usually within a few hundred meters of shore, ranging from 10 m to 30 m in width given slope, depth, and light penetration sufficient to sustain the eelgrass, but generally in 2.5 to 3.5 m of water. In South San Francisco Bay, the eelgrass meadows along the eastern shoreline are rarely if ever exposed at low tide, making these meadows suitable for brown smoothhound shark and some leopard shark parturition, but at the same time exposing them to avian predators at low tide (Russo 2015).

Non-eelgrass meadows or open Bay secondary nursery habitat was more difficult to quantify as the topography of the South Bay from the East Bay shoreline to the San Francisco Peninsula is a gently tapering mud-covered slope that gradually becomes deeper to about 20 m near the Peninsula shoreline. Therefore, no clear demarcation lines or shear drop-offs help define a secondary nursery boundary. Evidence of secondary nursery site activity can be deduced only from species composition and size combined with catch-event locations.

Based on analysis of trawl and rod and reel data collected in this study, past observations of avian predators capturing neonate and YOY leopard sharks in marsh sloughs and channels (Russo 2015), eyewitness reports of leopard sharks mating in marsh sloughs and channels (T. Laine, personal communication, Mowry Slough, 23 June 1978; L. Fancher, personal communication, Newark Slough, 29 June 1981) and a report of a kayaker in Newark Slough seeing "baby" leopard sharks (L. Jones, personal communication, 18 June 1986; R. Russo unpublished data), the primary nursery sites for leopard sharks are salt marsh sloughs and channels in the East Bay and extreme southern end of the Bay, especially those that retain water at low tide, as well as adjoining eelgrass meadows. Evidence also indicates a large number of neonates concentrated near Coyote Creek and Alviso and Guadalupe Sloughs south of the Dumbarton Bridge (Figures 1, 2).

Collection data also indicate that the primary nursery sites for brown smoothhound sharks are limited to near-shore eelgrass meadows of the East Bay, largely between the Oakland Airport and the San Mateo Bridge, but possible elsewhere along the western shoreline where eelgrass may grow. Because brown smoothhound shark neonates were not captured south of the Dumbarton Bridge or observed among the commercial shrimp trawls of May 1979 (Russo 2015) in the Alviso Slough area, the neonates of this species appear to have a more restricted primary nursery area than leopard sharks, at least in the East Bay.

The 20-hectare Arrowhead Marsh (Figure 3) in San Leandro Bay along the northeastern shoreline of South San Francisco Bay under the management of the East Bay Regional Park District is a significant primary nursery for leopard sharks north of the Dumbarton Bridge, as evidenced by two May trawl events capturing 47 neonates estimated to be <10 d old given their physical condition.

The secondary nursery sites for YOY of both species appear to be a large portion of the South Bay in water <8 m deep with some overlap. Leopard shark YOY appear to wander more from primary nursery sites than do brown smoothhound shark YOY who appear to stay within a few km of eelgrass meadows based on where they were captured (Table 1). The deep-water channel is from 15 to 20 m deep and generally within 1 km of the West Bay shoreline. This deep-water habitat is dangerous for smaller sharks as sevengill sharks 2 to 3 m long patrol the area and have been known to attack sharks caught on long-lines (Russo 2015). Only juveniles and adults of both species were caught in this environment.

Since tag studies indicate leopard sharks are largely residential in San Francisco Bay (Smith et al. 2003) and considering San Francisco Bay is the largest estuarine environment in the range of this species (Conomos et al. 1985), this Bay may well represent the largest primary and secondary nurseries for leopard sharks and perhaps brown smoothhound sharks throughout their range. There are an estimated 20,234 hectares of salt marsh habitat in San Francisco Bay (M. Salomon, San Francisco Estuary Institute, personal communication 13 March 2018). While not all marshland sloughs and channels and eelgrass meadows may function in this manner, there are some that are worthy of evaluation. The western shoreline areas adjoining Palo Alto, Redwood City, and San Mateo may also serve as primary nursery sites for these two species, but must be studied to confirm this usage (Heupel et al. 2007). Similarly, the marshland and eelgrass meadows of the North Bay near Tiburon and the Napa and Petaluma Rivers along with the vast marshlands west of Mare Island may have similar value.

Finally, 17 years have passed since this research, and physical changes in the available marshes and eelgrass meadows, especially in the southern extreme of South San Francisco Bay, may have occurred due to human impacts or environmental changes, compromising their value. The potential for primary nursery grounds for both shark species may have degraded or may be far more extensive than described herein and should be explored to develop a much more comprehensive understanding. The marsh sloughs and channels and shallow-water eelgrass meadows of San Francisco Bay should be considered ever more important in light of these findings in the overall management of these sharks.

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Literature Cited

Aca, E. Q., and J. V. Schmidt. 2011. Revised size limit for viability in the wild: neonatal and young of the year whale sharks identified in the Philippines. Asia Life Sciences 20(2):361-367.

Ackerman, L. T. 1971. Contributions to the biology of leopard sharks, *Triakis semifasciata* (Girard) in Elkhorn Slough, Monterey, California. M.A. Thesis, Sacramento State College, Sacramento, California. USA.

Adams, D. H., and R. Paperno. 2007. Preliminary assessment of a near-shore nursery ground for the scalloped hammerhead off the Atlantic Coast of Florida. American Fisheries Society Symposium 50:165-174.

Bass, A. J. 1978. Problems in the studies of sharks in the southwest Indian Ocean. Pages 545-594 *in* E. S. Hodgeson and R. F. Mathewson, editors. Sensory biology of-sharks, skates, and rays. Department of the Navy, Office of Naval Research, Arlington, Virginia. USA.

Brewster-Geisz, K. K., and T. J. Miller. 2000. Management of the sandbar shark, *Carcharhinus plumbeus*: implications of a stage-based model. Fishery Bulletin 98:236-249.

Carlisle, A., A. King, G. M. Cailliet, and J. S. Brennan. 2007. Long-term trends in catch composition from elasmobranch derbies in Elkhorn Slough, California. Marine Fisheries Review, NOAA 69:25-45.

Carlisle, A. B., and R. M. Starr. 2009. Habitat use, residency, and seasonal distribution of female leopard sharks *Triakis semifasciata* in Elkhorn Slough, California. Marine Ecology Progress Series 380:213-228.

Conomos, T. J., R. E. Smith, and J. W. Gartner. 1985. Environmental setting of San Francisco Bay. Hydrobiologia 129:1-12.

Duncan, K. M., and K. N. Holland. 2006. Habitat use, growth rates and dispersal patterns of juvenile scalloped hammerhead sharks *Sphyrna lewini* in a nursery habitat. Marine Ecology Progress Series 312:211-221.

Ebert, D. A. 1989. Life history of the Sevengill shark, *Notorynchus cepedianus* Peron 1807, in two northern California bays. California Fish and Game 75:102-112.

Ebert, D. A. 2003. Sharks, rays, and chimaeras of California. California Natural History Guide 71. University of California Press. Berkeley, California. USA.

Ebert, D. A., and T. B. Ebert. 2005. Reproduction, diet, and habitat use of leopard sharks, *Triakis semifasciata* (Girard), in Humboldt Bay, California, USA. Marine and Freshwater Research 56:1089-1098.

Francis, M. P., and J. D. Stevens. 2000. Reproduction, embryonic development, and growth of the porbeagle shark, *Lamna nasus*, in the southwest Pacific Ocean. Fishery Bulletin 98:41-63.

Heithaus, M. R. 2007. Nursery areas as essential shark habitats: a theoretical perspective. Pages 3-13 *in* McCandless, C. T., N. E. Kohler, and H. L. Pratt Jr. editors. Shark nursery grounds of the Gulf of Mexico and the East Coast waters of the United States. American Fisheries Society Symposium 50:35-43.

Heupel, M. R., J. K. Carlson, and C. A. Simpfendorfer. 2007. Shark nursery areas:concepts, definition, characterization and assumptions. Marine Ecology Progress Series 337:287-297.

Hughes, B. B., M. D. Levey, J. A. Brown, M. C. Fountain, A. B. Carlisle, S. Y. Litvin, C. M. Greene, W. N. Heady, and M. G. Gleason. 2014. Nursery functions of U. S. west coast estuaries: the state of knowledge for juveniles of focal invertebrates and fish species. The Nature Conservancy, Arlington, Virginia. USA.

Hussey, N. E., J. D. McCarthy, S. F. J. Dudley, and B. Q. Mann. 2009. Nursery grounds, movement patterns and growth rates of dusky sharks *Carcharhinus obscurus*: a long-term tag and release study in South African waters. Marine and Freshwater Research 60:571-583.

Hussey, N. E., S. P. Wintner, S. F. Dudley, G. Cliff, D. T. Cocks, and M. A. MacNeil. 2010. Maternal investment and size-specific reproductive output in carcharhinid sharks. Journal of Animal Ecology 79:184-193.

Lewallen, E. A., T. W. Anderson, and A. J. Bohonak. 2007. Genetic structure of leopard shark (*Triakis semifasciata*) populations in California waters. Marine Biology 152:599-609.

Lucifora, L. O., R. C. Menni, and A. H. Escalante. 2005. Reproduction, abundance and feeding habits of broadnose sevengill shark *Notorhynchus cepedianus* in north Patagonia, Argentina. Marine Ecology Progress Series 289:237-244.

McCandless, C. T., N. E. Kohler, and H. L. Pratt, Jr. 2007a. Shark nursery grounds of the Gulf of Mexico and the East Coast waters of the United States. American Fisheries Society, Bethesda, Maryland, USA.

McCandless, C. T., H. L. Pratt, Jr., N. E. Kohler, R. R. Merson, and C. W. Recksiek. 2007b. Distribution, localized abundance, movements, and migrations of juvenile sandbar sharks tagged in Delaware Bay. Pages 45-62 in C. T. McCandless, N. E. Kohler, and H. L. Pratt, Jr., editors. Shark nursery grounds of the Gulf of Mexico and the East Coast waters of the United States. American Fisheries Society, Bethesda, Maryland, USA.

Merson, R. R., and H. L. Pratt, Jr. 2007. Sandbar shark nurseries in New Jersey and New York: evidence of northern pupping grounds along the United States East Coast. Pages 35-43 *in* McCandless, C. T., N. E. Kohler, and H. L. Pratt, Jr., editors. Shark nursery grounds of the Gulf of Mexico and the East Coast waters of the United States. American Fisheries Society, Bethesda, Maryland, USA.

Mollet, H. F., G. Cliff, H. L. Pratt, Jr., and J. D. Stevens. 2000. Reproductive biology of the female shortfin mako, *Isurus oxyrinchus*, Rafinesque 1810, with comments on the embryonic development of lamnoids. Fishery Bulletin 98:299-318.

Nosal, A. P., A. Caillat, E. K. Kisfaludy, M. A. Royer, and N. C. Wegner. 2014. Aggregation behavior and seasonal philopatry in male and female leopard sharks *Triakis semifasciata* along the open coast of southern California, USA. Marine Ecology Progress Series 499:157-175.

Perez-Jimenez, J. C., and O. Sosa-Nishizaki. 2008. Reproductive biology of the brown smoothhound shark *Mustelus henlei*, in the northern Gulf of California, Mexico. Journal of Fish Biology 73:782-792.

Rechisky, E. L., and B. M. Wetherbee. 2003. Short-term movements of juvenile and neonate sandbar sharks, *Carcharhinus plumbeus*, on their nursery grounds in Delaware Bay. Environmental Biology of Fishes 68:113-128.

Russo, R. A. 1975. Observations on the food habits of leopard sharks, *Triakis semifasciata* and brown smoothhounds, *Mustelus henlei*. California Fish and Game 61:68-81.

Russo, R. A. 2015. Observations of predation and loss among leopard sharks and brown smoothhounds in San Francisco Bay, California. California Fish and Game 101:149-157.

Russo, R. A. 2018. Prey of neonate leopard sharks in San Francisco Bay, California. California Fish and Game 104:173-179.

Smith, S. E., and N. J. Abramson. 1990. Leopard shark *Triakis semifasciata* distribution, mortality rate, yield, and stock replenishment estimates based on a tagging study in San Francisco Bay. Fishery Bulletin 88:371-381.

Smith, S. E., R. A. Mitchell, and D. Fuller. 2003. Age-validation of a leopard shark, *Triakis semifasciata*, recaptured after 20 years. Fishery Bulletin 101:194-198.

Smith, S. E. 2005. Leopard shark mating observed off La Jolla, California. California Fish and Game 91:128-135.

Springer, S. 1967. Social organization of shark populations. Pages 149-174 *in* P. Gilbert, R. F. Mathewson, and D. P. Rall, editors. Sharks, Skates, and Rays. Johns Hopkins Press: Baltimore, Maryland. USA.

Talent, L. G. 1985. The occurrence, seasonal distribution, and reproductive condition of elasmobranch fishes in Elkhorn Slough, California. California Fish and Game 71:210-219.

Yudin, K. G., and G. M. Cailliet. 1990. Age and growth of the gray smoothhound, *Mustelus californicus*, and the brown smoothhound, *Mustelus henlei*, sharks from Central California. Copeia 1:191-204.

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