

Abstract—Information on the seasonal abundance and distribution of whale sharks (*Rhincodon typus*) is largely unknown throughout range of the species. Between 1989 and 1998, three spatially and temporally intensive aerial surveys were conducted by the National Marine Fisheries Service, Mississippi Laboratories that provided information on seasonality, distribution, and aggregations of whale sharks in the northern Gulf of Mexico. Transects totaling 89,369 km were surveyed over the course of the study and a total of 119 whale sharks were counted during 81 sighting events. There was no statistical difference in the sightings per unit of effort (SPUE) of whale sharks between the eastern and western continental slope waters of the Gulf of Mexico. In the continental slope waters of the eastern Gulf of Mexico, whale sharks were more abundant during the summer than in the winter. In the western Gulf of Mexico, whale shark SPUE was significantly greater in the summer than during the fall or winter; there was no significant difference between summer and spring. There was also no significant difference in whale shark SPUE among spring, fall, and winter in the western Gulf of Mexico. Aggregations of whale sharks were seen only during the winter and summer, and there were significantly more individuals per aggregation during the summer. The largest aggregation of whale sharks observed during the study consisted of 23 individuals.

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Abundance and distribution of whale sharks (*Rhincodon typus*) in the northern Gulf of Mexico

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Whale sharks (*Rhincodon typus*) are distributed in all tropical and subtropical marine waters of the world, with the exception of the Mediterranean Sea (Compagno, 1984). This species is considered vulnerable to extinction according to the World Conservation Union (IUCN)¹ partly because of a lack of information pertaining to its life history. Although the seasonality of whale sharks has been examined in two geographically discrete areas (Taylor, 1996; Duffy, 2002), no information exists for the seasonal distribution or relative seasonal abundance of this species over a broad spatial scale. The paucity of such information is probably attributable to logistical difficulties associated with collecting required data or to the expense of surveying large areas.

Whale sharks aggregate in areas of high biological productivity, and seasonal abundance of whale sharks could result from increased localized prey abundance. Whale sharks feed on a variety of organisms including invertebrates and teleosts (Compagno, 1984). Unlike basking (*Cetorhinus maximus*) and megamouth (*Megachasma pelagios*) sharks, which passively filter prey from the water column, whale sharks are capable of suction filter feeding (Colman, 1997). Although this feeding strategy enables whale sharks to capture a wider range of prey in terms of size, mobility, and diversity than other filter feeding elasmobranchs, this feeding strategy requires dense aggregations

of prey in order for whale sharks to meet their energetic demands (Compagno, 1984). Feeding aggregations of whale sharks have been reported in the Atlantic, Indian, and Pacific Oceans and specifically in the waters off Belize, Western Australia, the Galapagos Islands, Mexico, New Zealand, and Thailand (Taylor, 1996; Clark and Nelson, 1997; Colman, 1997; Eckert and Stewart, 2001; Heyman et al., 2001; Wilson et al., 2001; Duffy, 2002).

The whale shark was first described in 1828 from a type specimen collected off the coast of South Africa (Penrith, 1972). The first record of a whale shark in the western North Atlantic Ocean was not reported until 1902 and it was 1937 before this species was documented in the Gulf of Mexico (Gudger, 1939; Baughman and Springer, 1950; Breuer, 1954). Since 1937 several authors have reported sightings of whale sharks in the Gulf of Mexico (Gudger, 1939, 1941; Baughman, 1947, 1950, 1955; Gunter and Knapp, 1951; Breuer, 1954; Springer, 1957; Clark and von Schmidt, 1965; Hoffman et al., 1981; Hoffmayer et al., 2005). However, these reports are restricted to spatially discrete areas, and most are primarily anecdotal and largely based on isolated observations of few individuals. In the present study we report the seasonality, rela-

¹ The World Conservation Union. 2005. <http://www.redlist.org> [accessed 5 January, 2006].

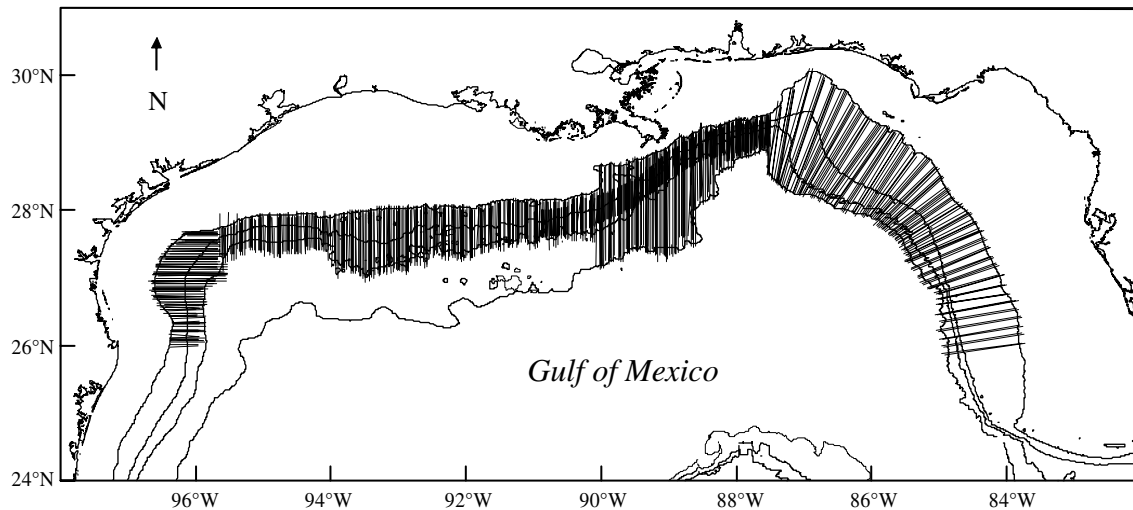


Figure 1

Transect lines surveyed by aircraft during three aerial studies conducted in the northern Gulf of Mexico from 1989 to 1998. Note that some lines overlap others, particularly in the eastern Gulf of Mexico. Bathymetric contours represent the 100-, 500-, 1000- and 2000-meter contours.

tive seasonal abundance, distribution, and aggregations of whale sharks observed in the northern Gulf of Mexico during three spatially and temporally intensive aerial surveys conducted by the National Marine Fisheries Service, Mississippi Laboratories.

Materials and methods

Between 1989 and 1998, three aerial surveys were conducted in the northern Gulf of Mexico with a DeHavilland Twin Otter turbine engine aircraft. The primary objective of one of these surveys, referred to as the Upper Continental Slope (UCS) Survey, was to examine species composition, distribution, and seasonality of cetaceans in the north-central Gulf of Mexico (Mullin et al., 1994). The purpose of the other two surveys, referred to as the Gulf of Mexico Cetacean Studies I (GulfCet I) and Gulf of Mexico Cetacean Studies II (GulfCet II) (Mullin and Hoggard²) surveys, was to assess possible impacts of petroleum industry activities on cetaceans and sea turtles in the Gulf of Mexico. Standard line-transect sampling methods were used for each survey (Buckland et al., 1993). Surveys were flown at a constant altitude and air speed of 229 m and 200 km/h, respectively. The aircraft was modified with a Plexiglas observation bubble on the port and starboard sides of the fuselage to permit an unobstructed view of the area along transect lines and a lateral view to each horizon. When fauna

of interest were sighted, the pilot circled the area until all observed fauna were identified to the lowest possible taxa and the latitude and longitude of the sighting and numbers of conspecifics sighted were recorded. All survey effort was limited to waters associated with the continental slope in Beaufort sea states less than 4 and restricted to areas within the United States Exclusive Economic Zone (EEZ; Fig. 1). For all analyses and discussion, seasons were defined as spring (April–June), summer (July–September), fall (October–December), and winter (January–March).

The UCS survey was conducted from the summer of 1989 through the spring of 1990 and was carried out during all four seasons. The study area was located in the central northern Gulf of Mexico along the continental shelf break (~200-m isobath) south of the Mississippi River Delta and extended from the DeSoto Canyon (87°00'W) to the western edge of the Mississippi Trough (90°05'W). GulfCet I surveys occurred from 1992 to 1994 over continental slope waters in the western Gulf of Mexico between the United States and Mexico border (25°57'N) and the Mississippi–Alabama border (88°25'W) and were conducted during all four seasons (Mullin et al., 2004). GulfCet I transects began at the 100-m isobath and extended to the 1000-m isobath west of 90°00'W, and to the 2000-m isobath east of 90°00'W. GulfCet II surveys were conducted only during the winter and summer between 1996 and 1998 in the northeastern Gulf of Mexico and covered continental slope waters (100–2000 m deep) and a portion of the continental shelf (Mullin and Hoggard²). The entire spatial range of the three areas was surveyed within each season of operations. Because of the spatial overlap of the UCS and GulfCet II surveys, the central northern Gulf of Mexico and the western Gulf of Mexico were treated as a single region, referred to as “the western

² Mullin, K. D., and W. Hoggard. 2000. Visual surveys of cetaceans and sea turtles from aircraft and ships. In OCS Study MMS 96-0027, vol. II, Cetaceans, sea turtles and seabirds in the northern Gulf of Mexico: distribution, abundance and habitat associations (R. W. Davis, W. E. Evans, and D. Würsig, eds.), p. 111–172. Minerals Management Service, Gulf of Mexico OCS Region, New Orleans, LA 70123.

Table 1

Summary of survey effort, number of whale shark (*Rhincodon typus*) sightings, and sightings per unit of effort (SPUE) by region, season, and survey. UCS=upper continental survey; GulfCetI=Gulf of Mexico Cetacean Studies I; GulfCet II=Gulf of Mexico Cetacean Studies II.

Survey and region covered	Season	Effort (km)	Number of sharks	SPUE
UCS—western Gulf of Mexico	winter	4382	1	0.23
	spring	7615	8	1.05
	summer	5321	14	2.63
	fall	3275	0	0.00
GulfCet I—western Gulf of Mexico	winter	12,645	13	1.03
	spring	12,645	20	1.58
	summer	12,942	43	3.32
	fall	11,756	7	0.60
GulfCet II—eastern Gulf of Mexico	winter	8348	3	0.36
	summer	10,440	10	0.96

Gulf of Mexico,” in this article. Mobile Bay, Alabama (88°00'W) was considered to be the dividing line between the eastern and western Gulf of Mexico.

Sightings per unit of effort (SPUE) were calculated to correct for unequal effort among regions by dividing the number of sightings per season by the total survey effort during the same season and then multiplying the resulting value by 1000. Because aerial surveys were limited to summer and winter in the eastern Gulf of Mexico, data from these two seasons in this region were compared (by using a *t*-test) to data collected during surveys in the same two seasons in the western Gulf of Mexico to determine if mean whale shark SPUE was significantly different between the two areas. To determine if there was a season of peak whale shark SPUE in the western Gulf of Mexico a one-way analysis of variance (ANOVA) and the Student-Newman-Keuls test were employed. The Mann-Whitney test was used to determine if there was a significant relationship between season and number of individuals per aggregation. This test was selected because of the non-Gaussian distribution of these data. The location of each whale shark sighting was plotted on navigational charts, produced by the National Oceanic and Atmospheric Administration (Chart numbers 11006, 11300, 11340), to examine the associations of whale sharks with bathymetric features such as reefs and salt diapirs. Statistical tests were performed according to the methods of Zar (1999) at a significance level of $P \leq 0.05$.

Results

Transects totaling 89,369 km were surveyed over the course of the study (Table 1). A total of 119 whale sharks were counted during 81 sighting events (Fig. 2). There was no statistical difference in the SPUE of whale sharks between the eastern and western continental slope waters of the Gulf of Mexico (*t*-test, $df=4$, t -value=1.06,

$P=0.35$). Because survey effort in the eastern Gulf of Mexico was limited to summer and winter, it was not possible to quantitatively analyze whale shark seasonality in this region. However, results indicated that whale sharks are more abundant in the eastern Gulf of Mexico during the summer (SPUE=0.96) than in the winter (SPUE=0.36). There was a statistically significant difference in whale shark SPUE among seasons in the western Gulf of Mexico (ANOVA, $df=7$, F -ratio=12.97, $P=0.02$). The Student-Newman-Keuls test indicated that whale shark SPUE was significantly greater in the summer ($\bar{x}=2.98$, $SD=0.49$) than during the fall ($\bar{x}=0.30$, $SD=0.18$) or winter ($\bar{x}=0.63$, $SD=0.32$). However, there was no significant difference between summer and spring ($\bar{x}=1.32$, $SD=0.38$). There was no significant difference in whale shark SPUE among spring, fall, and winter.

Of the 119 whale sharks sighted over the course of the study, 45 were observed in aggregations—an aggregation being defined as the presence of two or more whale sharks in close proximity to one another. Seven aggregations, ranging in size from 2 to 23 individuals, were observed. Aggregations of whale sharks were seen only during the winter and summer and there were significantly more individuals per aggregation during the summer (Mann-Whitney test, $W=12.0$, $P=0.05$). Sixty-two percent ($n=74$) of whale sharks were not observed in association with conspecifics.

The majority of whale sharks observed were not associated with discrete areas of high bathymetric relief. Thirty-four of the whale sharks sighted were in close proximity to relatively small, high relief diapiric features dominated by coralline algae (Rezak et al., 1990); Ewing Bank (28°06'N, 91°02'W), Bright Bank (27°53'N, 93°18'W) and 28 Fathom Bank (27°55'N, 93°26'W). Of the seven aggregations observed during the surveys, three were associated with the aforementioned banks including the aggregation consisting of 23 individuals. The area of highest whale shark abundance was located in an area of approximately 16,800 km² and

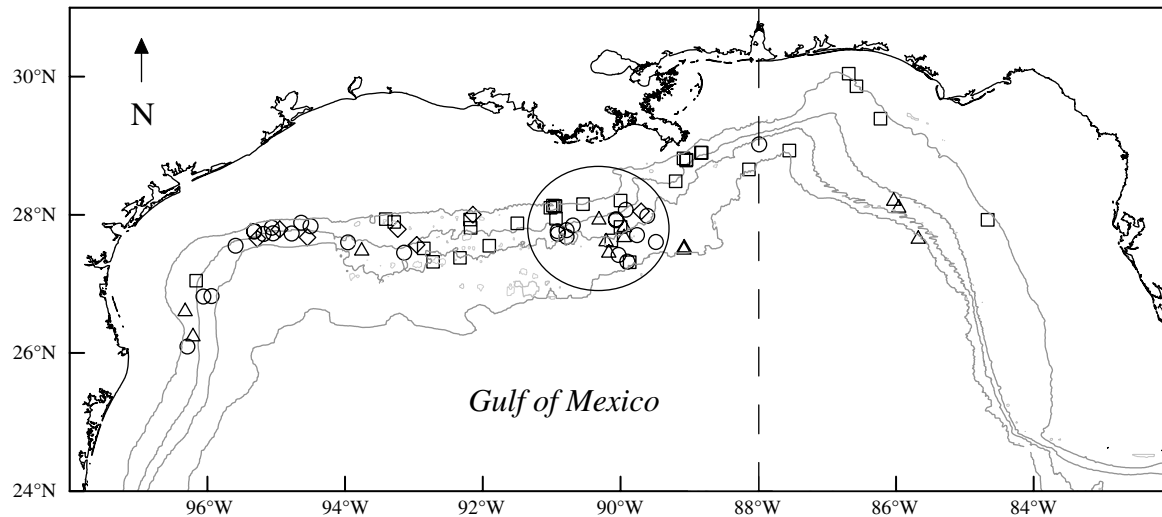


Figure 2

Locations ($n=81$) of whale sharks (*Rhincodon typus*) observed during aerial surveys in the northern Gulf of Mexico from 1989 to 1998. Dashed line demarks the separation between the eastern and western Gulf of Mexico as defined in our study. Area contained within the circle indicates region of highest observed whale shark abundance. Bathymetric contours represent the 100-, 500-, 1000- and 2000-meter contours. Location and season of sighting symbols: \triangle = winter, \circ = spring, \square = summer, \diamond = fall.

the center of their distribution was approximately 140 km southwest of the Mississippi River Southwest Pass (Fig. 2). Twenty-seven whale sharks were observed in this region over a four-year period.

Discussion

We observed whale sharks throughout the year in the Gulf of Mexico, and our study is the first to identify a broad region where whale sharks are present during all seasons and where they are perhaps resident throughout the year. The highest SPUE values that we observed occurred during the summer. Therefore, given the reported seasonality of whale sharks in the western Caribbean Sea (Heyman et al., 2001) and southeastern Gulf of Mexico (Gudger, 1941), it is reasonable to assume that a portion of the population migrates into the northern Gulf of Mexico during the spring and in winter moves into lower latitude waters, such as the Bay of Campeche and waters off the coast of Cuba. The only entrances to the Gulf of Mexico are through the Yucatan Channel and the Straits of Florida; therefore research with telemetry and satellite tagging in these regions would help determine the timing and routes of whale shark migrations and the period of residency within the Gulf of Mexico.

Whale sharks are more abundant in the western than in the eastern Gulf of Mexico. However, because the aerial surveys were limited to two seasons in the eastern Gulf of Mexico, little can be inferred from our data, except confirmation of the presence of whale sharks in the eastern Gulf of Mexico during the winter and the addition of summer to the seasonality of occurrence in

this region. Because the survey reported in our study focused solely on continental slope waters, it is possible that whale sharks in the eastern Gulf of Mexico use continental shelf waters to a greater extent and, thus, were outside of the sampled area. Despite extensive effort over the broad upper continental slope off the west coast of Florida, no whale sharks were observed south of 27°38'N. However, at higher latitudes, 13 individuals were sighted in continental slope waters at depths ranging from 70 to 180 m. Because the upper continental slope is broader in the eastern than in the western Gulf of Mexico, it is possible that whale shark distribution in the eastern Gulf of Mexico is more diffuse than would be expected, especially if this species is associated with steep bathymetric relief, which promotes upwelling of nutrient rich waters. During our study, two whale sharks were observed at the head of the DeSoto Canyon, an upwelling area south of the Florida panhandle. A large aggregation (30–100 individuals) was found in this same area by Hoffmayer et al. (2005).

In the western Gulf of Mexico, whale sharks were observed in all sampled depth strata, and the spatial distribution of sightings was fairly continuous along the continental slope from Mobile Bay (88°00'W) to the United States/Mexico border (96°30'W; Fig. 2). Seasonally, whale sharks were present year round in the western Gulf of Mexico, except between 94°00'W and 95°35'W where they were observed only during spring and fall. Bimodality in seasonal occurrence in this region could be attributed to seasonal fluctuations in biological productivity and, thus, to prey availability resulting from ephemeral mesoscale phenomena such as Loop Current eddy formation, current reversals, and coastal jetting. For example, in the western Gulf of Mexico the Texas Current is capable of

generating localized upwelling on the continental shelf break, thus increasing primary productivity and the availability of prey species (Sahl et al., 1993). However, the Texas Current occasionally flows in a direction opposite to its normal eastward course because of wind forcing (Sahl et al., 1997). Such a reversal of direction in the Texas Current could affect productivity in this area and thus influence the seasonal abundance of whale sharks in this region. Given the stochastic nature of the physical oceanography of this region, additional research will be needed to determine if whale sharks make limited use of this area during discrete times of the year or if they are in fact present year round.

From observations made by commercial mariners in transit between the southern tip of Florida and unidentified ports in Texas, Gudger (1941) reported sightings of 68 whale sharks from a circular area in the north-central Gulf of Mexico with a diameter of approximately 280 km; however no specific locations were given. He concluded that the density of whale sharks in this area must be related to high prey densities. The area of highest regional abundance during the present study occurred in a circular area, bounded by 89°30'W and 91°00'W longitude, and having a diameter of approximately 165 km (Fig. 2). Three aggregations of between 30 and 100 whale sharks in this same area were reported by Hoffmayer et al. (2005). The safety fairway used by shipping traffic transiting between the eastern and western Gulf of Mexico crosses this area. It is probable, therefore, that the observations of whale sharks by commercial mariners reported by Gudger (1941) were in the same area. Because of nutrient loading from the Mississippi and Atchafalaya rivers, primary productivity is higher in this region of the Gulf of Mexico than in any other region (Lohrenz et al., 1999) and may explain the high localized abundance of whale sharks in this region. Other highly productive areas where whale sharks are known to be present in relatively large numbers include Ningaloo Reef, Australia, and Gladden Spit, Belize (Taylor, 1996; Heyman et al., 2001).

The sighting of 23 whale sharks on 9 August 1993 was the largest aggregation observed during our study. The sharks, which were observed for about 35 minutes, were distributed over an area of approximately 2.6 km². Coral spawning occurred on 9 August 1993 at the East Flower Gardens (27°55'N, 93°36'W; Gittings³) which is approximately 33 km due west of the location of the aggregation sighting. A similar relationship between coral spawning events and increased localized abundance of whale sharks has also been noted to occur off the coast of Western Australia (Taylor, 1996). Future efforts should examine the relationship between annual coral spawning events and whale shark occurrence near the East Flower Gardens to determine if there is an annual migration of whale sharks to this area.

There are inherent difficulties associated with examining the seasonality of marine organisms using aerial surveys. This is particularly true when the species of interest is not obligated to surface waters where visual observations can be made. Because the whale shark is not a surface obligate species, factors such as changes in feeding behavior resulting from seasonal variability in the vertical distribution of prey species could have introduced significant bias into our sighting data, subsequent analyses, and data interpretation. We assumed that no differences exist among seasons in the amount of time whale sharks spend at or in close proximity to the surface. Using telemetry and archival tags, Gunn et al. (1999) determined that whale sharks spend 17–53% of their time at the surface during daylight hours off the coast of Australia. Over periods ranging from 28–1144 days, Eckert and Stewart (2001) tracked vertical movements of whale sharks through the water column in the Sea of Cortez using satellite tags. They concluded that during all seasons whale sharks spend greater than 80% of their time at depths of 10 m or less during all seasons—depth well within the photic zone of continental slope waters of the Gulf of Mexico. The findings of both Gunn et al. (1999) and Eckert and Stewart (2001) support our assumption.

Due to the economic value of their meat, fins, and liver oil, whale sharks have recently been designated as vulnerable to harvesting-induced extinction by the IUCN (Stewart and Wilson, 2005). Furthermore, the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) has placed the whale shark under Appendix II, which limits the trade of whale shark products among cooperating nations (Stewart and Wilson, 2005). Within the United States EEZ, the retention of whale sharks caught commercially or recreationally is prohibited (NMFS, 1993). However, because whale sharks are highly migratory and their movements cross numerous boundaries, detailed information on their abundance and seasonal distribution is needed to ensure their well being.

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³ Gittings, S. R. 1993. Personal commun. Science Program Manager, NOAA Office of National Marine Sanctuaries, 1305 East West Hwy, Silver Springs, MD 20910.

Literature cited

- Baughman, J. L.
1947. Fishes not previously reported from Texas, with miscellaneous notes on other species. *Copeia* 1947:280.
1950. Random notes on Texas fishes. *Tex. J. Sci.* 2:117-138.
1955. The oviparity of the whale shark, *Rhincodon typus*, with records of this and other fishes in Texas waters. *Copeia* 1955:54-55.
- Baughman, J. L., and S. Springer.
1950. Biological and economic notes on the sharks of the Gulf of Mexico with special reference to those of Texas and with a key for their identification. *Am. Midl. Nat.* 44:96-152.
- Breuer, J. P.
1954. The littlest biggest fish. *Tex. Game Fish.* 12:29.
- Buckland, S. T., D. R. Anderson, K. P. Burnham, and J. L. Laake.
1993. Distance sampling: estimating abundance of biological populations, 446 p. Chapman and Hall, London.
- Clark, E., and D. R. Nelson.
1997. Young whale sharks, *Rhincodon typus*, feeding on a copepod bloom near La Paz, Mexico. *Environ. Biol. Fishes* 50:63-73.
- Clark, E., and K. von Schmidt.
1965. Sharks of the central Gulf coast of Florida. *Bull. Mar. Sci.* 15:13-83.
- Colman, J. G.
1997. A review of the biology and ecology of the whale shark. *J. Fish. Biol.* 51(6):1219-1234.
- Compagno, L. J. V.
1984. Sharks of the world. FAO Fisheries Synopsis no. 125, part 4:210-211.
- Duffy, C. A.
2002. Distribution, seasonality, lengths, and feeding behavior of whale sharks (*Rhincodon typus*) observed in New Zealand waters. *N.Z.J. Mar. Freshw. Res.* 36:565-570.
- Eckert S. A., and B. S. Stewart.
2001. Telemetry and satellite tracking of whale sharks, *Rhincodon typus*, in the Sea of Cortez, Mexico and the north Pacific Ocean. *Environ. Biol. Fishes* 60:299-308.
- Gudger, E. W.
1939. The whale shark in the Caribbean Sea and the Gulf of Mexico. *Sci. Monthly* 48:261-264.
1941. The food and feeding habits of the whale shark (*Rhincodon typus*). *J. Elisha Mitchell Sci. Soc.* 57:57-72.
- Gunn, J. S., J. D. Stevens, T. L. O. Davis, and B. M. Norman.
1999. Observations on the short-term movements and behaviour of whale sharks (*Rhincodon typus*) at Ningaloo Reef, Western Australia. *Mar. Biol.* 135:553-559.
- Gunter, F., and F. T. Knapp.
1951. Fishes, new, rare or seldom recorded from the Texas coast. *Tex. J. Sci.* 1:134-138.
- Heyman, W. D., R. T. Graham, B. Kjerfve, and R. E. Johannes.
2001. Whale sharks *Rhincodon typus* aggregate to feed on fish spawn in Belize. *Mar. Ecol. Prog. Ser.* 215:275-282.
- Hoffman, W., T. H. Fritts, and R. P. Reynolds.
1981. Whale sharks associated with fish schools off south Texas. *Northeast Gulf Sci.* 5:55-57.
- Hoffmayer, E. R., J. S. Franks, and J. P. Shelley.
2005. Recent observations of the whale shark (*Rhincodon typus*) in the northcentral Gulf of Mexico. *Gulf Caribb. Res.* 17:117-120.
- Lohrenz, S. E., D. A. Wiesenburg, R. A. Arnone, and X. Chen.
1999. What controls primary production in the Gulf of Mexico? In *The Gulf of Mexico large marine ecosystem* (H. Kumpf, K. Steidinger, and K. Sherman, eds.), p. 151-170. Blackwell Science, Oxford, UK.
- Mullin, K. D., W. Hoggard, and L. J. Hansen.
2004. Abundance and seasonal occurrence of cetaceans in outer continental shelf and slope waters of the north-central and northwestern Gulf of Mexico. *Gulf Mex. Sci.* 22:62-73.
- Mullin, K., W. Hoggard, C. Roden, R. Lohofener, C. Rogers, and B. Taggart.
1994. Cetaceans on the upper continental slope in the north-central Gulf of Mexico. *Fish. Bull.* 92:773-786.
- NMFS (National Marine Fisheries Service).
1993. Fishery management plan for sharks of the Atlantic Ocean, 166 p. U.S. Dep. Commerce, Washington, D.C.
- Penrith, M. J.
1972. Earliest description and name for the whale shark. *Copeia* 1972:362.
- Rezak, R., S. R. Gittings, and T. J. Bright.
1990. Biotic assemblages and ecological controls on reefs and banks of the northwest Gulf of Mexico. *Am. Zool.* 30:23-35.
- Sahl, L. E., W. J. Merrell, and D. C. Biggs.
1993. The influence of advection on the spatial variability of nutrient concentrations on the Texas-Louisiana continental shelf. *Cont. Shelf Res.* 13:233-251.
- Sahl, L. E., D. A. Wiesenburg, and W. J. Merrell.
1997. Interactions of mesoscale features with Texas shelf and slope waters. *Cont. Shelf Res.* 17:117-136.
- Springer, S.
1957. Some observations on the behavior of schools of fishes in the Gulf of Mexico and adjacent waters. *Ecol. Monogr.* 38:166-171.
- Stewart, B. S., and S. G. Wilson.
2005. Threatened fishes of the world: *Rhincodon typus* (Smith 1828) (Rhincodontidae). *Environ. Biol. Fishes* 74: 184-185.
- Taylor, J. G.
1996. Seasonal occurrence, distribution and movements of the whale shark, *Rhincodon typus*, at Ningaloo Reef, Western Australia. *Mar. Freshw. Res.* 47:637-642.
- Wilson, S. G., J. G. Taylor, and A. F. Pearce.
2001. The seasonal aggregation of whale sharks at Ningaloo Reef, Western Australia: currents, migrations and the El Nino/Southern Oscillation. *Environ. Biol. Fishes* 61:1-11.
- Zar, J. H.
1999. Biostatistical analysis, 620 p. Prentice-Hall, Inc. Englewood Cliffs, NJ.