Studies suggest multiple stocks of Australian barramundi

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RESEARCHERS in the CSIRO Division of Fisheries Research are utilizing electrophoresis, a biochemical technique for analysing proteins, to study barramundi fish stocks in northern Australia.

Their results, indicating the existence of several stocks, should allow fishery biologists to formulate future policies to protect and manage the existing fishery.

Biology and fishery

Many important aspects about the basic biology of barramundi have recently come to light as the result of research projects carried out by the Fisheries Research Branch of the Queensland Department of Primary Industries, the Fisheries Division of the Northern Territory Department of Primary Production, and the Division of Fisheries Research of CSIRO (see *Australian Fisheries* July 1982, pp. 27-28).

These studies have revealed that barramundi change sex, first maturing as males at about age three and later becoming females in about their fourth or fifth year. The main spawning period is generally from September through February and individual females may produce as many as 10 million eggs. Because successful fertilization and embryonic development require at least 50 per cent seawater, adults living in freshwater streams and billabongs must migrate to the ocean during the spawning season. Tag-recapture studies in both the Northern Territory and Queensland have indicated that there is some movement of adult fish among neighbouring river systems.

Commercial barramundi fisheries generally are centred at river mouths along the coasts of Queensland and the Northern Territory. Current management policies restrict the length and mesh size of the gill nets used and a closed season during the peak of the spawning season further limits the commercial catch.

In recent years reports from fishermen have suggested that the composition of the commercial catch has changed, with smaller individuals comprising an ever-increasing percentage of the total catch.

This shift in the catch may have particularly profound effects on the future of the barramundi resource for two reasons.

First, as with any fishery, when the larger individuals have been removed, the reproductive potential of the species is decreased because large individuals usually produce the greatest number of eggs and are the most successful spawners.

Second, in the case of barramundi (where all large individuals are females), any shift in size and age composition brought about by the fishery can also result in a significant change in the sex ratio. In fact many catches of barramundi presently consist of 60 to 90 per cent males. This distorted sex ratio may further limit reproduction and thus recruitment of new generations to the fishery.

Given the ever-increasing demand for barramundi, the apparent shift in size and sexual composition of the catch, and the declining commercial catch (official figures indicate a decrease from about 3 200 tonnes in 1978-79 to slightly more than 1 000 t in 1980-81) there is a great deal of concern about the nature and viability of barramundi stocks in Australia and the future management of this fishery.

One important aspect of barramundi biology about which virtually nothing is known is the number of different stocks or sub-populations which can contribute to the barramundi fishery.

Fish stocks and management

Since a fish stock can be considered a self-reproducing unit within a fishery, the number and characteristics of such component stocks can be of critical importance to the management and long-term future of the entire fishery.

At one extreme, we can imagine that all barramundi in northern Australia could be members of a single large interbreeding stock. In this case, fishing harvest in any one location can actually affect the species throughout its range since all individuals contribute to the single large stock. In such a situation, one overall management program for the species would be appropriate.

At the other extreme, we can imagine that the barramundi fishery could be comprised of numerous smaller sub-populations, each associated with a major river system, and each more or less independent and reproductively isolated from the others. In this situation, the effects of the fishery on any one stock would be localized or semi-isolated so that the viability of other stocks should not be affected.

Given a situation where several barramundi stocks exist, the management of the entire fishery must be structured in such a way as to reflect the multiplicity of stocks

contributing to the overall harvest.

The barramundi fishery is presently managed on the assumption that it is composed of a single large stock. For this reason, certain streams are closed to all fishing to act as reserves — functioning as nursery grounds to stimulate the recruitment of juveniles into the fishery.

If only a single stock of barramundi actually exists, such a management policy would be expected to enhance the entire fishery.

On the other hand, if the barramundi fishery is, in reality, composed of many smaller stocks, this policy of setting aside small reserves may only strengthen certain isolated stocks and not benefit the overall fishery.

There are many ways to investigate the stock structure of a species. These include: tag-recapture programs; the study of biological features such as reproductive traits, life history characteristics, and behaviour; and the search for differences in parasites or anatomical characters.

However one of the most direct methods is to examine the genetic interrelationships of the fish in different areas.

We expect individuals within a stock to be genetically related to one another due to random interbreeding within the stock. Individuals from different stocks should be genetically different because of partial or complete reproductive isolation between stocks. Therefore genetic characteristics can provide considerable insight into the stock structure of the fishery.

In our laboratory at present we are studying the pattern of genetic variation of proteins in barramundi to investigate this problem of stock structure.

It first involves field sampling of tissues from a large number of individual fish from several localities. This aspect of the research is being conducted by biologists with the Fisheries Research Branch of the Queensland DPI and the Northern Territory Fisheries Division. The tissue samples are frozen and sent back to the CSIRO Division of Fisheries Research laboratory at Cleveland (Brisbane), where the actual biochemical tests are done. Extracts of each tissue (in this case muscle, liver and eyes) are prepared and subjected to electrophoretic analysis.

Electrophoresis

Electrophoresis is a procedure that depends upon the movement of charged molecules in an electric field. The rate of movement depends on the voltage applied and the overall electrical charge of each molecule. Protein molecules move in an electrical field because they are composed of amino acids, many of which are charged.

Each tissue of a fish contains thousands of different kinds of proteins which form the basis for both the structure and metabolism of the tissue. Electrophoresis provides a means of separating protein molecules that have different electrical charges. Therefore it can be used (in conjunction with a general protein stain which allows the separated proteins to be easily seen) to determine the pattern of proteins characteristic of a species of fish.

Because different species have different general protein patterns in, for example, muscle tissue, this procedure can be used to identify fish fillets and detect substitution. This simple application of the technique for identifying barramundi fillets has recently been described in *Australian Fisheries* (July 1982, pp. 19-20— and is being used by several agencies (including the CSIRO Tasmanian Food Research Laboratory, The Queensland Government Chemical Laboratory and the Australian Government Analytical Laboratory) to monitor the barramundi substitution problem.

We are utilizing this same basic technique — electrophoresis — together with biochemical and genetic studies, to investigate the stock structure of barramundi.

In our case, we take advantage of the fact that the amino acid composition of each protein is determined by the gene in the DNA specifying that protein. Any change in protein structure detected by a different rate of movement during electrophoresis indicates a change in the gene encoding that protein. Such different forms of a gene are called alleles.

By monitoring many proteins by electrophoresis, we can determine the genetic characteristics of individual fish. However, since each tissue contains several thousand different kinds of protein molecules, we restrict our analysis to one class of protein — enzymes.

Because each enzyme catalyses one and only one biochemical reaction, we employ specific enzyme staining following electrophoresis to show up and identify one type of enzyme at a time. This makes the approach more sensitive and allows us to make genetic interpretations of the resulting patterns seen after electrophoresis.

When the analysis is done repeatedly for many different enzymes and many individual fish from several localities, we can describe the genetic characteristics of the fish populations sampled in each area and determine whether or not different samples come from different stocks or breeding groups.

Genetic differences

To date we have examined the genetic characteristics of barramundi from three general localities: eastern Queensland (Princess Charlotte Bay), the Gulf of Carpentaria (Staaten and Nassau Rivers in the south-eastern Gulf), and the Northern Territory (Daly River).

Samples of fish from each locality have been electrophoretically analysed on starch gels for at least 15 different enzymes. Figure 1 schematically illustrates the pattern of variation seen for the enzyme esterase (EST) in fish from the Northern Territory (NT) and the east coast of Queensland (PCB).

Although we have detected four different esterase types (alleles) in our study of barramundi, only three were common in these samples and these three (labelled **+**, **m**, **s**) are shown in the figure.

The proportions of all four types (**f**, **+**, **m** and **s**) in the samples are shown in the 'pie' diagrams in Figure 2.

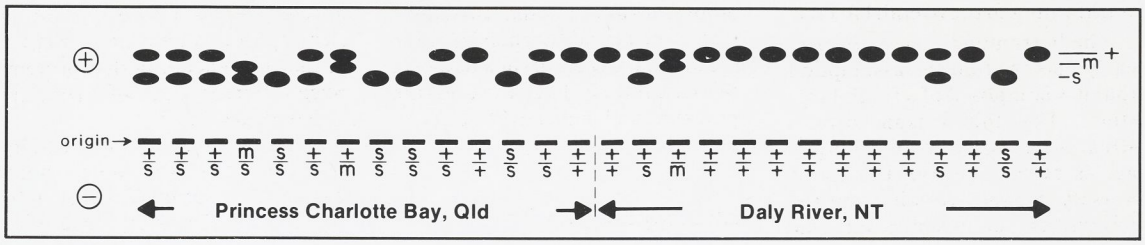

Figure 1. *Electrophoretic analysis of barramundi esterases (schematic drawing). Tissue extracts from 28 individual fish (14 from Queensland and 14 from the Northern Territory) were loaded onto a starch gel at the sample origin and electrophoresed for six hours. A slice of the gel was then stained for esterase. Three esterase types — **+**, **m** and **s** —each due to a different allele of the esterase gene were observed. The allelic composition of each fish is indicated at the bottom of the figure. Note that approximately equal numbers of **+** and **s** alleles occur in the eastern Queensland sample while the **+** allele predominates in the Northern Territory sample. The Gulf sample is somewhat intermediate.*

In the sample of barramundi from the Northern Territory, only three types were observed (the **f** allele was absent). The **+** type made up 84 per cent of the total while the **s** allele contributed only 11 per cent.

In contrast, the barramundi samples from the south-eastern Gulf and from Princess Charlotte Bay each had all four alleles present and the contribution of the **s** type was much greater (making up 34 per cent of the total in the Gulf sample and 43 per cent in the PCB sample) than in the NT sample.

Statistical tests of these data for esterase indicate that the three samples are significantly different from each other, implying that each barramundi sample was derived from a different stock. Preliminary studies of a barramundi esterase by Dr Barry J. Richardson (formerly of the Australian National University) also suggested such stock differences.

We have completed similar electrophoretic analyses for an additional 14 enzymes. Genetic variation has been observed for at least five of these (isocitrate dehydrogenase-IDH in both liver and muscle, lactate dehydrogenase-LDH, phosphogluconate dehydrogenase-PGDH and umbelliferase-UMB). Four of these enzymes also show evidence of genetic differences among the three areas.

Taken together, these data indicate that at least three separate stocks of barramundi exist in northern Australia. How many additional stocks, and what their boundaries may be, can be determined only by additional investigations (which are planned and in progress).

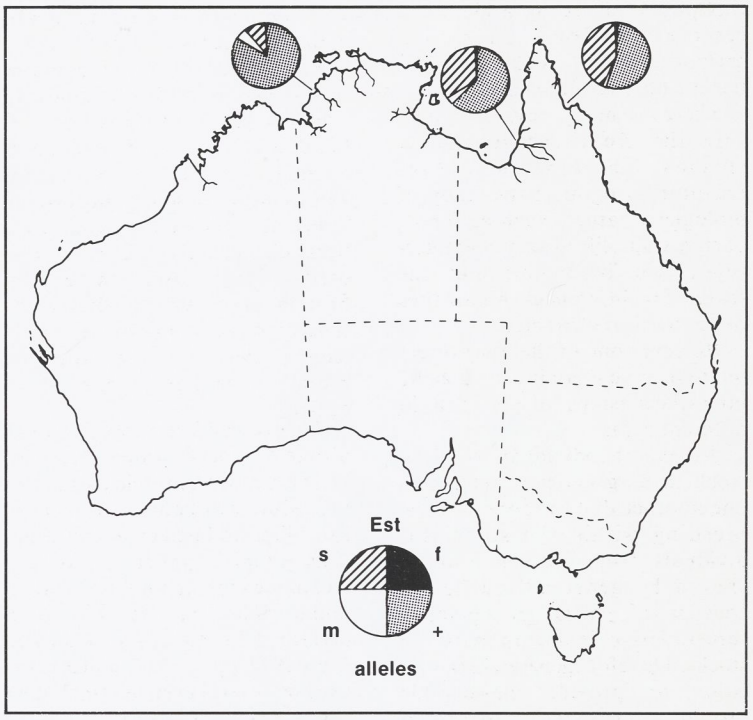

Figure 2. *Esterase allele proportions in barramundi from three localities: Princess Charlotte Bay, Queensland (58 fish); south-eastern Gulf of Carpentaria, Queensland (84 fish); Daly River, Northern Territory (48 fish). The proportions of each allele (**f**, **+**, **m** and **s**) in each sample are represented by the size of the wedge in each pie diagram.*

These results emphasize two major points.

The first, which is specific to barramundi, is that several stocks exist. This means that a single uniform management policy for the entire species is undoubtedly non-ideal and possibly quite inappropriate.

The second point is that biochemical genetic studies of fishes utilizing electrophoresis can provide valuable insight regarding the number, characteristics, and boundaries of fish stocks and thus make a significant contribution to fisheries management in Australia.

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PHYSIOLOGICAL RESPONSES OF NEWBORN SMOOTH DOGFISH, *Mustelus canis,* DURING AND FOLLOWING TEMPERATURE AND EXERCISE STRESS

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Abstract: Glucose, lactate, and hematocrit levels were noted for 24 hours in newly pupped smooth dogfish, *Mustelus canis,* subjected to stresses of high (28°C) water temperatures and vigorous exercise. Male lactate levels increased statistically following exercise but decreased in females. Glucose levels increased in both sexes but the differences were not significant. Hematocrit (Hct) levels decreased in both sexes at 0 hour post exercise and returned to original levels in 24 hours. The slight Hct differences by sex varied significantly. Exercise and stress should be considered important variables when interpreting blood chemistry observations.

Key Words: smooth dogfish; *Mustelus canis*; physiology; stress; exercise.

INTRODUCTION

A large and growing mass of literature treats fish physiology and stress (Hunn, 1967; Hoar and Randall, 1971; Hawkins and Mawdesley-Thomas, 1972; Hickey, 1976; Murru, 1984), yet most deals with the health and stress of cultivated and natural populations of teleosts (Hickey, 1982; Ellesaesser and Clem, 1986). Few note changes in blood level parameters of freshwater fishes following induced or angling exercise (Black, 1955, 1957; Connor et al., 1964; Barnhart, 1969; Fletcher, 1975; Beggs and Holeton, 1980; Mulligan and McDonald, 1988) or over prolonged periods of time (Bridges et al., 1976; Van Vuren and Hartingh, 1978). Only Jolly and Irby (1979) studied stress conditions of captured pelagic marine sailfish, *Istiophorus platypterus.*

Little physiological stress literature pertained to elasmobranchs, especially sharks. Caillouet (1971), Lenfant and Johansen (1966), and Martini (1978) noted shark blood constituent variations in relation to capture stress, respiration, and starvation. Bushnell et al. (1982) was one of the few reporting hematocrit increases during exercise in large lemon sharks (*Negaprion brevirostris*). Emery (1986) compared endothermal versus ectothermal sharks and found hematocrit levels in endothermal sharks were significantly greater than in ectothermal sharks. Cliff and Thurman (1984) examined blood variables of capture stressed dusky sharks (*Carcharhinus obscurus*) wherein blood lactate and glucose levels were elevated during stress, acidosis was evident from the onset of stress minutes before lactate levels rose, and the sharks required a recovery period of almost 24 hours before most parameters regained pre-stress levels. Conversely, Wells and Davie (1985)

reported captured mako sharks (*Isurus oxyrinchus*) failed to exhibit Root or Bohr effects. Piper and Baumgarten (1969) observed the blood lactate levels and acid base balance in *Scyliorhinus stellaris* following exhaustive activity.

While a plethora of literature deals with many aspects of the smooth dogfish, *Mustelus canis,* or spiny dogfish, *Squalus acanthias,* biology, distribution, and physiology, only Wintrobe (1951) reported blood hematocrit values for the smooth dogfish while Murdaugh et al. (1965) commented on lactate metabolism in the spiny dogfish.

We therefore examined glucose, lactate, and hematocrit responses in newly pupped smooth dogfish, by sex, subjected to exercise and high water temperature stresses.

METHODS

Newly pupped smooth dogfish were trawled 27 April 1987 from the Atlantic Ocean just south of Shackleford Banks, North Carolina. Trawl dimensions were: 12.1 m headrope, constructed of 19 mm nylon twine. Tow time was 0.25 hour to minimize catch compaction of the captured sharks. Aboard ship the captured sharks were promptly placed in a 1.5 × 1 m deep oblong tank supplied with flow through water pumped from the capture site. Transfer to the laboratory, 8 km away, took about one hour. Ashore the specimens were transferred to covered, oblong 4.1 × 12 m stainless steel tanks to prevent their jumping out and were supplied with flow through water pumped from nearby Bogue Sound. The water depth was maintained at 0.5 m. Salinities varied 32–34 ppt. The tanks were housed in a plastic covered shed which was open at one end to permit additional air circulation. A 0.6 m diameter circulating fan moved the air within the shed to keep it from becoming excessively hot during the peak heat of the day. Water temperatures, during the holding and testing period, ranged 27 to 28°C 15 June 1987.

The fish were fed small bits of fish daily except 24 hours before testing. The sexes were kept together and testing was by random selection.

Well over a month elapsed between capture and testing to permit the fish to recover from any capture or tank holding stress. Each test fish was grasped, while actively swimming, with rubber gloved hands as preliminary observations indicated that just momentary direct handling with ungloved hands influenced the blood parameters markedly. Unexercised free-swimming fish were not handled except for the few seconds it took to draw a blood sample. Handled specimens were those grasped and held for a few minutes prior to blood sampling, but were not subjected to exercise. Exercised fish were those that had been handled and subjected to stress agitation by a mop being vigorously passed back and forth throughout the holding tank for five minutes prior to blood withdrawal.

Blood, for analyses, was obtained by direct heart puncture using heparinized syringes fitted with 23 ga needles. Following blood extraction, all fish were measured to the nearest millimeter fork length (FL), weighed to nearest 0.1 g on a Mettler 3000 electronic balance, tagged, and released into nearby Bogue Sound. No fish was reused during any test although several were held for up to four months, grew in size, and exhibited no ill effects from the direct heart puncture sampling procedure or a second blood withdrawal.

Blood for hematocrit analysis was spun in unheparinized microhematocrit cap-

Table 1

Number, range, lengths, weights of unstressed, handled and stressed newly pupped male and female smooth dogfish determined 0, 6, and 24 hours following stress. $\bar{x}$ = mean; ( ) = number and range of specimens studied.

	Length (FL)				Weight (G)			
	M		F		M		F	
	$\bar{x}$	n	$\bar{x}$	n	$\bar{x}$	n	$\bar{x}$	n
Unexercised	322	(2, 295–350)	298	(4, 260–325)	150	(2, 148–150)	102	(4, 65–149)
Handled only	323	(2, 310–335)	310	(8, 285–330)	137	(2, 120–154)	131	(8, 100–155)
Handled and exercised								
Post exercise								
0 hours	316	(4, 310–335)	323	(6, 290–350)	135	(4, 113–188)	154	(6, 99–189)
6 hours	321	(4, 315–339)	315	(5, 310–325)	149	(4, 109–189)	142	(5, 128–170)
24 hours	321	(7, 290–330)	316	(3, 300–330)	152	(5, 94–190)	143	(3, 98–188)

Table 2

Lactate, glucose, and hematocrit values (mean and ranges) for Male (M) and Female (F) smooth dogfish unexercised, handled, and post exercise. * 5% significance; ** 95% significance; NS, not significant.

	Lactate mg/dl		
	M	F	F value
Unexercised	34.4 (2, 24.4–44.3)	15.1 (4, 514–27.6)	Between sexes**
Handled only	12.0 (2, 12.0–12.1)	17.7 (4, 14.3–21.4)	Between hours NS
Post exercise 0 hours	17.0 (5.7–32.3)	13.4 (2, 13.2–13.6)	
6 hours	12.1 (2, 22.0–13.3)	11.5 (6.0–14.3)	
24 hours	15.1 (5, 12.6–19.3)	10.0 (1)	
	Glucose mg/dl		
	M	F	F value
Unexercised	86.4 (2, 81.1–91.7)	89.8 (4, 632–132.6)	Between hours NS
Handled only	81.7 (2, 90.2–107.2)	92.1 (4, 716–109.3)	Between sexes NS
Handled + 5 min exercise			
Post 0	90.0 (4, 618–118.0)	84.5 (4, 71.1–103.1)	
6	95.6 (4, 840–108.2)	96.1 (5, 850–106.2)	
24	118.0 (88.7–129.6)	103.5 (3, 90.1–14.8)	
	Hct (%)		
	M	F	F value
Unexercised	16.7 (15.5–18.0)	16.6 (5, 15.7–21.0)	Between sexes*
Handled only	23.9 (21.7–26.1)	22.6 (19.9–26.8)	Between hours**
Handled + 5 min exercise			
Post 0	18.3 (4, 16.4–26.1)	18.6 (4, 146–21.6)	
6	19.4 (4, 18.5–21.2)	26.1 (4, 19.2–23.6)	
24	19.9 (6, 18.2–21.9)	16.0 (3, 19.6–26.6)	

illary tubes in a Clay-Adams centrifuge at 4500 rpm for four min. Boehniger-Mannheim Lactate UV test 19 and Preciset Glucose Trender test kits were used to determine glucose and lactate levels.

All data were compared using ANOVA with disproportionate subclass analyses.

OBSERVATIONS

The sizes and weights of the test specimens ranged 260–350 mm fork length and 65–190 g respectively (Table 1). Although chosen at random, the unexercised and handled females were smaller in both size and weight than those used during other test periods (Table 1). These size differences did not differ statistically between sexes.

Contrary to lactate observations in the blacktip shark (Cliff and Thurman, 1984), where lactate levels rose markedly following exercise, prior to return to "normal," the smooth dogfish male lactate levels increased following exercise while those for females tended to decrease at a more rapid rate following exercise. The response results were statistically different between sexes but not by hour post exercise (Table 2).

Glucose levels increased following exercise for male smooth dogfish as did those for females, but female values were lower throughout the test periods (Table 2). The wide range differences noted were not significant between post exercise ob-

servation periods as well as between sexes (Table 2). Cliff and Thurman (1984) also noted rises in glucose levels following exercise for at least 24 hours.

Hematocrit values for males and females, while appearing similar (Table 2), increased in handled fish, decreased at 0 hours post exercise, and then returned to original levels within 24 hours. The slight differences in hematocrit values were statistically different between exercise period as well as between sexes.

Thus, when or how one conducts a stress experiment, while important for a myriad of influences, should also be taken into consideration when interpreting what the values obtained mean and when the blood chemistry was influenced in that animal. Exercise (stress) is just one variable that is or can influence the blood chemistry of a species. Length of time post exercise should also be considered. Only then will we begin to grasp the full meaning of stress in a species, be it shark or other animal. Stressing an animal may influence or even cause its death, depending on how long or how severe the influence.

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EXTREME HABITAT OCCURRENCES FOR TWO SPECIES OF HAMMERHEAD SHARKS (FAMILY SPHYRNIDAE) IN NORTH CAROLINA AND WESTERN ATLANTIC OCEAN WATERS

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Abstract: Two species of hammerhead shark, scalloped hammerhead (*Sphyrna lewini*) and bonnethead (*S. tiburo*) are now known to utilize diverse habitat extremes. The scalloped hammerhead has been seen just off the bottom during a submersible dive to 431 m depths. The bonnethead now also frequents inland freshwater habitats of 0 ppt.

Key Words: hammerhead sharks; *Sphyrna lewini*; *S. tiburo*; North Carolina; fresh water; deep oceanic waters.

INTRODUCTION

Fishes occupy the world's fresh and marine waters to depths of 7,000 to 8,370 m, the deepest by the brotulid *Bassogigas profundissimus* (Nielsen and Munk, 1964; Staiger, 1972; Nelson, 1984). Sharks, similarly, occupy habitats to depths of 9,938 m, the deepest by the squaloid *Euproctomicrus bispinatus* (Compagno 1984). Sharks like the bull shark *Carcharhinus leucas* are known to penetrate inland fresh waters for hundreds of kilometers (Thorson, 1976; Compagno, 1988) and to endure 0 ppt freshwater for extended periods of time (see the excellent review of freshwater occurrences of sharks in Taniuchi and Shimizu, 1991). We report the sighting, by submersible, of the scalloped hammerhead shark, *Sphyrna lewini,* from deep Atlantic Ocean marine waters off the Point, Dare County, near Cape Hatteras, and the capture of a young bonnethead shark, *S. tiburo,* in fresh waters of the Trent River, a tributary of the Neuse River at New Bern, Craven County, North Carolina.

OBSERVATIONS

A @ 1,600 mm fork length scalloped hammerhead, *Sphyrna lewini,* sex unknown, was observed just off the bottom (off the Point, North Carolina, at 35°28.5'N, 74°47.9'W) in the Western Atlantic during a daytime (0930 hr) Johnson-Sea Link II submersible dive #2471, 5 September 1992, at a depth of 431.8 m. Surface air temperature was 28°C, while surface waters were 29°C, bottom 5°C, and sea state calm. Visible bottom organisms were red crabs, *Geryon quinquedens* and *Cerianthid* sea anemones.

A young 438 mm fork length bonnethead shark (*S. tiburo*), that had been freshly wounded by a boat propeller, was found 2 June 1993, in the Trent River boat basin of the Sheraton Hotel at New Bern, Craven County, North Carolina; the Trent River joins the Neuse River 1 km east of the boat basin. Occurrence in the

Trent River constitutes an inland penetration, northwest of the Atlantic Ocean, of 64.4 km to New Bern, via Pamlico Sound and the Neuse River. Salinities of the Trent and Neuse Rivers at New Bern were 0 ppt, freshwater, from 1–25 June 1993. The nearest and earliest recorded saline water, 5 ppt, occurred in the Neuse River 15 June 1993, at Cherry Point–Havelock, North Carolina, 32 km to the southeast.

DISCUSSION

Carey and Scharold (1990) reported blue sharks, *Prionace glauca,* making vertical excursions to 600 m and 7°C waters off Cape Hatteras, North Carolina, while Randall (1977) reported the white tip reef shark *Triaenodon obesus,* from 330 m deep Kyukyu Island, Japan waters. Clark et al. (1986) and Clark and Kristoff (1990) reported submersible observations of six gill shark (*Hexanchus griseus*) and other sharks at depths to 610 m, yet no scalloped hammerhead sharks were noted from deep ocean waters. MacKenzie (1986) reported sharks biting transoceanic cables laid 1,700 m deep, but did not implicate scalloped hammerheads as possible bite culprits. Nakaya and Shirai (1992) compared world deep-water chondrichthyan faunas below 200 m but did not list *S. lewini* frequenting those depths. Grey (1956) noted few deep water occurrences of sharks, while *S. lewini* was absent from the compilation. To date, the scalloped hammerhead, a cosmopolitan species, was thought to frequent ocean waters to at least 275 m depths (Compagno, 1984) although fall surface migrants are often well offshore in waters hundreds of meters deep. Recently Klimley (1993) and Klimley et al. (1993) reported a 1,250 mm total length radio tagged female scalloped hammerhead making a night time vertical excursion to a 450 m depth off Las Animas Island in the lower Gulf of California. Water temperatures ranged 14–20° for all his sharks' excursions.

Schwartz (1994) noted 22 species of elasmobranchs, 10 sharks, and 12 rays, entered sound and river waters of North Carolina, yet they rarely penetrated inland or fresh waters. Radcliffe (1913) reported hammerhead sharks from lower Sound and high saline (28–32 ppt) river areas of the Newport River, North River, and Town Creek, North Carolina, while Gudger (1913) reported only *S. zygaena* from Newport River and Beaufort, North Carolina. Schwartz (1994) noted only bull sharks, *Carcharhinus leucas,* as summer occurrences of the Neuse River at New Bern while the bonnethead shark, *S. tiburo,* was known only from higher saline Core Sound and nearby Ocracoke Inlet waters of North Carolina (Schwartz 1989).

Thus, occurrences of young bonnethead and adult scalloped hammerhead sharks from freshwater or deep (5°C) ocean waters provide evidence of their endurance of several habitat extremes. Continued research will broaden our knowledge of habitats utilized by these and other sharks.

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OCCURRENCE OF AN ADULT MALE REEF SHARK, *Carcharhinus perezi* (CARCHARHINIDAE) OFF NORTH CAROLINA

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Abstract: A 45 kg adult male reef shark, *Carcharhinus perezi,* 1901 mm total length, was captured 20 July 1995 in the Atlantic Ocean approximately one kilometer east of Cape Hatteras Lighthouse, North Carolina. The specimen provided the first documented data for an adult male reef shark. Morphometric and meristic comparisons revealed few differences between the male and similar-sized female reef sharks. Capture extended its range at least 1200 km north of Florida.

Key Words: reef shark, *Carcharhinus perezi,* North Carolina, range extension, adult male, morphometric and meristic comparisons.

INTRODUCTION

The reef shark, *Carcharhinus perezi* (=*C. springeri*), occurs to depths of 30 m in tropical inshore continental shelf and insular waters of the western Atlantic Ocean. Its life history is poorly known, although it is a demersal carcharhinid that commonly frequents coral reefs from Florida and Bermuda to southern Brazil, and possibly the northern Gulf of Mexico (Bigelow and Schroeder 1944, 1948; Castro 1983; Clark and Von Schmidt 1975; Compagno 1984; Garrick 1982; Randall 1968; Springer 1960). Garrick's (1982) revision of the genus *Carcharhinus* contains the only detailed information regarding *C. perezi,* a species often confused with several other sharks: bignose (*C. altimus*), dusky (*C. obscurus*), Galapagos (*C. galapagensis*), and sandbar (*C. plumbeus*). Bonfil (1989) mentions

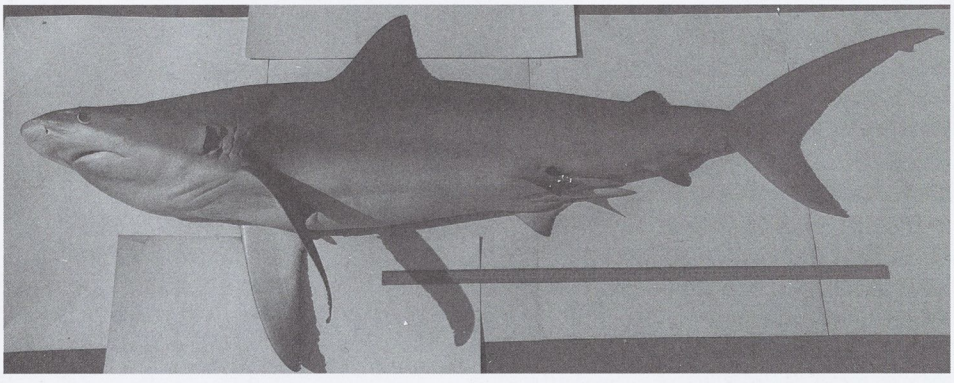

FIG. 1. Adult male *Carcharhinus perezi* captured on 20 July 1995 near Cape Hatteras, North Carolina.

Table 1. Proportional dimension comparisons, expressed as percent total length (TL) for an adult male and four female *Carcharhinus perezi* (>1,000 mm TL).

Sex	Male	Female*			
Location	North Carolina	Jamaica	Bahamas	Venezuela	Grand Bahama
Length (mm TL)	1901	1023	1082	1900	2950
Catalogue No.	UNC 17493	USNM 197361	UMML (uncat)	—	—
Snout tip to:					
Outer nostrils	2.5	3.0	2.8	2.9	2.6
Eye	6.1	6.9	6.7	—	6.1
Mouth	5.6	7.1	6.9	6.5	6.1
1st gill opening	18.7	19.3	18.1	—	18.6
3rd gill opening	21.9	21.4	19.7	—	21.3
5th gill opening	23.9	23.1	21.1	—	22.2
Pectoral origin	22.7	21.7	20.3	—	22.2
Pelvic origin	49.3	49.3	48.2	—	53.6
1st dorsal origin	30.7	31.5	30.5	33.6	33.2
2nd dorsal origin	63.3	60.6	60.2	66.5	65.7
Anal fin origin	63.6	61.8	59.9	—	66.1
Upper caudal origin	75.1	72.0	71.1	—	75.8
Lower caudal origin	74.1	71.2	70.2	—	75.5
Nostrils					
Distance between inner corners	6.4	6.8	6.9	—	5.9
Mouth					
Width	9.6	9.7	9.9	9.6	8.9
Length	6.1	5.1	5.7	4.8	4.7
Labial furrow lengths					
Upper	0.3	0.3	0.5	—	0.3
Lower	0.4	0.4	0.6	—	0.6
Gill opening lengths					
1st	3.2	2.4	2.6	3.2	2.7
3rd	4.0	2.9	3.4	4.0	3.3
5th	3.0	2.3	2.2	2.3	1.2
Eye					
Horizontal diameter	1.5	2.0	2.5	1.8	1.2
1st dorsal fin					
Length of base	10.2	8.7	9.7	10.1	11.1
Length posterior margin	2.6	3.4	3.4	—	3.3
Height	10.7	10.7	11.2	10.3	10.7
2nd dorsal fin					
Length of base	4.1	4.1	3.9	3.9	3.6
Length posterior margin	3.9	4.1	3.9	—	4.2
Height	2.7	3.0	3.2	3.1	2.9
Anal fin					
Length of base	4.4	4.3	4.2	4.1	4.2
Length posterior margin	3.1	3.7	3.6	—	3.5
Height	3.9	3.4	3.7	3.7	3.7
Pectoral fin					
Length of base	5.7	6.1	5.6	—	7.1
Length anterior margin	19.7	20.3	20.3	20.8	21.7
Length distal margin	16.6	16.5	16.8	19.4	20.2
Greatest width	10.3	—	9.6	—	—

Table 1. Continued.

Sex	Male	Female*			
Location	North Carolina	Jamaica	Bahamas	Venezuela	Grand Bahama
Length (mm TL)	1901	1023	1082	1900	2950
Catalogue No.	UNC 17493	USNM 197361	UMML (uncat)	—	—
Pelvic fin					
Length of base	6.1	5.3	4.9	—	5.5
Length anterior margin	6.1	6.2	6.1	—	6.1
Length distal margin	6.8	5.7	5.7	—	6.9
Caudal fin					
Length upper lobe	27.0	28.3	29.2	30.6	27.0
Length lower lobe	14.6	13.6	13.9	14.3	13.9
Trunk at pectoral margin					
Width	15.3	11.4	10.3	—	—
Height	10.8	13.4	12.7	—	—

* Female data from Garrick (1982, Table 71, p. 149).

head, eye, and gill filament deformities for an abnormal embryonic *C. perezi* from Yucatan.

This report presents new morphometric and meristic data for an adult male *C. perezi* captured off Cape Hatteras Lighthouse, North Carolina. We compare the male features to extant data, based only on females. The capture also represents a range extension north of Florida of at least 1200 km.

MATERIALS AND METHODS

An adult 45 kg male *C. perezi* (Fig. 1) was captured off North Carolina by the commercial longline vessel F/V *Water Sport* on 20 July 1995 at 35°13.4′N, 75°28′W, about one kilometer east of Cape Hatteras Lighthouse. The specimen measured 1418 mm standard length (SL), 1546 mm fork length (FL), and 1901 mm total length (TL). The shark was caught on a longline (24.6 km long, 862 hooks) set in waters 7.8–21.9 m deep. Surface water temperatures ranged 27.7–29.1°C during the night set. Other sharks captured during the set were: three female blacknose (*C. acronotus*), one male bull (*C. leucas*), three female blacktip (*C. limbatus*), one female dusky (*C. obscurus*), five (2M, 3F) adult sandbar (*C. plumbeus*), one female tiger (*Galeocerdo cuvier*), and 132 Atlantic sharpnose (*Rhizoprionodon terraenovae*).

The reef shark was weighed at the dock and frozen until measured 25 October 1995. We follow Garrick (1982) for morphometric and meristic data comparisons and Robins et al. (1991) in common name usage, reef shark, as well as use of a single "i" when spelling *perezi*. Vertebral counts were determined from radiographs produced using a Fisher unit and varying exposures between 64–70 kv, 200 ma, $\frac{1}{5}$ to $\frac{1}{4}$ sec for the monopondylous portion of the vertebral column (prepelvic) and 40–64 kv, 200 ma, $\frac{1}{20}$ to $\frac{1}{60}$ sec for the diplospondylous portion. Kodak CSGI film was developed for 90 sec.

OBSERVATIONS

Specific morphometric and meristic data, expressed in percent TL (Table 1), for the male *C. perezi* from North Carolina were computed and compared to known female data of similar length (Garrick 1982). Additional new male data were: *claspers*—left 169 mm, right 168 mm;

$$\textit{dental formula}\ \frac{\text{12-0-13}}{\text{11-1-12}};$$

$$\frac{\text{length}}{\text{diameter}}\ \text{penultimate monospondylous centrum 0.70;}$$

$$\frac{\text{length penultimate monospondylous centrum}}{\text{length first diplospondylous centrum}}\ 122;$$

and *vertebrae* — precaudal 106, caudal 102, total 208.

DISCUSSION

Garrick (1982, Table 71, p. 149) presented detailed morphometric and meristic data for seven female *C. perezi* (726–2950 mm TL) captured throughout the Caribbean Sea. He also mentioned that males were known by only two immature specimens, 780 and 800 mm TL, and two embryos, 265 and 290 mm. Neither he, nor Poey (1876, in Garrick 1982), elaborated or measured the male specimens. Garrick (1986) commented on the similarity of *C. perezi* to bignose, dusky, and sandbar sharks, species that possess an interdorsal ridge and a first dorsal fin that originates above to slightly behind the pectoral fin inner margin (M. Grace, pers. comm.; pers. obs.). Meristic and morphometric data for the *C. perezi* from North Carolina compared favorably (Table 1) to that of four similar >1000 mm TL females reported by Garrick (1982), indicating few differences between sexes. Most male data fell within the variation noted for young or adult females, except that the posterior margin length of the first dorsal fin and the anterior margin of the pectoral fin were longer. Likewise, the dental formula lacked an upper interstitial tooth. Otherwise the upper and lower tooth counts fell within the variation known for *C. perezi,*

$$\frac{\text{13-1-13}}{\text{12-1-12}}\quad \text{or at most}\quad \frac{\text{12 or 13-1 or 2-12 or 13}}{\text{11 or 12-1-11 or 12}}\quad \text{(Garrick 1982).}$$

Teeth of *C. perezi* differed from morphologically similar sharks in that the anterior lateral teeth were serrated, narrow, and strongly notched versus the broad and laterally concave teeth similar in other similar species.

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Florida State Museum, University of Florida, Gainesville, Florida, and J. Smith, NMFS, Southeast Fisheries Lab, Beaufort, North Carolina reviewed the manuscript and provided helpful comments for improvement. L. White (IMS) typed the manuscript, and R. Barnes (IMS) produced Fig. 1.

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TOOTH SURFACE AREA COMPARISONS, BY SEX AND AGE, FOR ATLANTIC SHARPNOSE SHARKS (*Rhizoprionodon terraenovae*, CARCHARHINIDAE) FROM NORTH CAROLINA

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Abstract: Upper and lower jaw teeth of a newborn and adult male and female Atlantic sharpnose sharks, *Rhizoprionodon terraenovae,* were examined to note if differences existed between their surface areas, tooth position, and jaw shape. "Normalized tooth surface areas" and "normalized tooth position" were highly correlated revealing that the jaws were widest, in both sexes, at their lateral tooth position. Upper jaw teeth surface areas were greater (statistically) than lower jaw teeth in both sexes. Males exhibited a cross bite condition that may affect their feeding behavior. Similar, but shallower, tooth areas, positions, and jaw shapes existed for a newborn male. A strong fork length to lower jaw length was determined. Feeding behavior may be correlated or influenced by jaw configuration, tooth position in the jaw, and surface area of each type of tooth.

Key Words: Atlantic sharpnose shark, *Rhizoprionodon terraenovae,* North Carolina, tooth surface area, tooth position, jaw shape.

INTRODUCTION

Naylor and Marcus (1994) identified carcharhinid shark teeth and noted their relevance in tracking phylogenetic changes through the fossil record. Applegate (1965) established shark tooth terminology. Breder (1942), James (1953), Cadenat (1962), Strasburg (1963), Moss (1967, 1972, 1977), Randall (1973), and Luer et al. (1990) noted tooth shedding mechanisms and tooth–body length relationships for several sharks. Compagno (1984, 1988) determined tooth number, shape, and jaw formulas for all known sharks. Yet, little or no attention has been given tooth surface area, tooth jaw position, or jaw shape in sharks, as they might affect shark feeding behavior. We examined two dimensional tooth surface areas and tooth position relationships of upper (palatoquadrate) and lower (Meckel's cartilage) right side jaw teeth of male and female Atlantic sharpnose sharks (*Rhizoprionodon terraenovae*) to determine if differences existed between their surface areas, tooth position, and jaw shape.

METHODS

Atlantic sharpnose sharks (a newborn male 450 mm Fork Length (FL), nine adult males, 740–820 mm FL, and 10 adult females, 770–890 mm FL) were captured during longline and otter trawl operations 14, 28 September and 12, 26 October 1995. Most sharks were captured on the longline (48 km long, 0.006 cm diameter) fished in the Atlantic Ocean three and 11 km south of Shackleford Banks, Carteret County, North Carolina, in waters 14–20 m deep. Otter trawl tows (12 m wide) were of 0.25 hr in similar depth waters.

Sharks, following capture, were measured (FL) and sexed. Their heads were severed, rinsed in sea water, and placed in labeled plastic bags for analyses ashore. Ashore, the position of a tooth in a jaw was determined by measuring along the right outer curved aspect of each jaw from the jaw symphysis to the midjoint of each tooth. The jaws were then removed and placed in freshwater for two weeks to soften the connective tissues surrounding the teeth bases. Once loosened, surface areas were determined for seven or eight representative teeth (symphyseal, anterior, lateral, and posterior) located on the outer row of each male and female right upper and lower jaw.

Two-dimensional tooth surface areas were automatically calculated for the selected teeth using the image analysis JAVA program (Jankel Video Analysis Software, Jandel Scientific). The enameled surface area of each tooth was "normalized" by dividing its surface area by the shark FL. Tooth position was "normalized" by dividing tooth distance from the symphysis by the curved length of each jaw. Graphs (69 points for adult males, 71 for females, and 15 for the newborn male) relating "normalized surface areas" to "normalized tooth position" were plotted and compared by jaw, sex, and shark age (Fig. 1). The graphed curves were determined using the 4th degree polynomial formula $y = a + bx + cx^2 + dx^3$. A linear regression $y = a + bx$ described the newborn vs. adult male lower jaw relationship (Fig. 2).

RESULTS

"Normalized tooth surface areas" versus "normalized tooth positions" of the right side adult male and female upper and lower jaws were highly correlated (male, upper r = 0.9396, lower r = 0.9110; female upper r = 0.9424, lower r = 0.9420, Fig. 1). The polynomial curves (Fig. 1) were expressed by the formulas: male, upper jaw $y = 0.0051 + 0.0792x - 0.1728x^2 + 0.0833x^3$, lower jaw $y = 0.0045 + 0.0690x - 0.1551x^2 + 0.0818x^3$; females, upper jaw $y = 0.0053 + 0.0876 - 0.1988x^2 + 0.0998x^3$, lower jaw $y = 0.0046 + 0.0808x - 0.1895x^2 + 0.1029x^3$. They revealed that the jaws were widest in both sexes at their lateral teeth position (Fig. 1). If one superimposed the upper on the lower jaw, by sex, males had wider jaws than did females (Fig. 2). Likewise, a cross-bite condition existed at the junction of the two jaws in males.

Comparing tooth surface area, tooth position, and jaw shape of the newborn

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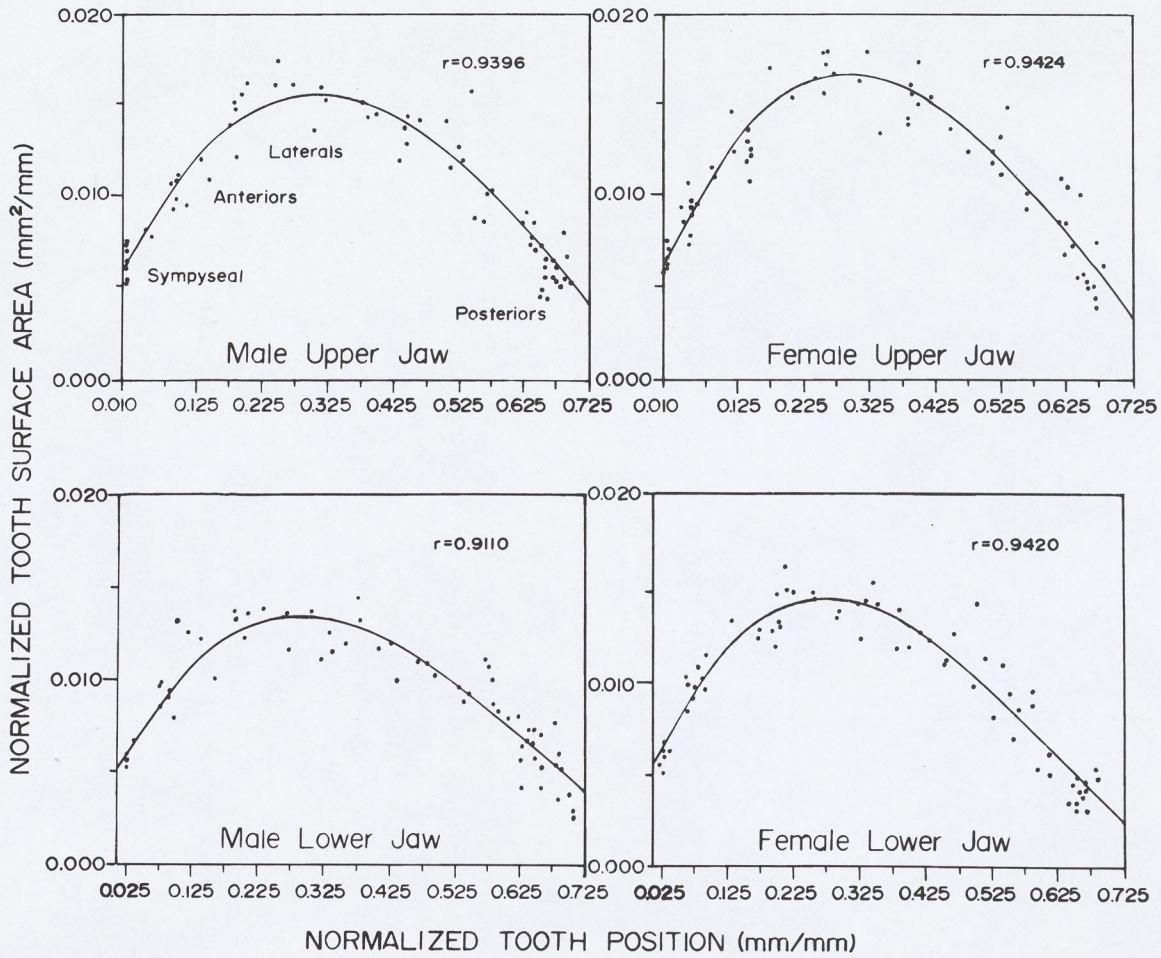
FIG. 1. "Normalized tooth surface areas"/"Normalized tooth position" comparisons of various upper and lower male (9 specimens) and female (10) Atlantic sharpnose shark teeth (69 data points for males, 71 for females).


NORMALIZED TOOTH SURFACE AREA (mm²/mm)
NORMALIZED TOOTH POSITION (mm/mm)
r=0.9396
Laterals
Anteriors
Sympyseal
Posteriors
Male Upper Jaw
r=0.9424
Female Upper Jaw
r=0.9110
Male Lower Jaw
r=0.9420
Female Lower Jaw
0.020
0.010
0.000
0.010
0.025
0.125
0.225
0.325
0.425
0.525
0.625
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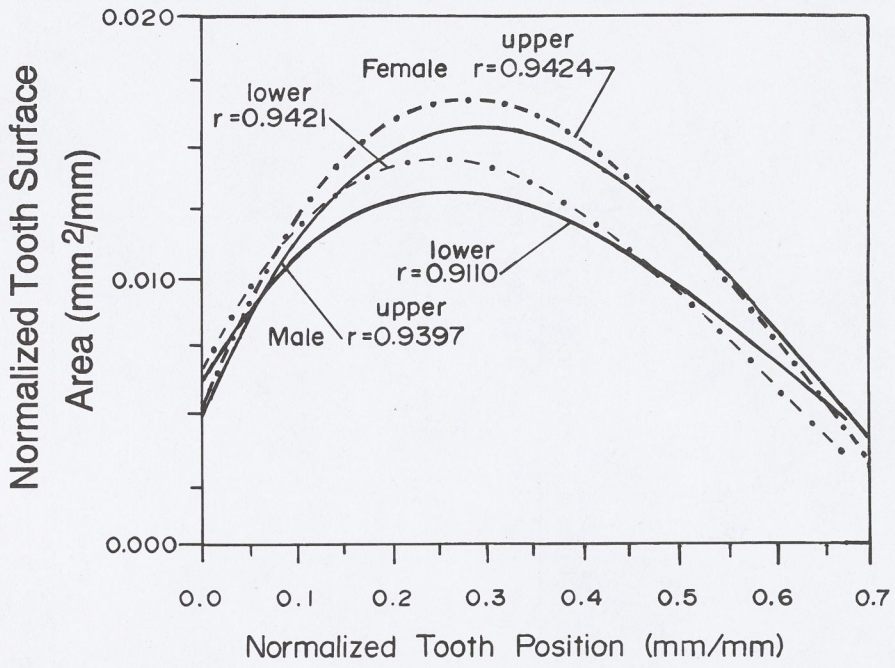

FIG. 2. Comparisons of "Normalized tooth surface areas"/"Normalized tooth positions" of male and female upper and lower Atlantic sharpnose shark teeth illustrating variations in jaw shapes and size/positions of their teeth.

male to adult male Atlantic sharpnose sharks found: "normalized tooth position" vs. "normalized tooth area" of the newborn was also highly correlated: upper jaw r = 0.9854, lower jaw r = 0.9516. The polynomial plot of the newborn tooth area/position relationship was: upper jaw $y = 0.0024 + 0.0472x - 0.0804x^2 + 0.0262x^3$, lower jaw $y = 0.0042 + 0.0319x - 0.0653x^2 + 0.0262x^3$. The shape of the newborn male's right side jaw was different, shallower, than that of adult males as the widest part of the upper jaw was at the level of the lateral teeth, whereas the lower jaw was widest slightly posterior of the midpoint of the jaw, nearer the rear of the laterals (Fig. 3). The upper jaw was statistically wider, using ANOVA analyses, than the lower jaw of both the adult and newborn specimens.

Comparing the length of the lower right side jaw of the newborn male to that of adult males revealed a linear relationship of r = 0.9959 existed and was best expressed by the formula $\log y = 1.0389 \log x - 3.2815$.

DISCUSSION

Between sexes: Upper and lower jaw teeth, tooth formula $\frac{12\text{-}1\text{-}12}{12\text{-}12}$, of the Atlantic sharpnose sharks, except for size, were serrated and undifferentiated, agreeing with descriptions of Compagno (1984) and Frazzetta (1988); smooth only in young, as noted by Meek and Hildebrand (1923). Female sharks had larger teeth (surface areas) per body FL than did males (Table 1). Surface areas of lateral

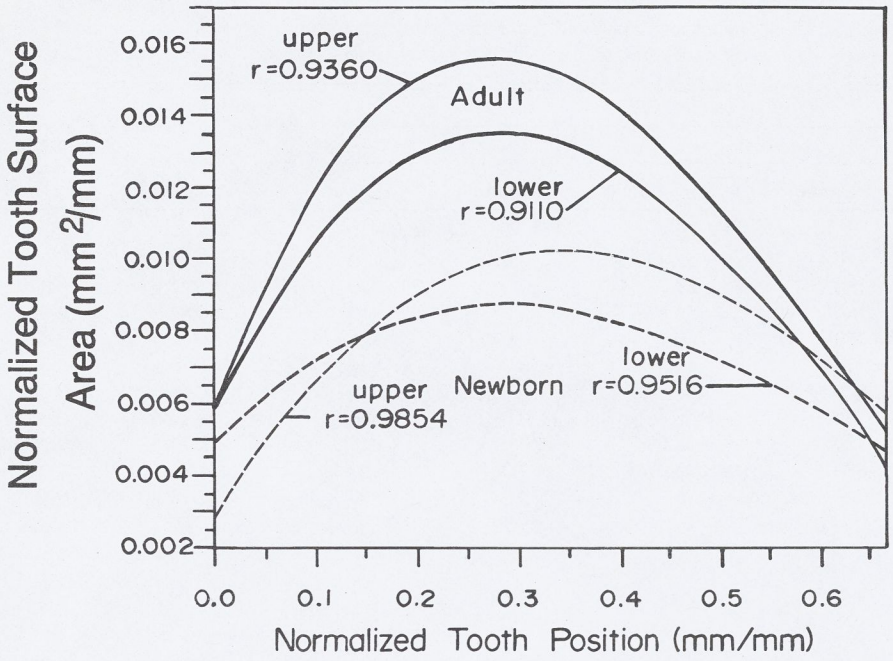

FIG. 3. Comparisons of adult and a newborn male Atlantic sharpnose shark upper and lower jaw shapes and tooth areas and positions.

teeth were largest, regardless of sex. Upper jaw tooth areas were greater than lower jaw tooth areas in both sexes (Table 1).

To explain these differences, we suggest that the female has a shallower bite than do males as the female's symphyseal, anterior, and lateral teeth are larger and more laterally positioned in the jaw vs. males (Fig. 1). This condition would produce a more even bite. Conversely, males might use their larger and wider rear positioned posterior teeth when they bite. This would permit them to penetrate their prey easier and to maintain a firmer grip on their food or a female when mating. The serrated aspect of the Atlantic sharpnose shark teeth helps them penetrate their prey better than pointed teeth would (Frazzetta 1994). Likewise, during feeding penetration of the smaller area lower teeth would permit easier penetration as the lower jaw strikes the prey. This behavior would be similar to that noted by Moss (1972, 1977), Springer and Gold (1989), and Frazzetta (1994).

FL versus low jaw length.—Applegate (1965), Randall (1973), and Springer and Gold (1989) noted a linear relationship in a number of species between shark tooth height and shark body length. Moss (1967) and Strasburg (1963) related tooth width to total body length. A strong 1:1 FL and lower jaw length relationship was evident for Atlantic sharpnose from North Carolina. This adds another means of determining shark length when the lower jaw length is known.

Behavior patterns.—Sharks exhibit a variety of feeding behaviors: gougers, suckers, crushers, graspers, biters, and filterers (Moss 1972, 1977; Springer 1961; Frazzetta 1994). This study strongly suggests that the feeding behavior of each sex and age of the Atlantic sharpnose shark may be correlated or influenced by

Table 1. Comparisons of upper and lower jaw tooth areas (cm^2), "normalized areas"/FL, for a newborn male, adult male, and adult female Atlantic sharpnose sharks.

Adult Male			Adult Female		
Tooth		Normalized area/FL	Tooth		Normalized area/FL
FL mm	Area cm^2	cm^2/mm	FL mm	Area cm^2	cm^2/mm
		Upper Jaw			
740	55.45	0.074	770	57.18	0.074
750	59.72	0.080	780	61.72	0.079
750	54.87	0.073	810	66.67	0.082
760	60.15	0.079	815	59.12	0.072
770	49.53	0.064	830	63.56	0.077
770	43.92	0.057	830	68.46	0.082
770	46.46	0.060	860	58.30	0.068
780	58.69	0.075	870	58.73	0.068
820	73.07	0.089	890	65.74	0.074
			890	97.18	0.109
Mean	55.76	0.072	Mean	65.67	0.079
	Newborn male				
450	26.43	0.059			
		Lower Jaw			
740	48.06	0.066	770	49.88	0.065
750	46.20	0.064	780	47.23	0.061
750	44.56	0.059	810	55.77	0.069
760	46.29	0.061	815	53.03	0.065
770	47.22	0.061	830	54.10	0.065
770	40.83	0.053	830	55.11	0.064
770	45.26	0.059	860	64.23	0.075
780	50.44	0.064	870	50.54	0.058
820	47.14	0.057	890	61.99	0.070
			890	61.66	0.069
Mean	46.22	0.060	Mean	55.35	0.066
	Newborn				
450	19.61	0.044			

its morphological jaw configuration, teeth position in the jaw, and surface area of each type of tooth. Studies examining similar features in other sharks may refine or explain the influence of a shark's dentition on its feeding behavior characteristics.

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A NORTH CAROLINA CAPTURE OF THE BRAMBLE SHARK, *Echinorhinus brucus,* FAMILY ECHINORHINIDAE, THE FOURTH IN THE WESTERN ATLANTIC

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Abstract: A 200.25 kg, 2408 mm TL female bramble shark, *Echinorhinus brucus,* is reported from North Carolina. It becomes the fourth specimen captured in the western Atlantic Ocean. Morphometric data are presented and compared to specimens captured elsewhere. Body–organ weight relationships are reported as well as comments concerning eggs and vertebrae.

Key Words: bramble shark; *Echinorhinus brucus*; North Carolina; western Atlantic Ocean.

INTRODUCTION

Debate still persists whether *Echinorhinus brucus,* the bramble shark, family Echinorhinidae, a cosmopolitan species, is different from *E. cookei,* the prickly shark, of the Pacific (Garrick, 1960; Compagno, 1984; Bass and Compagno, 1986). Recently Crane and Heine (1992a,b) reported seeing up to 30 individuals of *E. cookei* during any one observation in Monterey Canyon off California. *E. brucus,* supposedly the slimmer of the two species (Garrick, 1960), is known in the western Atlantic from three specimens captured between the late 1880s and 1969 off Massachusetts, Virginia, and Argentina, and occasionally by one or two individuals from other parts of the world (Bigelow and Schroeder, 1948; Musick and McEachran, 1969; Compagno, 1984). A fourth, *E. brucus,* has now been captured in the western Atlantic off North Carolina. Morphometric, body–organ weight relationships, and comments on eggs and vertebrae are compared to those reported in the literature.

A 2,400 mm FL, 2,808 TL, 200.25 kg female bramble shark (UNC 17387) was captured commercially by longline 15 March 1992 in the western Atlantic at 35°22.5′N latitude, 74°52′W longitude off Dare County, North Carolina. Capture was 69.2 km ENE of Cape Hatteras at a depth of 111 m, maximum water depth was 121 m. Bait was an "albacore," *Euthynnus alletteratus.* Morphometric data (Table 1) were similar to those reported for *E. brucus* from other localities (Bigelow and Schroeder, 1948; Garrick, 1960; Nair and Lal Mohan, 1971; Silas and Selvaraj, 1972; Somasekharan and Thulesidas, 1984) and the female captured off Virginia (Musick and McEachran, 1969).

EXTERNAL FEATURES

Body coloration was uniform light tan except under the snout and around the mouth where white prevailed (Fig. 1). Black spots (Garrick, 1960) were absent. Instead, four or five horizontal chocolate-brown stripes were present above the

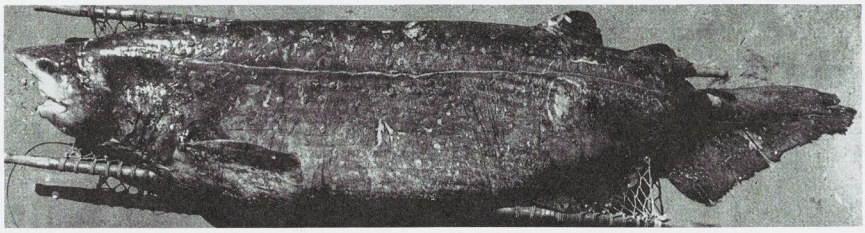

FIG. 1. Lateral view of a 200.25 kg, 2,408 mm TL female bramble shark captured in North Carolina. The bend in caudal peduncle unnatural and a result of body extending beyond stretcher on which shark rests.

lateral line, and 11 similar stripes, spaced 25–30 mm apart, were located below the lateral line, including the belly. Striping extended from the gill covers onto the caudal peduncle, where they blended with the brown color of the peduncle and tail. A prominent, closed-open lateral line described by Garrick (1960) extended from the level of the last gill slit, along the length of the body, onto the tip of the dorsal lobe of the caudal fin (Fig. 1). Pectoral- and pelvic-fin rear margins, as well as the trailing edge of the ventral caudal-fin lobe, were dusky to black. Single or clustered dermal denticles, often 28 × 30 mm in area, were scattered irregularly about the body, few were located on the snout and near the mouth, unlike the fine closely-positioned denticles of *E. cookei.* Teeth counts: upper jaw 11–11, lower 8–10 and similar in shape to those depicted by Bigelow and Schroeder, 1948; Garrick, 1960; Nair and Lal Mohan, 1971; Silas and Selvaraj, 1972; and Compagno, 1984. Discrepancy in the lower jaw tooth count stemmed from apparent damage at the mandible symphysis, perhaps a result of an earlier capture, for all the usual rows of teeth were missing and the symphysis had healed slightly askew. A large 12 cm white ring or spot, perhaps the result of the shark's encounter with an octopus or giant squid, was evident on the left side of the body just below the lateral line and between the dorsal and pelvic fins (Fig. 1).

INTERNAL FEATURES

No food was found in the intestinal tract; however, the stomach lining was orangish-red, similar to that reported by Silas and Selvaraj (1972) suggesting the North Carolina specimen had fed on crustaceans. No mention of body–organ weight relationships has been made in the literature. However, Silas and Selvaraj (1972) reported liver weights of 3 g and 5 g in 150 cm (20 kg) and 162 cm (29 kg) male *E. brucus* from India. Nair and Lal Mohan (1971) noted liver weight of 7.2 kg for a 1,790 mm (35.5 kg) male from the Gulf of Mannar, Southeast India. Musick and McEachran (1969) noted that each lobe of the liver in the 78.2 kg, 2,159 mm TL female *E. brucus* from Virginia was gray and weighed 8.1 kg. Right and left lobes of the gray liver in the North Carolina specimen weighed 8.2 and 13.9 kg respectively (Table 1). Thus, as body weight increased, liver weights increased yielding a body weight–liver percent weight change from 15, 17.2, 20.3 in specimens from India, to 20.7 in Virginia, and 22 percent in North Carolina. Weights of fins and other internal organs listed in Table 1 were similar to body–

Table 1

Original lengths (mm), percent total length, original weight (kg), and percent total weight for various morphometric and body-organ weight relationships of the female bramble shark captured off North Carolina.

	Total Length			Total Weight	
	mm	% Length		kg	% Total Weight
Total length	2,808	—	Total weight	200.25	—
Fork length	2,480	88.3	Liver left	13.9	6.9
Snout–D_1 Distance	688	24.5	Liver right	8.2	4.1
Snout–D_2 Distance	995	35.4	Intestine	3.9	1.9
Snout–P_1 Distance	729	26.0	Spleen	0.155	0.07
Snout–P_2 Distance	1,797	64.0	Kidney	0.122	0.06
Snout–upper caudal lobe	2,159	76.9	Caudal fin	3.727	1.9
Snout–lower caudal lobe	2,160	76.9	Gonad	3.141	1.7
Snout–in front outer nostrils	135	4.8	Heart	0.152	0.08
Snout–in front inner nostrils	156	5.6	D_1	0.398	0.20
Distance between D_1–D_2	129	4.6	D_2	0.247	0.12
Distance between D_1–upper caudal lobe	881	31.4	P_1	0.552	0.28
Distance between D_2–upper caudal lobe	317	11.3	P_2	0.995	0.50
Distance snout to 1st gill slit	534	19.0			
Distance snout to 2nd gill slit	579	20.6			
Eyes, diameter, height	50, 35	1.8, 1.2			
Interorbital distance	133	4.7			
D_1 base, height	190, 130	6.8, 4.6			
D_2 base, height	156, 134	5.6, 4.7			
P_1 length, breadth	392, 250	14.0, 8.9			
P_2 outer posterior, inner margin	362, 270, 260	12.9, 9.6, 9.3			
Mouth width, height	267, 82	9.5, 2.9			
Trunk at P_1 origin	514	18.3			
Trunk at P_2 origin	658	23.4			
Trunk at D_2 origin	317	11.3			
Gill length 1	126	4.5			
Gill length 2	142	5.1			
Gill length 3	160	5.7			
Gill length 4	191	6.8			
Gill length 5	187	6.7			
Distance between gill slit 1–2	5.1	1.3			
Distance between gill slit 2–3	5.7	1.2			
Distance between gill slit 3–4	6.8	1.8			
Distance between gill slit 4–5	6.7	1.7			
Teeth Upper	11–11				
Lower	8–10				

organ weight relationships noted in other large sharks (Schwartz, 1978; Winner and Schwartz, 1989, 1991).

Nair and Lal Mohan (1971) depicted a gill arch of an *E. brucus* from India with three gill rakers, the largest raker being about 5 mm long. The North Carolina

specimen's first gill arch weighed 460 g and had five gill rakers varying from 7.75, 14.25, 14.90, 13.00, to 7.55 mm in length. There were 100 gill filaments on the arch of which filaments 1–10 were 2–4 mm long, whereas every 10th filament, measuring dorsally–ventrally, for filaments 20–100, were 58.65, 61.20, 70.80, 69.80, 65.35, 65.00, 59.30, and 12.80 mm in length respectively.

Silas and Selvaraj (1972) commented that a Gulf of Mannar bramble shark contained a 30 cm long embryo. Others noted varying numbers of young comprised a litter (Compagno, 1984; Bass and Compagno, 1986). The North Carolina bramble shark contained two large egg envelopes. Each envelope was surrounded by a thin golden-grey membrane, similar to that surrounding ray eggs, and contained three greenish-cream colored yolks. Despite care the envelopes were easily ruptured permitting the tapioca-like consistency egg yolks to break up and ooze out of the envelope. No embryos or embryonic development was evident. Only Collyer (1953) commented on eggs, probably of a prickly shark, *E. cookei,* as being 3.3 cm in size in a 267 cm Guadeloupe, Mexico specimen. Each egg envelope in the North Carolina specimen was about 50 cm long, while each yolk was about 9 × 4 cm wide. Only one large egg (8.1 cm) was evident in the ovary; others were 1.5–2.0 cm in size.

Musick and McEachran (1969) and Springer and Garrick (1964) mention their inability to obtain radiographs of vertebrae in embryo and adult bramble sharks. Similar frustrations occurred when the North Carolina specimen was radiographed. At most slanted compartments (vertebrae?), visible externally, were evident on the radiographs of all areas of the completely cartilaginous vertebral skeleton. The skeleton, when dissected from the base of the skull to the upper caudal fin base, contained a gelatinous substance that occupied each "vertebral" compartment and flowed back and forth between compartments via 5 mm diameter holes located at each end of the compartment. If each compartment represented a vertebra (not as in other elasmobranchs or teleosts) then there were 58 vertebrae from the skull to the base of the upper caudal-fin lobe; 41 occurred from the base of the lower caudal-fin lobe to the tip of the upper caudal-fin lobe for a total of 94 "vertebrae." Five "vertebrae" occupied the space between the beginning of the lower and upper caudal-fin lobes. No comments can be made regarding number of mono- or diplospondylous vertebrae.

Frozen tissue samples of the liver, spleen, muscles, skin, and kidney have been deposited at the Smithsonian Institution, Laboratory of Molecular Systematics, USNM, Suitland, Maryland, and are available for study. Head, tail, fins, and body organs mentioned herein are preserved in the University of North Carolina, Institute of Marine Sciences, curated fish collection, Morehead City, North Carolina.

Acknowledgments: Thanks go to commercial fisherman Ted James of Buxton, NC, who captured the North Carolina bramble shark and had the great forethought to retain it and, realizing its scientific value, iced it and delivered it within hours of capture to Morehead City, some 595 km away for scientific study. J. Purifoy of IMS assisted with the autopsy. Dr. Michael Braun, Smithsonian Molecular Systematics Laboratory, advised regarding tissue sampling and care. Dr. V. Springer, Division of Fishes, USNM, reviewed the manuscript. Andre Share (IMS) took Figure 1. L. White typed the manuscript.

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CORONETFISHES (*Fistularia,* FISTULARIIDAE) AS FOOD OF THE DUSKY SHARK, *Carcharhinus obscurus* (CARCHARHINIDAE), FROM NORTH CAROLINA, AND PROBLEMS IDENTIFYING FISTULARIDS FROM ONLY HEADS

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Abstract: Eleven partially digested and five disarticulate heads of coronetfishes were among the stomach contents of an adult female dusky shark captured off North Carolina. Species identification was difficult as important characteristics of head bone serrations or body proportions were lacking or confusing when compared to intact undigested *Fistularia petimba* and *F. tabacaria.* On the basis of head bone serrations, four partially digested heads represented *F. petimba* while seven represented *F. tabacaria.* Body proportion ratios suggested all heads represented *F. tabacaria.* Only orbit length in snout length and eye in snout length ratios should be used to identify Atlantic Ocean fistularids; especially when head bone serrations are inconspicuous or absent. Better methods to distinguish coronetfishes are needed regardless of state of the specimen.

Key Words; coronetfishes; *Fistularia petimba; Fistularia tabacaria;* North Carolina; dusky shark; head features.

INTRODUCTION

Two coronetfishes (Fistulariidae) that attain 2 m lengths occur along the western North Atlantic coast and in North Carolina waters (Fritzsche, 1976; Robins and Ray, 1986; Schwartz, 1989). The bluespotted coronetfish (*Fistularia tabacaria*) occurs in coastal and shelf waters to depths of 200 m, while the red coronetfish (*F. petimba*) occurs in deeper waters (Schwartz, 1989). The shallow water, often schooling (Fritzsche, pers. comm.), *F. petimba* of the Marshall Islands is *F. commersonii* (Hiatt and Strasburg, 1960; Fritzsche, 1967). Both *Fistularia* of the Atlantic Ocean are easily distinguished from the smaller (to 1 m) trumpetfish, *Aulostomus maculatus,* that frequents weedy inshore and shallow reef habitats, as they lack the chin barbel of the trumpetfish and possess an elongate median caudal fin element. Little is known regarding any *Fistularia* other than species distinctions and distributions (Fritzsche, 1976; Schwartz, 1989). We report the occurrence of a mixture of *F. petimba* and *F. tabacaria* heads as stomach contents of a female dusky shark (*Carcharhinus obscurus*), comment on problems in identifying the fistularids, and discuss the depths frequented by the shark and the coronetfishes.

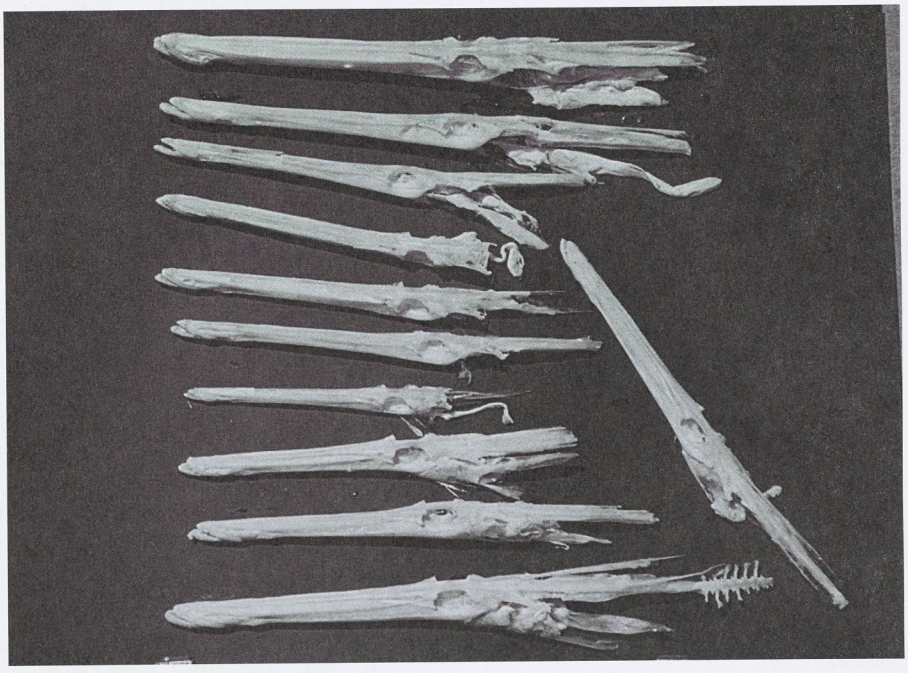

FIG. 1. Eleven partially-digested heads (top to bottom), four are *Fistularia petimba,* and seven *F. tabacaria,* see text for further identity comments.

MATERIALS AND METHODS

An adult female dusky shark, 250 cm fork length, 300 cm total length, was captured 15 March 1996 in the western Atlantic Ocean off North Carolina at 33°58.1′N, 76°42′W on a bottom longline set by the F/V *Reel Action* II. Water temperature was 16.4°C at the depth of capture (55 m). The female shark's stomach contained numerous coronetfish heads. Eleven heads were partially digested, some with vertebrae, gills, and viscera still attached (UNC 17507, Fig. 1); five additional heads were disarticulated. One honeycomb cowfish (*Lactophrys polygonia*), and a bluefish (*Pomatomus saltatrix*) also comprised the stomach contents.

Species identification of the heads was attempted by two methods; 1) head measurements consisted of measuring the snout from the tip of the premaxillary to the anterior rim of the orbit (SN), from the tip of the premaxillary to the rear of the epiotic bone (Ep, see Gregory, 1959 for bone delineation), orbit length (OR), and interorbital width (IO), and 2) examining the lateral snout, preorbital, postorbital, and post-temporal bones for the presence or absence of serrations (Fritzsche, 1976). Graphic plots of the partially digested head measurement relationships SN/Ep, SN/OR, SN/IO, and orbit length in SN were then compared to intact curated specimens of *F. petimba* (UNC 2710 [1 specimen], 4764[1], 10570[2], 15981[1], 16077[2]), and *F. tabacaria* (UNC 2477[3], 4658[2], 10234[1], and 17496[1]). Linearity was evident by the measurement relationships and calculated using the formula $\log y = a + b \log x$. Where graph differences seemed apparent between the heads and curated *Fistularia,* statistical ANOVA analyses compared SN/OR, SN/I0, and eye in SN relationships.

OBSERVATIONS

Identification of the heads, on the basis of presence or absence of head bone serrations (Fritzsche, 1976), was difficult as the presence of serrations was often inconspicuous or absent, an erosion condition that could have resulted during partial digestion. Only four of the 11 heads possessed serrations on the snout ridge (specimens 1, 5, 6, 7, Fig. 1), whereas those bones were smooth on the other seven heads. Thus, four heads were identified as *F. petimba* and seven as *F. tabacaria.* Otherwise, the preorbital ridges were smooth on all heads, as described for *F. tabacaria*; not serrated as in *F. petimba* (Fritzsche, 1976). Postorbital ridges were serrate on heads 5, 7, 8, and 9, suggesting they were *F. petimba*; *F. tabacaria* postorbital bones are smooth (Fritzsche, 1976). Heads of preserved intact *F. petimba* have head ridges and bones as described by Fritzsche (1976). On the basis of the variations noted in the digested head ridges, doubt still persists regarding the identities of the four heads as *F. petimba* and the seven heads as *F. tabacaria.*

Further, plotting the various head length measurement ratios of the partially digested *F. petimba,* and *F. tabacaria* heads also suggested that the head features commonly used in separating *F. petimba* and *F. tabacaria* (Fritzsche, 1976) should be reexamined, as linearity was noted between several ratios. The SN/Ep length ratio relationship was linear and expressed by the formula $\log y = 0.0912 + 1.0063 \log x$, $r = 0.9982$ (Fig. 2a). This ratio was not significantly different between the heads and intact curated specimens. When comparing the partially-digested heads to intact *F. petimba,* and *F. tabacaria* heads (Fig. 2b) the SN/OR ratio was also linear: $\log y = -1.0443 + 1.0476 \log x$, $r = 0.9440$, and highly significant, $f = 68.61^{**}$ $df = 13$. The eye in SN relationships of head and curated specimens varied between 9 and 40 and were highly significantly different, 56.36^{**}, $df = 13$ and expressed by the linear formula: $\log y = 1.0450 + -0.4794 \log x$, $r = -0.1296$ (Fig. 2c). The SN/Ep ratio ranged between 0.640 and 0.830, $\log y = -0.0617 + -0.0205 \log x$, $r = -0.2060$ and was not significant (Fig. 2d). SN/I0 width measurement relationships for the heads and preserved specimens (used by Meek and Hildebrand, 1923) were also linear: $\log y = -1.4467 + 1.0650 \log x$, $r = 0.9639$, and not significant $f = 0.043$, $df = 13$ (Fig. 2e). On the basis of the above ratios and employing the eye in SN ratio, all heads should be *F. tabacaria,* as *F. petimba* has a smaller eye than *F. tabacaria.* On the basis of OR/SN ratios (Fig. 2b) all heads should likewise be *F. tabacaria,* as *F. petimba* has a smaller OR/SN ratio (Fig. 2b).

DISCUSSION

Compagno (1984) mentions that only two sharks, the blacktip shark (*Carcharhinus limbatus*) and the longnose sawshark (*Pristiophorus cirratus*) have fed on coronetfishes. The fast-swimming *C. limbatus* feeds deeper than 30 m, while the longnose sawshark of the Australian Pacific Ocean occurs deeper than 311 m (Compagno, 1984). This suggests that *F. tabacaria* was the food fish of *C. limbatus* and *F. petimba* the sawshark. Randall (1967) noted *F. tabacaria* in the stomach of a 920 cm SL black grouper (*Mycteroperca bonaci*) in the West Indies. *M. bonaci* rarely frequents depths below 30 m (Bullock and Smith, 1991).

Dusky sharks are usually considered slow-moving sharks that frequent coastal

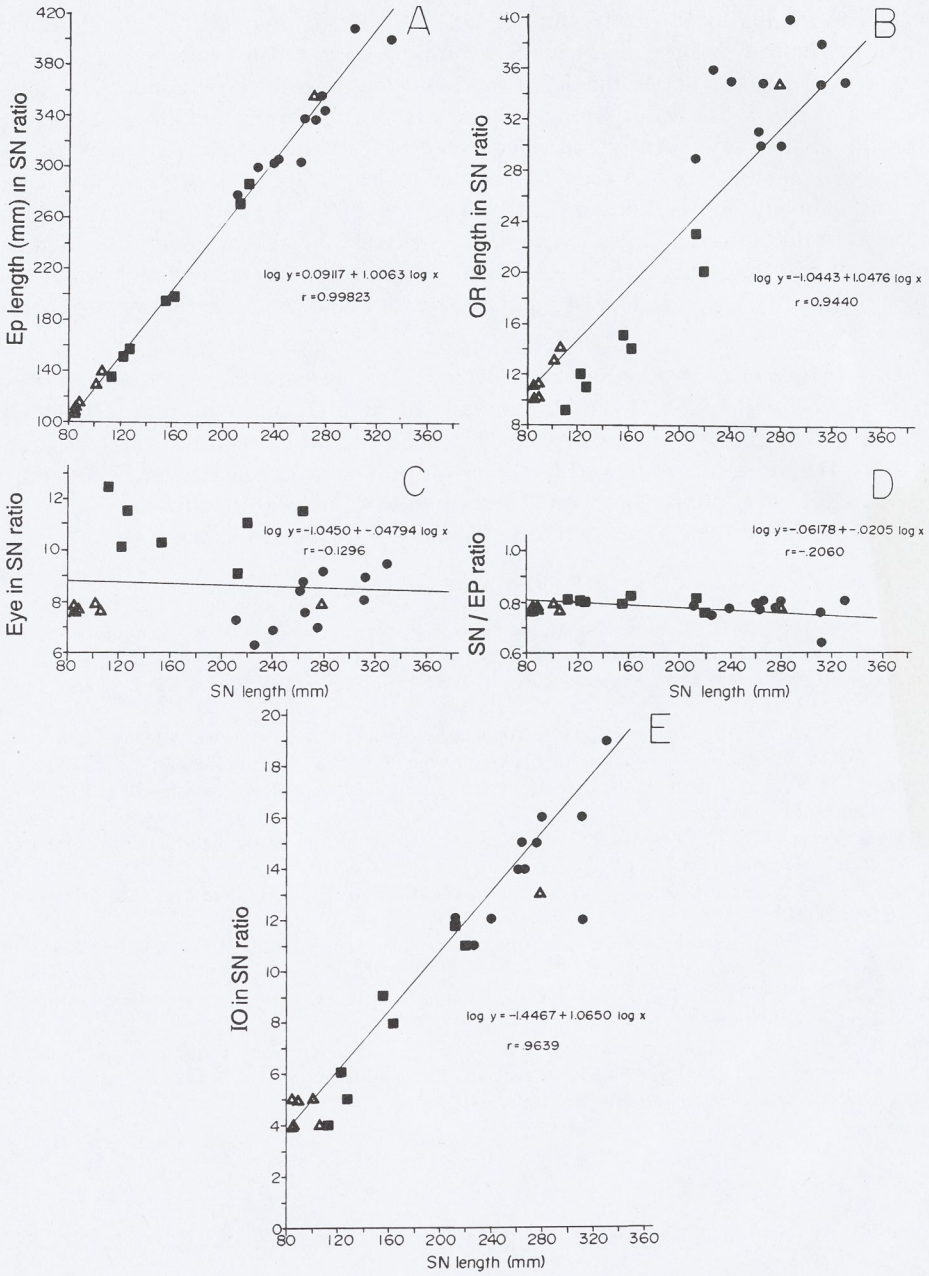

FIG. 2. Linear regression comparisons of: a) Snout length (mm) to Ep length (mm) ratio, b) SN to OR length in SN ratio, c) SN to Ep in SN ratio, d) SN to SN/Ep ratio, and e) SN and IO in SN ratio. Dots represent partially-digested heads, preserved ■ *F. petimba,* and △ *F. tabacaria* head features and measurement ratios.

waters to depths to 400 m (Compagno, 1984). The capture of the female dusky shark in shallow water (55 m), with the mixed coronetfish heads, presents interesting new insight about the shark and its depth feeding behavior. The large number of *Fistularia* heads, along with portions of their gills and viscera, suggests that the shark had recently fed. Occurrence of so many heads of each of the coronetfishes suggests that they may occur in larger aggregations and at greater depths than previously known. Lastly, because of the possible erosion of head bone serrations during digestion, and the linearity noted for several head measurement features, only the OR length in snout or eyes in snout ratios should be used to identify Atlantic Ocean fistularids, when head bone serrations are inconspicuous or absent.

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NOTE

EFFECTS OF THE SHARKSUCKER, *Echeneis naucrates,* FAMILY ECHENEIDIDAE, ON CAPTIVE SHEEPSHEAD, *Archosargus probatocephalus*

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Key Words: sharksucker; sheepshead; *Echeneis naucrates*; *Archosargus probatocephalus.*

To date, only Schwartz (1977) has noted the effects of the sharksucker, *Echeneis naucrates,* family Echeneididae, on captive fishes (48 species in 21 families) and sea turtles (three species). Cownose rays, *Rhinoptera bonasus* and striped mullet, *Mugil cephalus,* were shown to be the easiest to have their skin or scales abraded by sharksuckers while all other test fishes outswam or sluffed the sharksuckers. The abraded fishes died once abrasion proceeded through their skin or scales to the muscles. Sheepshead, *Archosargus probatocephalus,* responded by shedding the sharksucker, by outswimming it, or by scraping along the substrate to dislodge the hitchhiker.

Recently, the same (as in 1977) 1.2 million liter, 9.1 × 18.2 × 0.75 m deep, concrete holding tank now half filled with pea-sized gravel and supplied with flow through Bogue Sound, North Carolina, 30–34 ppt saline waters, was used to note the further effects of sharksuckers on sheepshead. A 145 mm standard length (SL) sharksucker, *E. naucrates,* captured 8 July 1991, was released into the holding tank occupied by two adult and one 152 mm (SL) yearling sheepshead (Schwartz, 1990) and two sea robins (*Prionotus carolinus* and *P. tribulus*) that had resided in the tank for over a year (since 14 May 1990). The sharksucker had been attached to a 1,378 mm fork length blacktip shark, *Carcharhinus limbatus,* captured in the Atlantic Ocean 5 km southeast of Morehead City, North Carolina. Colorations of the tank-held sheepshead were the usual dark black and silvery banding on a darkened black body background. All fish were in good physical health.

The sharksucker paid no attention to the smaller two sea robins (±180 mm SL), instead immediately associated itself with a 365 mm (SL) sheepshead. It moved characteristically all over the head and darkened body of the sheepshead seeking a firm place to attach. At first abrasions by the sharksucker disk were evident, in four days, on the opercle and nape. Subsequently, body scales were abraded on the nape and dorsally along each side of the spinuous dorsal fin base. Once those areas were abraded through to the skin of the now light-colored and banded sheepshead, the sharksucker next abraded the body scales, beginning at the pectoral fin base and moving onto the mid-lateral scaled body. Eventually the skin and scales were rasped away, especially on the left side of the sheepshead, as were those of the gular, breast area, and opercles (Fig. 1).

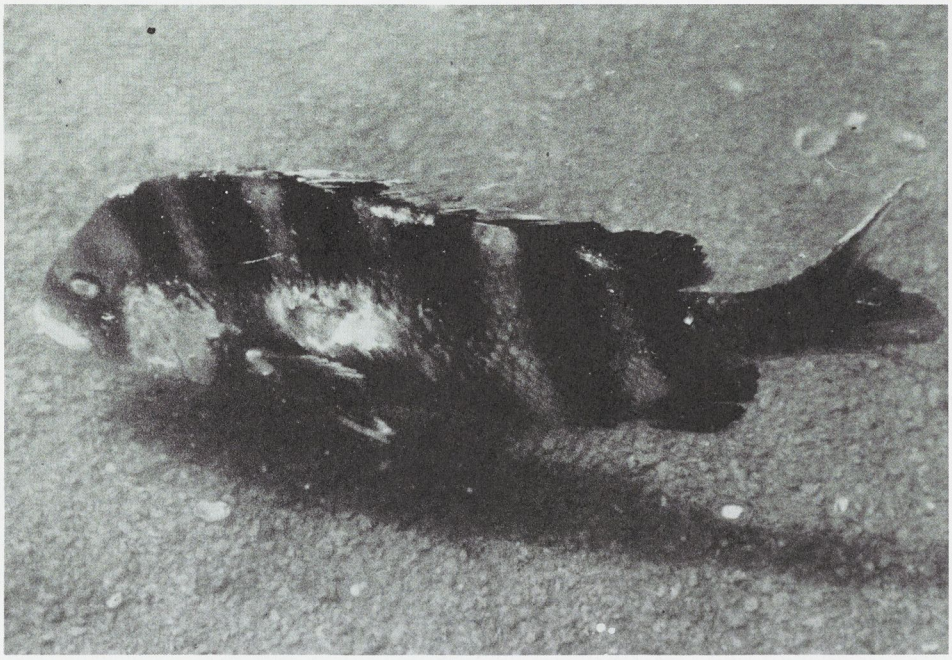

FIG. 1. Sheepshead, *Archosargus probatocephalus,* illustrating body abrasion and scale removal following 55 days of attachment activities by the sharksucker, *Echeneis naucrates.*

The affected sheepshead stopped feeding once pursued by the sharksucker and increased its swimming and scraping against the tank substrate in efforts to dislodge the fish with little success. The sheepshead lived 55 days, dying 1 September 1991. The sharksucker was then transferred to another similar sized, sans gravel, tank that contained loggerhead sea turtles, *Caretta caretta,* in order to spare the remaining sheepshead. The sharksucker, as in 1977, attached itself to the turtles. Months later no abrasions were evident as a result of its attachment activities.

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BIOLOGY OF THE CLEARNOSE SKATE, *RAJA EGLANTERIA,* FROM NORTH CAROLINA

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ABSTRACT: *Clearnose skates,* Raja eglanteria, *were trawled in 1993 and 1994 from the western Atlantic Ocean off Shackleford Banks, Carteret County, North Carolina. Aspects studied were: age and growth, food, environmental features, body surface areas and several body-organ weight and morphometric relationships. New data expand prior information on this common yet neglected skate. ANOVA analyses, by sex and year, did not substantiate specimens from two populations being sampled. Females were heavier than males and possessed slightly shorter tails than did males, even with increasing total lengths. Female disk widths were slightly smaller than in males. Male surface areas were larger than those of females. Clearnose skates were apparently more active than previously believed. A variety of foods were eaten.*

PRIOR to 1963 and even today meager literature refers to the wide ranging, Massachusetts to Florida and west in the Gulf of Mexico, clearnose skate, *Raja eglanteria,* (Bigelow and Schroeder, 1953; McEachran and Musick, 1975, Luer and Gilbert, 1985). Previous studies pertain to seasonal or range occurrences, distribution and environmental factors or limited aspects dealing with morphology and biology (Breder, 1924; Fahey, 1966; Fitz, 1956; Fitz and Daiber, 1963; Fowler, 1916; Hildebrand and Schroeder, 1928; Price, 1967; Schwartz, 1981, 1995 in press; Schwartz et al. 1981; Shaefer, 1967; Wilk and Silverman, 1976). This study examines clearnose skates trawled in the western Atlantic Ocean off Shackleford Banks, Carteret County, North Carolina in 1993 and 1994. It resolves whether they represented members of a southern subspecies of the skate, and enlarges upon age and growth, food, environmental features, body surface areas, and several body-organ weight and morphometric relationships.

METHODS—Clearnose skates were captured up to 11.5 km offshore of Shackleford Banks during 0.5 hr daylight tows of a 12.5 m head-rope semi balloon otter trawl, at depths of 10.7 to 19.8 m between 15 April and 31 October 1993 and 1994. Near surface water temperatures and depths were recorded continuously by the 16.5 m R/V Capricorn via temperature and depth recorders mounted 1.5 m below the water surface.

Specimens were frozen for subsequent examinations, measurement, and study. Each individual was sexed and various body features measured in millimeters. Body measurements were: total length (TL), disk length (DL), disk width (DW), pelvic fin length, and tail length (from junction with pelvic fin to tail tip). Total body weight (BW) was recorded in grams (g), using a triple beam balance while organ weights were recorded, to the nearest 0.001 g, by an electronic Mettler balance for: heart, liver, intestine, gonads, kidneys, spleen, and eyes. Each year male and female gonads were examined to note extent of seasonal development. Fish and

body organs were patted dry of excess moisture prior to weighing. Percent body-organ weight relationships were calculated for each sex. ANOVA, single classification, analyses tested TL, DW, and tail length data for differences between sexes and sample years. Vertebra, 5–10th, were excised and air dried or after soaking in glycerine, anise oil, and isopropyl alcohol for several days, examined for age analyses. Instead age determinations were estimated from DW frequencies following Fitz (1956) and Fitz and Daiber (1963, Table 2).

A DW-TL factor X was calculated for each specimen following the formula of Daiber (1960) where TL = X·DW + 5CM. Surface areas and body and disk factor were determined following the methods of Musick and co-workers (1990) and Schwartz and co-workers (1993) where surface area SA = X·(G·TL), SA = total body plus pelvic fins (and clasper in case of males), and tail surface areas, G = girth (an addition of upper and lower DW measurements), and TL = total body length. Surface areas were determined from templates made of 100% rag Albenene tracing paper outlines of the dorsal and ventral sides of the body disk, pelvic fins, tail and/or clasper surfaces of each specimen. Templates were washed of excess blood or mucous and air dried prior to weighing. An average weight of 0.006 g/cm^2 was determined by weighing 1 × 1 or 10 × 10 cm pieces of the tracing paper. Total body disk, fin, tail and/or clasper template weights × 0.006 g/cm^2 determined the surface area desired.

Linear regressions determined male and female: length-weight, TL-total body surface area, disk surface-total body surface areas, BW-heart weight, BW-liver weight, BW-intestine weight, BW-gonads weight, BW-kidneys weight, BW-spleen weight, BW-eyes weight, TL-gonad weight, TL-male clasper length, TL-DL, and TL-DW relationships (Table 1).

Stomach and intestine food contents were determined for only clearnose skates caught in 1994. Foods were determined to the lowest possible taxon.

RESULTS—Nine males and 16 females (8 males and 15 females were immature) were captured in 1993 while 44 males and 45 females (39 males and 35 females were immature) were captured in 1994 (Table 1). Size ranges were: TL mm, 1993 males 290–579, females 386–570; 1994 males 255–614, females 361–687. Weights (g) ranged: 1993 males 118–1095, females 223–1267; 1994 males 78–1547, females 193–2070 (Table 1). Captures occurred in waters 20–30°C in 1993 and 19–29°C in 1994. No clearnose skates were caught when near waters were cooler than 18.9°C or warmer than 30°C in summer. Spring caught males were largest in May, 1994, 614 mm TL. Fall caught males were largest in October 1993, 570 mm TL. Spring caught females were largest, 657 in May 1994 versus 570 mm TL in October 1993. Generally, most large specimens prevailed in fall rather than spring samples (Table 1). DL's were similar each year but DW's were larger in 1994 than 1993 caught specimens (Table 1).

Morphometric observations—Linear regressions defined male and female TL-weight relationships in 1994 as: male log weight = −4.9320 + 2.8808 log TL, r = 0.9118, female log weight = −5.7680 + 3.1869 log TL, r = 0.9565 (Table 2), substantiating females attained heavier weights and total lengths than did males (Fig. 1).

TL-tail length relationships were linear for both sexes caught in 1994 (Table 2), male r = 0.9187, females r = 0.9295 even though females possessed slightly shorter tails at all sizes. Tail lengths of both sexes were proportionally smaller with increasing TL, decreasing from 50% of the TL in small specimens to about 45% in mature clearnose skates.

TABLE 1. Catch, by date, sex, size TL, disk length and width, and weight (W, in g) of *R. eglanteria* off Shackleford Banks, NC, in 1993 and 1994, water temperature °C.

	Males								Females						
Date	N	$\bar{x}$	TL	DL	DW	W	°C	Date	N	$\bar{x}$	TL	DL	DW	W	°C
						1993									
15 May	1	—	341	190	228	182	23.8	15 May	1	431	390–550	198–293	253–365	254–883	23.8
1 June	2	336	290–382	155–201	192–248	118–258	23.9	17 May	3	522	386–473	386–473	237–303	474–1267	23.9
7 June	2	535	545–562	286–300	346–380	768–1074	29.8	1 June	1	386	386	190	238	233	23.9
11 Oct	3	478	295–579	230–300	253–379	302–1095	23.9	7 June	1	470	470	255	312	500	29.8
26 Oct	1	540	540	285	353	890	20.8	26 Oct	4	473	386–473	202–252	257–303	223–258	20.8
	9								16						
						1994									
18 Apr	3	442	394–530	211–277	253–353	302–792	18.9	18 Apr	5	496	431–553	221–295	262–357	352–967	18.9
3 May	4	480	397–561	210–294	258–354	288–1013	22.6	3 May	8	509	353–687	186–366	226–465	200–2070	22.6
16 May	30	487	255–614	190–329	176–404	214–1547	22.5	16 May	28	463	361–657	177–338	224–419	193–1496	22.5
20 Jun	0	—	—	—	—	—	28.6	20 Jun	1	438	438	226	268	353	28.5
28 Jun	1	362	363	230	228	214	27.0	28 Jun	0	—	—	—	—	—	27.0
17 Oct	2	428	255–600	136–315	171–385	78–1274	20.0	17 Oct	2	—	600–618	318–335	400–419	1509–1565	20.0
20 Oct	1	450	450	240	298	526	20.0	20 Oct	1	613	613	393	394	1115	20.0
31 Oct	3	552	540–562	277–296	353–368	526–1145	21.4	31 Oct	0	—	—	—	—	—	21.4
	44								45						

Linear TL-DL regressions for 1993 and 1994 caught specimens (Table 2) revealed females in 1993 possessed larger body disks than did males longer than 450 mm TL. Small sample sizes in 1993, 9 males, 16 females, may account for this difference since no TL-DL surface area dissimilarities existed for males (44) and females (45) caught in 1994 (Fig. 2).

TL-DW relationships were similar for both years except 1993 female disk widths were slightly smaller than DW's in males 300–550 mm TL.

TL-clasper analyses (Table 2, Fig. 3) of specimens caught in 1994 revealed a typical abrupt upward flexure in the relationship in mature males longer than 550 mm TL. North Carolina males matured earlier than those noted off Block Island, Massachusetts, 750–770 mm TL, by Bigelow and Schroeder (1953).

Surface areas and factors—Solving for Daiber's (1960) TL-DW X factor relationship found: X factors for males captured in 1993 were $\bar{x}$ = 1.50 (range 1.47–1.56), females $\bar{x}$ = 1.53 (range 1.45–1.61); 1994 males $\bar{x}$ = 1.50 (range 1.29–1.63), females $\bar{x}$ = 1.52 (range 1.41–1.63), factors all larger than the 1.45 determined for clearnose skates of Delaware Bay.

Surface area X factors, an addition of dorsal and ventral disk widths, were determined by the formula SA = X (G·DL), G = girth. Surface areas were similar for 1993 males $\bar{x}$ = 0.0060 (range 0.0036–0.0083), females $\bar{x}$ = 0.0062 (range 0.0044–0.0065), while 1994 factors were much higher: males $\bar{x}$ = 0.0076 (range 0.0058–0.0087), females $\bar{x}$ = 0.0070 (range 0.0050–0.0084). Both sexes in 1994 had larger total body surface areas than in 1993, with male surface areas being larger, at all sizes, greater than 260 mm TL, whereas 1993 male surface areas were larger in specimens less than 530 mm TL (Fig. 3).

Comparing disk surface areas to total surface areas, 1993 male disk areas were about $\bar{x}$ = 84% (range 76.7–87.9) of the total body surface area, females $\bar{x}$ = 85.3% (range 82.6–87.7); 1994 male disk surface areas were $\bar{x}$ = 81.6% of total body surface area (range 74.1–86.5), females $\bar{x}$ = 82.9% (range 75.7–88.1), again larger disk surfaces were possessed by 1994 than 1993 caught males.

TL-total body surface areas were constantly larger in 1994 males larger than 320 mm TL than females. But 1993 males smaller than 530 mm TL, had larger body surface areas than did females (Table 2).

Body organ-weight relationships—Body-organ heart, liver, and intestine weights for 1994, as a percent of body weight, were usually larger in females; gonads, kidney, spleen, and eye relationships were similar between sexes (Tables 2, 3).

BW-heart weight (BW) relationships were larger in 1994 for both sexes. Male hearts were always larger than female hearts in specimens longer than 200 mm TL, whereas the reverse was true in 1993, as female hearts were

TABLE 2. Linear regressions and correlation coefficients of various disk-TL surfaces and body-organ weight relationships of male and female *Raja eglanteria* captured in 1993 and 1994.

	1993		
Male (N = 9)		Female (N = 16)	
Body-organ weight relationships			
Log heart = −2.8449 + 0.8847 log body wgt.	r = 0.9359	Log heart = −2.9826 + 0.9528 log body wgt.	r = 0.8679
Log liver = −2.1982 + 1.2047 log body wgt.	r = 0.9477	Log liver = −1.9127 + 1.1340 log body wgt.	r = 0.9346
Log intestine = −1.6170 + 0.9899 log body wgt.	r = 0.9436	Log intestine = −2.1063 + 1.1860 log body wgt.	r = 0.8811
Log gonad = −6.7525 + 2.5262 log body wgt.	r = 0.8938	Log gonad = −5.2182 + 1.9710 log body wgt.	r = 0.8761
Log kidney = −4.7747 + 1.7154 log body wgt.	r = 0.8656	Log kidney = −3.3293 + 1.1273 log body wgt.	r = 0.8702
Log spleen = −3.3972 + 1.1044 log body wgt.	r = 0.9748	Log spleen = −2.0140 + 0.7433 log body wgt.	r = 0.7212
Log eye = −0.9320 + 0.3026 log body wgt.	r = 0.4906	Log eye = −1.4959 + 0.5048 log body wgt.	r = 0.6957
Body feature-TL relationships			
Log gonad = −21.5636 + 8.1190 log TL	r = 0.8719	Log gonad = −20.6593 + 7.7909 log TL	r = 0.8902
Log disk length = −0.5329 + 9.1377 log TL	r = 0.9758	Log disk length = −0.9337 + 1.2488 log TL	r = 0.9678
Log disk width = −0.1431 + 0.9833 log TL	r = 0.9920	Log disk width = −0.4019 + 1.0780 log TL	r = 0.9802
	1994		
Male (N = 44)		Female (N = 45)	
Surface area-TL relationship			
Total length log surface = −2.1435 + 1.9641 log TL	r = 0.9696	Total length log surface = −2.8512 + 2.2102 log TL	r = 0.9794

TABLE 2. Continued.

Male (N = 44)		Female (N = 45)	
Body-organ weight relationships			
Log heart = −3.6257 + 1.2073 log wgt.	r = 0.9481	Log heart = −3.1823 + 1.0354 log wgt.	r = 0.9164
Log liver = −2.4224 + 1.3040 log wgt.	r = 0.9433	Log liver = −2.4763 + 1.3445 log wgt.	r = 0.9458
Log intestine = 1.3380 + 0.8565 log wgt.	r = 0.9492	Log intestine = −1.7527 + 1.0358 log wgt.	r = 0.9587
Log gonad = −5.4959 + 2.0711 log wgt.	r = 0.7920	Log gonad = −5.3677 + 2.0028 log wgt.	r = 0.8402
Log kidney = −2.5659 + 0.9325 log wgt.	r = 0.8741	Log kidney = −2.6468 + 0.9753 log wgt.	r = 0.8984
Log spleen = −3.2652 + 1.1613 log wgt.	r = 0.9039	Log spleen = −2.7692 + 1.0092 log wgt.	r = 0.8588
Log eye = −2.4610 + 0.8237 log wgt.	r = 0.9379	Log eye = −2.6536 + 0.8909 log wgt.	r = 0.9391
Body feature-TL relationships			
Log gonad = −19.1811 + 7.2512 log TL	r = 0.7991	Log gonad = −17.0428 + 6.4253 log TL	r = 0.8196
Log clasper = −7.7513 + 3.5142 log TL	r = 0.9010	none	
Log disk length = −0.1294 + 0.9452 log TL	r = 0.9691	Log disk length = 0.3434 + 1.0247 log TL	r = 0.9835
Log disk width = 0.1428 + 0.9848 log TL	r = 0.9779	Log disk width = 0.1947 + 1.0031 log TL	r = 0.9873
Log tail L = −0.2852 + 0.9885 log TL	r = 0.9187	Log tail L = 0.0781 + 0.8472 log TL	r = 0.9295
Surface areas			
Log total surface = −2.3855 + 2.0398 log TL	r = 0.9719	Log total surface = −2.0890 + 1.9291 log TL	r = 0.9860
Log disk surface = −0.0559 + 0.9526 log total surface	r = 0.9945	Log disk surface = −0.0584 + 0.9925 log total surface	r = 0.9963
Length-Weight			
Log weight = −4.9320 + 2.8808 log TL	r = 0.9118	Log weight = −5.7680 + 3.1869 log TL	r = 0.9565

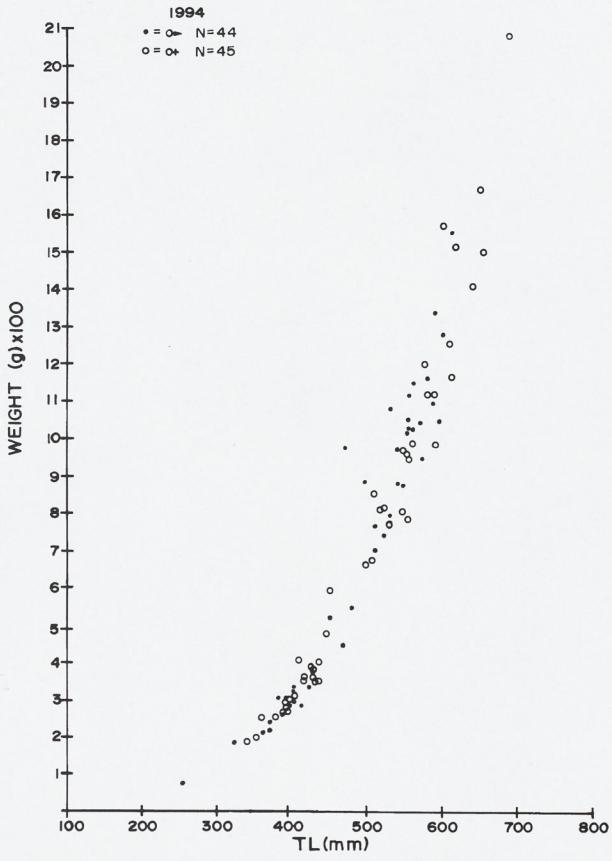

FIG. 1. Length-weight relationships for male and female clearnose skates captured in 1994.

always larger than male hearts at all sizes (Tables 2,3), perhaps the latter an influence of the small 1993 sample sizes.

BW-liver relationships revealed livers were heaviest in males weighing more than 800 g in 1993 and 600 g in 1994. The largest liver weighed 90.75 g in a 1877 g female caught in 1994. The heaviest male liver weighed 60.49 g in a 1547 g, 1994 specimen.

BW-intestine relationships found female 1993 intestine weights were, overall, heavier than male intestine weights (Table 2), whereas 1994 female intestines were heavier than male weights if the body weight was in excess of 400 g (Table 2).

BW-gonad weights were variable. Male 1993 gonad weights were heavier at all sizes than female gonads, whereas 1994 gonads always weighed more if the body weight was in excess of 400 g (Table 2).

Both sexes of 1994 fall caught specimens exhibited enlarged gonads.

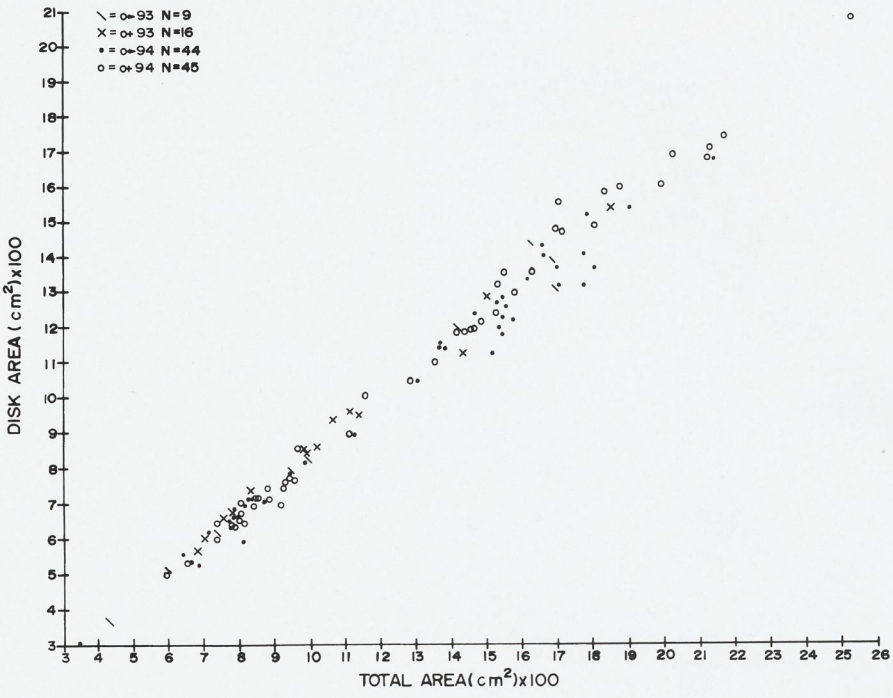

FIG. 2. Total and surface area relationships for clearnose skates captured in 1993 and 1994.

Females reflected this condition in their TL-weight regressions, enlarged shell glands, and externally an enlargement of their cloacas. The largest bulbous cloacas were evident in more mature, fall caught females.

BW-kidney weights. Male kidney weights were always heavier in 1993 than in females. Female kidneys weighed more in 1994 than did male kidneys, if females weighed more than 700 g (Table 2).

BW-Spleen-BW. Female spleen weights in 1993 exceeded male weights at all body weights whereas in 1994 male kidneys were heavier in specimens up to 700 g (Table 1).

Eye-BW. Eye weights were variable. Female eyes in 1993 were heavier than male eyes in specimens heavier than 150 g, whereas female eyes of 1994 specimens were heavier in specimens weighing less than 900 g (Table 2).

Age and growth—Attempts at aging vertebra proved hopeless. Instead Fitz (1956) and Fitz and Daiber's (1963) DW age designations were used to designate fish with DW's up to 210 mm as age 1 fish, 280 mm age 2, 340 mm age 3, 400 mm age 4, 420 mm age 5, and 460 mm age 6 (Table 4). Analyses of North Carolina specimens caught in 1993 consisted of four males and seven females age 1, one male, four females age 2, two males,

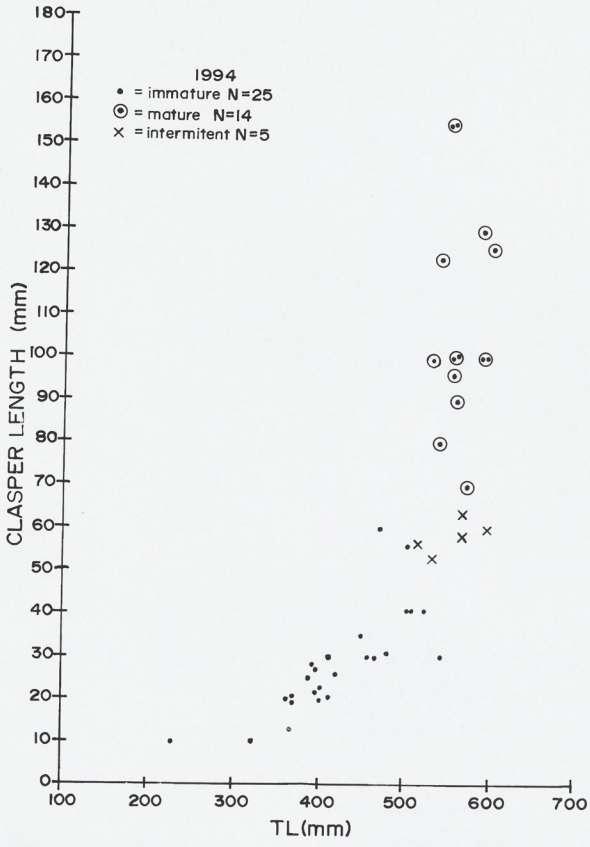

FIG. 3. Clasper length-total length relationships for clearnose skates captured in 1994.

TABLE 3. Male and female body-organ weight relationships for six body organs, as percent mean and ranges noted in specimens caught in 1994.

	Male		Female	
Body organ	$\bar{x}$	% Range	$\bar{x}$	% Range
Heart	0.07	0.01–0.27	0.08	0.03–0.14
Liver	2.78	1.66–4.60	3.19	0.93–5.24
Intestines	1.97	1.31–4.99	2.29	0.73–3.77
Gonad	0.73	0.03–3.42	0.57	0.02–6.17
Kidneys	0.19	0.08–0.75	0.19	0.008–0.34
Spleen	0.16	0.07–0.47	0.19	0.01–0.46
Eyes	0.12	0.05–0.32	0.12	0.03–0.19

TABLE 4. Number of males (M) and females (F) captured in 1993 and 1994. Disk width (DW) age designations follow Fitz and Daiber, 1963. (See text for explanation of ages.)

	Number					Fitz and Daiber (1963)
	1993		1994			
DW (mm)	M	F	M	F	Age	DW mean age (mm)
160			1			
180	1					
200						
220	1	2	4	2		
240	2	3	5	6		
260		2	6	9	1	
280	1	4	3	3	2	265
300		2	1	1		294
320		1	2	3		
340	2		8	8	3	359
360	1	1	9	3		
380	1	1	3	5		
400			2	3	4	401
420				1	5	439
440						
460				1	6	477
Total	9	16	44	45		

three females age 3, two males, two females age 4 while for 1994, 16 males and 17 females were age 1, three males and three females age 2, 11 males and 12 females age 3, 14 males and 11 females age 4, one female age 5, and one female age 6 (Table 4). No regression compared immature vs. mature specimens, by year, as none were mature in 1993 vs. two in 1994. Small sample size in 1993 (9M,16F) prevented comparison to clearnose skates caught (44M,45F) in 1994 (Table 4).

Food—Nine food items were noted only in the 1994 specimens. Recognizable food was found in the stomach, it appeared as chyme in the intestines. Blackcheek tonguefish, *Symphurus plagiusa,* were the most frequently eaten food, occurring in six males (403–590 mm TL) and 10 females (594–639 mm TL). Lengths of the tonguefish ranged 60–120 mm TL in males and 100–150 mm TL in females. Two male and two female clearnose skate stomachs contained two each, striped anchovies, *Anchoa hepsetus* (M, 28–80 mm SL, F, 80–100 mm SL). One 100 mm SL croaker, *Micropogonias undulatus,* was found in a 470 mm TL male and fish remains occurred in two female clearnose skates, 366 and 613 mm TL respectively. One spot, *Leiotomus xanthurus* (less than 150 mm SL), was found in each of two female clearnose skates 549 and 556 mm SL, respectively. One mantid shrimp, *Squilla empusa,* was found in a 540 mm SL male and one white shrimp, *Penaeus azetecus,* was eaten by a 540 mm SL male. A brief squid,

Loliguncula brevis, was eaten by a 445 mm SL clearnose skate. Crab remains were found in one male and two females 296–591 mm SL.

DISCUSSION—Bigelow and Schroeder (1953) suggested, based on lengths and disk sizes, that two subspecies might frequent Western Atlantic waters. Specimens of the subspecies north of Cape Hatteras, North Carolina would be larger while those south of the cape smaller. ANOVA analyses between sexes and years of DL, tail, and DW measurement differences indicated no significant differences. Thus, one population of skates comprised the 1993 and 1994 North Carolina samples. Morphologically North Carolina specimens were similar to Bigelow and Schroeder's (1953) subspecies south of Cape Hatteras, *R. eglanteria eglanteria* rather than the northern *R. eglanteria americanus.* Bigelow and Schroeder specimens DL's ranged 51.3–53.7, $\bar{x}$ 52.5, and DW's 65.7–66.8, $\bar{x}$ 66.25. Fitz (1956) likewise noted body length as percent of TL as 43.9 in males and 46.7 in females, DL's 46.0 in males, 46.6 in females, DW's were 58.1 in males and females, tail percentage was 55.8 in males and 53.6 in females. North Carolina specimens, in 1993, as percent of TL were, 58.2 in males, 53.1 in females, DW 64.0 in males and 65.2 in females, tail 48.0 in males and 45.1 in females.

Sizes—TL's and DW's of captured clearnose skates from North Carolina fell well within size limits noted by others: 130 mm TL (84 mm DW) for newborn (Bigelow and Schroeder, 1953; Fitz, 1956; Luer and Gilbert, 1985) and 949 mm TL for Atlantic Ocean (Schaefer, 1967) and 910 mm TL for Gulf of Mexico specimens (Hoese and Moore, 1977). Maximum DW's were reported as 480 mm by Daiber (1960) for Delaware Bay clearnose skates. DW's reported by Schwartz (1961) for clearnose skates from Chincoteague and Sinepuxent Bays, Maryland should have been 100–136 mm, not 1000–1300 mm. Maximum weights of North Carolina specimens were much less (1547 g male, 2070 g female), than noted (3473 g) by Bigelow and Schroeder (1953) for Block Island, Massachusetts specimens.

Environmental factors—Study specimens of clearnose skates were captured, in 1993 and 1994, in depths of 20 M, depths similar to those of 14 m noted by Price (1957) for the lower Chesapeake Bay, or western Atlantic continental shelf by Wilk and Silverman (1976). McEachran and Musick (1975) reported the maximum recorded depths for the species as 111 m south of Cape Hatteras.

Absences of clearnose skates in 1993 and 1994 June to October samples were attributed to water temperatures higher than those usually frequented by clearnose skates. Schwartz and co-workers (1981) reported clearnose skates frequenting the Cape Fear River, North Carolina, waters of 12–31°C, lowest salinity waters were at 12 ppt at Snow's Cut. Bigelow and Schroeder (1953) found clearnose skates in waters of 12–17°C off Cape Lookout, North Carolina. Breder (1924) captured specimens off Sandy Hook, New York, in

14°C water while Price (1967) noted specimens in Chesapeake Bay were caught in cool waters of 13 or 14°C. McEachran and Musick (1975) noted clearnose skates from Chesapeake Bay in waters 5–20°C, most abundantly in 9–20°C waters, while observations north of Cape Hatteras found skates in waters of 9–27°C. Hildebrand and Schroeder's (1928) Chesapeake Bay observations were of captures in 21°C waters. Fitz and Daiber (1963) recorded clearnose skates in 14°C (range 8–24°C) water temperatures for Delaware Bay. Off Sandy Hook, New York, clearnose skates occurred in waters colder than 14°C. Newsome and Long (1939) noted clearnose skates in waters of 27°C at the entrance of Chesapeake Bay.

Clearnose skates were captured off North Carolina in waters of 32–34 ppt salinity even though Bigelow and Schroeder (1953), Schwartz (1981, 1995 in press) and Schwartz and co-workers (1981), reported captures in salinities as low as 27 ppt. Fitz (1956) noted occurrences in 22–27 ppt salinities in Delaware Bay. Luer and Gilbert (1985) have maintained young and old clearnose skates in 30–35 ppt salinities.

Surface areas—Limited information exists on body surface areas as few have examined body surface area relationships in fishes. Grey (1953) devised a method to calculate surface areas of fishes. Musick and co-workers (1990) described an X factor and compared surface areas of several species of sharks. Schwartz and co-workers (1993) compared surface areas of the pelagic and benthic sharks, Atlantic sharpnose sharks, *Rhizoprionodon terraenovae* and smooth dogfish (*Mustelus canis*), as well as described an X factor to fit both species. Schwartz and co-workers (1993) disproved the universality of the x factor of 0.71, suggested by Musick and co-workers (1990), and suggested each species possesses its own X factor. X factors of clearnose skates from North Carolina were larger for both sexes than were those noted for sharks. The larger X factor found for clearnose skates not only reaffirms the idea that each species may possess its own range of X factors as well as suggests clearnose skates are much more active swimmers than currently believed. Even though the preponderance of tonguefish and other benthic and near benthic species comprised the foods eaten, greater skate surface areas apparently help them move about quickly in order to capture the varied foods eaten.

Body organ-weight relationships—Few body organ-weight relationships exist, other than for the oyster toadfish *Opsanus tau* (Robinson et al. 1960) and sharks (Schwartz, 1978; Winner and Schwartz, 1989, 1991). Examination of the study specimens revealed direct linearity, with little variation, in all of the relationships examined.

Food—Tonguefish dominated the stomachs that contained foods. Other foods were similar to the 29 noted in clearnose skates from Delaware Bay (Fitz and Daiber, 1963) and Chesapeake Bay (Hildebrand and Schroeder,

1928) or various *Raja* spp. from elsewhere (Soarces et al. 1992). Kimmel (1973) found mollusks, shrimp, and crabs as dominant foods of 19–44 mm (TL?) skates from Magothy Bay, Virginia. *Neomysis* and *Crangon* were not prevalent as they were in Delaware clearnose skates in North Carolina specimen stomachs.

Even though difficulties persisted when attempting to age clearnose skates, new aspects have been determined for the often ignored yet common clearnose skate. Statistically the sizes and surface area differences noted between specimens captured in 1993 and 1994 established that clearnose skates from North Carolina were members of one population and, as Luer and Gilbert (1985) pointed out, clearly a potentially useful research species.

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A SECOND RECORD OF A UROGENITAL SINUS UROLITH IN THE SAND TIGER SHARK (*Odontaspis taurus*)

The renal physiology of sharks is poorly known (Shuttleworth 1988). Uroliths are known from a variety of vertebrates (Walsh and Murru 1987). Only one incidence, a 9 g urolith, has been recorded in sharks, that being in a sand tiger held captive at Sea World, Florida for 3.5 years (Walsh and Murru 1987). I now report a second occurrence of a urolith from a healthy 2.3 m, 114.75 kg male sand tiger caught 16 December 1989 due east of Cape Lookout, North Carolina at Lat. 34°43′N, Long. 75°46′W, water depth 65.7 m. No food was in the stomach. Tissues surrounding the urolith were not abraded. Nothing can be said regarding whether the shark experienced any impaired renal function.

A large urolith of 44.4 g was discovered while cleaning the urogenital sinus of the sand tiger (Fig. 1). Dimensions of the concretion were: longest length 61.5 mm, next longest length 60.2 mm, maximum width 32.9 mm, and depth 29.0 mm. The whitish distal outer knobs measured 12.1 mm (left) and 10.8 mm (right) respectively. The white dorsal apron measured 21.0×17.1 mm. The groove separating the two whitish knobs was 26.0 mm long. The urolith was positioned horizontally in the urogenital sinus with the small end facing forward.

Dawson (1964, 1966, 1971) and Dawson and Heal (1971) as well as the worldwide literature have not reported large uroliths in any wild shark. Walsh and Murru (1987) found their captive sand tiger urolith was composed of 80% cryptocrystalline to fine orthorhombic crystals of magnesium ammonium phosphate hexahydrite (Struvite) and 15% was a random mixing of micro-crystalline calcium phosphate. No attempt was made to section or alter the cream colored urolith as the fisherman who discovered it desired its return. It is assumed its composition was similar to that noted by Walsh and Murru (1987). Occurrence of the urolith documents that sharks, although known for their resistance to disease and bodily dysfunction, can occasionally fall victim to ailments that could affect their well-being.

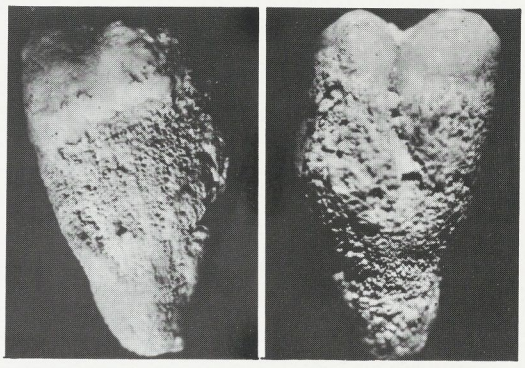

Figure 1. Urolith from urogenital sinus of sand tiger shark.

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Anatomy, Histology, and Development of the Cardiac Valvular System in Elasmobranchs

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ABSTRACT We report here on the anatomy, histology, and development of the three sets of cardiac valves in embryonic and adult elasmobranch fishes. The sinus venosus is the first segment of the heart to receive blood, and a pair of sinoatrial (SA) valves prevent backward flow of blood into the sinus venosus. The SA valves derive from two dorsolateral infoldings of the cardiac wall and consist of a simple endocardium covering transverse sheets rich in collagen. The SA valves are simple flaps of tissue without papillary muscles or chordae tendineae. Blood from the atrium passes the atrioventricular (AV; semilunar) valves, which are attached to papillary muscles in the ventricle by way of the chordae tendineae. A series of rows of conal or pocket valves (CV) in the conus arteriosus, equipped with chordae tendineae but no papillary muscles, prevent blood from reentering the ventricle. Chordae tendineae form in a similar fashion in both chambers. Elevations from the chamber wall emerge as a sheet covered on both surfaces with endocardium and separated by a core of connective tissue. Endocardial cells extend basal projections toward the opposing epithelium through their basal laminae. Basal cell projections make contact to create perforations that enlarge to produce spaces between the nascent chordae. Fibroblasts in the core of the chordae enlarge and strengthen the chordae by producing linear arrays of collagen fibers.

Partitioning the embryonic vertebrate heart into arterial and venous sides causes considerable internal remodeling, especially in the genesis of the valvular complexes that regulate the unidirectional flow through the heart. Early cardiac morphogenesis depends upon regulated interaction between cells and their environment. The immediate environment is an abundant extracellular matrix (ECM). The embryonic heart is composed of a wide variety of glycosaminoglycans, glycoproteins, collagens, and proteoglycans. ECM molecules are believed to play multiple roles in cardiac morphogenesis, including mediating cell shape changes, cell migration, proliferation, and differentiation (Little and Rongish, '95). It is likely that the ECM plays important roles in all embryonic morphogenetic processes.

The elasmobranch heart is typical of fishes in general. The chief collecting chamber, the sinus venosus, is thin-walled with considerable amounts of fibrous tissue and little muscle. It receives systemic blood and is filled by suction when the ventricle contracts. Blood gushes through the sinoatrial (SA) aperture into the atrium as soon as the latter begins to relax after emptying. The atrium is relatively large, thin-walled, and muscular. Blood from the atrium enters the ventricle through the atrioventricular (AV) aperture, which is guarded by valves. The ventricle has thick, muscular walls. The anterior end is prolonged as a muscular conus arteriosus, which passes to the cephalic end of the pericardial cavity, where it is continuous with the ventral aorta. A series of pocket valves in the conus prevent backflow of blood. Due to its contractility, the conus maintains a steady arterial pressure into and through the gills.

Aside from studies of chick and rat embryos, little attention has been paid to the structure and development of the valvular apparatus in lower vertebrates. We report here on the anatomy, his-

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tology, and development of the cardiac valvular apparatus in two elasmobranchs, the Atlantic sharpnose shark, *Rhizoprionodon terraenovae,* and the yellow spotted ray, *Urolophus jamaicensis,* and compare our results with data from other embryonic vertebrate systems.

MATERIALS AND METHODS

Female Atlantic sharpnose sharks, *R. terraenovae,* were obtained via long line from ocean waters near Morehead City, NC. Female yellow spotted rays, *U. jamaicensis,* were obtained via dip nets from ocean waters near Long Key, FL. Some newborn animals of both species were also obtained and used in this study. Gravid females containing embryos and fetuses were anesthetized with MS-222 and opened by a longitudinal ventral incision and the uteri isolated. The uteri were tied off anterior to the oviducal gland and near the entrance to the cloaca before being transected and removed. The uteri were opened with surgical scissors and the embryos and fetuses isolated by blunt dissection. Embryos and fetuses were likewise anesthetized and the hearts dissected out and placed directly in the primary fixative, which was 3% glutaraldehyde in 0.1 M phosphate buffer with 0.4 M sucrose.

For light microscopy (LM), tissue samples were fixed in the same fixative as above. Samples were dehydrated through a graded series of alcohols and embedded in JB-4 glycol methacrylate (Polysciences, Warrington, PA). Sections, 2μ thick, were made with glass knives and affixed to glass slides. Sections were stained with either toluidine blue or methylene blue-basic fuchsin.

For LM histochemistry, samples were fixed in Gendre fluid fixative, which preserves tissue mucopolysaccharides (Sheehan and Hrapchak, '80). Specimens were washed in two 5-min changes of 80% ethanol and routinely prepared for paraffin sectioning.

Two differential stains were used for histochemical evaluation of the ECM. These stains were (1) periodic acid-Schiff (PAS) and (2) Alcian blue (AB) followed by PAS. PAS stains molecules containing vincinal hydroxyl groups or a hydroxyl and adjacent carbonyl group combination (Humason, '72). The combined AB/PAS is of value in differentiating between neutral and acidic mucopolysaccharides in the same tissue sections (Humason, '72). Elastin was stained by Verhoeff's stain (Humason, '72).

Photomicrography

Photomicrographs were taken on a Nikon Optiphot-2 bright field microscope equipped with a green filter to increase contrast. The film used was Kodak 2415 technical film, and micrographs were printed on Kodak Polycontrast paper (Eastman-Kodak, Rochester, NY).

Electron microscopy

For scanning electron microscopy (SEM), tissues were immersed in a primary fixative consisting of 3% glutaraldehyde in 0.1 M phosphate buffer with 0.4 M sucrose. Fixation was carried out at room temperature for 6–8 hr. Tissues were then washed several times in fresh buffer, transferred to a secondary fixative (1.0% osmium tetroxide in 0.1 M phosphate buffer) and postfixed for 1.5 hr at room temperature. Specimens were washed with distilled water and dehydrated through a graded series of ethanols from 30% to 100%. Specimens were dried by the critical-point method with liquid carbon dioxide as the translational medium and mounted on double-sided plastic tape to which silver conductive paint had been added, coated with a thin layer of gold, and viewed on a JEOL JSM-T300 SEM at 10–25 kV.

RESULTS

The heart of the Atlantic sharpnose shark, *R. terraenovae,* consists of four chambers, the sinus venosus, atrium, ventricle, and conus arteriosus, each endowed with a valvular apparatus (Fig. 1).

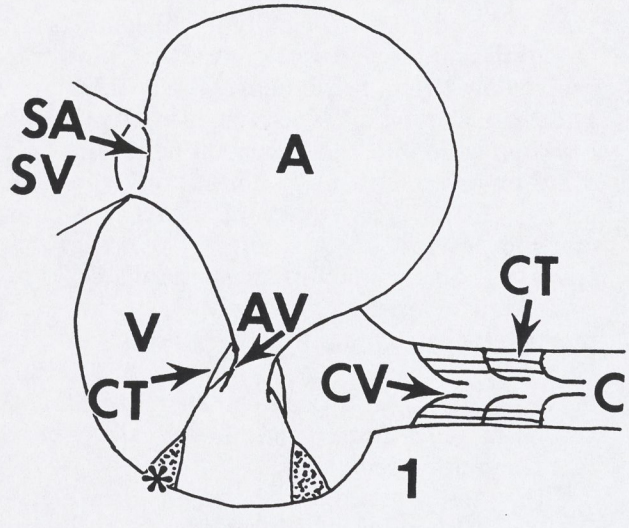

Fig. 1. Diagram of adult elasmobranch heart. A = atrium, AV = atrioventricular valve, C = conus arteriosus, CT = chordae tendineae, CV = conal valve, SA = sinoatrial valve, SV = sinus venosus, V = ventricle, asterisk = papillary muscle.

Massive migratory congregations of the cownose ray, Rhinoptera bonasus off North Carolina and of rhinopterids worldwide

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Five species of cownose rays, genus Rhinoptera, frequent temperate and tropical waters of the world. Massive schools or congregations have been sporadically noted for R. bonasus, R. javanica, and R. steindachneri. Dense R. bonasus schools were observed moving along the Sarasota, Florida, Gulf of Mexico coast toward Yucatan, Mexico in 1963 and in Chesapeake Bay or southward along the Delaware-Maryland-Virginia coasts in 1962-1964. Since then little has been recorded regarding large migratory aggregations of R. bonasus anywhere. Massive schools of R. bonasus, 6-7 each year, were sighted off Core and Shackleford Banks, NC during their fall, southerly migration in September 1985 and 1986 respectively. Each school, occupying 2.4-4.0 hectares, consisted of hundreds of thousands of rays often layered 6-10 rays deep. Schools usually frequented coastal waters 0.25-10.5 m deep. Layering extended from the ocean surface to the substrate, as evidenced by a trail of disturbed substrate. To date large-scale schooling is known only for R. steindachneri from the Pacific Galapagos Islands (in 1978) and R. javanica, on five occasions (1899-1973), between Sri Lanka (Gulf of Mannar) and Madras (Bay of Bengal) off eastern India. Whether R. marginata of the Mediterranean and West African coasts, R. neglecta off eastern Australia or R. javanica, in other parts of its Indopacific range, school is unknown.

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Cell and Tissue Research

Subcellular organization of the yolk syncytial-endoderm complex in the preimplantation yolk sac of the shark, *Rhizoprionodon terraenovae*

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Summary. The structure of the yolk syncytial-endoderm complex of the preimplantation yolk sac of the shark is examined by light- and transmission electron microscopy. The yolk syncytium is bounded by a membrane that is anchored to the plasmalemma of adjacent endoderm cells by desmosomes. Enlarged nuclei, rough endoplasmic reticulum, Golgi complexes, mitochondria, and other cellular organelles populate the syncytium. Microtubules and filamentous elements are also observed free in the syncytium. Yolk is present as pleomorphic droplets, the profiles of which are generally spherical but may be vesicular, especially at the periphery of large yolk droplets. Occasionally, large yolk droplets have a paracrystalline configuration. Small yolk droplets are modulated through the Golgi complex of the yolk syncytium, and it is suggested that acid hydrolases are added there. Small yolk droplets released from the maturing face of the Golgi complex are sequestered in membrane-limited packets. The membrane of the packets fuses with the membrane enveloping the yolk syncytium and the yolk droplets are released into the yolk syncytial-endoderm interspace. Subsequently, the yolk droplets are endocytosed by the endoderm. Yolk droplets disperse and fuse to form the large irregular yolk inclusions of the endoderm. Yolk metabolites are transported out of the endoderm through the yolk sac endothelium. The yolk sac endoderm thus mediates the transfer of metabolites from the yolk mass to the extraembryonic circulation.

Key words: Yolk sac – Endoderm – Fetal membranes – Endocytosis – Shark, *Rhizoprionodon terraenovae*

Embryogenesis in lower vertebrates requires raw materials and free energy, most of which is provided by yolk platelets sequestered in the yolk sac. These yolk platelets are synthesized during oogenesis to serve as the prime nutrient source (Williams 1967). However, in most mammals and some placental elasmobranchs, metabolites are delivered continuously from the mother to augment the yolk supply (Hamlett et al. 1985a–c), especially in the latter phases of gestation after the yolk reserves have been depleted. Yolk proteins of many nonmammalian vertebrates are generally similar in composition (Fuji 1960; Wallace 1963a, b; Wallace and Selman 1978, 1985) but there is considerable morphological diversity in the yolk platelets. Moreover, there may be different types of yolk in a given egg, as has been shown chemically by Panijel (1950) in amphibian eggs. Several works relating oocyte maturation and protein changes during vitellogenesis in *Fundulus heteroclitus* have appeared in the literature (Wallace and Selman 1978, 1981, 1985). Morphological studies of yolk resorption and utilization in lower vertebrates is rare because of the difficulty in preparing this material for histological or ultrastructural analysis (Karasaki 1963; Jurand and Selman 1964; Jollie and Jollie 1967; Walzer and Schonenberger 1979a, b). Numerous investigators (Van der Ghinst 1935; Yamagami 1960a, b; Yamamoto 1967; Vernier and Sire 1977; Walzer and Schonenberger 1979a, b) in studying fish yolk have shown that hydrolytic enzymes are present in the yolk syncytium and participate in yolk digestion. Fish eggs differ from avian eggs in the greater proportion of energy supplied by protein, this being associated with the ease of disposing of nitrogenous wastes in an aqueous environment (Needham 1942). Selachian eggs are heavily yolked and the yolk is digested both extracellularly in the yolk syncytium of the yolk sac and in the fetal gut (Williams 1967; Hamlett and Wourms 1984; Hamlett et al. 1985a–c).

In sharks that develop placentae, the embryos are maintained within the uterus until parturition (Hamlett et al. 1985a). The preimplantation yolk sac of placental viviparous sharks is composed of several distinct histological layers, viz.: (1) ectoderm; (2) somatic mesoderm; (3) a reduced extraembryonic coelom; (4) splanchnic mesoderm; (5) endoderm; and (6) yolk syncytium (Hamlett and Wourms 1983, 1984). The yolk sac encloses a large yolk mass. Yolk platelets are synthesized during oogenesis to serve as the nutrient source for the embryo prior to the differentiation and functional establishment of the yolk sac placenta (Hamlett 1986).

As development proceeds, yolk is utilized by the richly vascular yolk sac. It is also transmitted up the patent ciliated ductus vitellointestinalis, within the yolk stalk, directly to the gut (Schlernitzauer and Gilbert 1966; Baranes and Wendling 1981; Hamlett and Wourms 1984). As yolk is depleted, the yolk sac expands and increases in surface area (Te Winkel 1963). During the early stages of development, the external gill filaments may also play a role in nutrition (Hamlett et al. 1985) by absorbing material se-

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creted by the maternal uterus. The yolk sac then undergoes an ontogenetic transition and differentiates into a functional placenta (Hamlett et al. 1985a–c).

Mobbs and McMillan (1979, 1981) have demonstrated that yolk is endocytosed by endodermal cells of the chick yolk sac. Endodermal cells of the mammalian yolk sac incorporate exogenous tracers by a system of coated vesicles and canaliculi that subsequently bind to large membrane-limited vacuoles (Jollie and Seibel 1970; King and Enders 1970; Slade 1970; Wild 1970; Haar and Ackerman 1971; Wild et al. 1972; Moxon et al. 1976). No studies to ascertain the role of the endoderm in the nutrition of the shark embryo have been previously undertaken. This paper considers the subcellular organization and function of the yolk syncytial-endoderm complex in the preimplantation yolk sac of the shark prior to establishment of the placental connection.

Materials and methods

Female Atlantic sharpnose sharks, *Rhizoprionodon terraenovae*, were obtained via longline from ocean waters near Morehead City, North Carolina, USA. Gravid females containing embryos (4.5 cm total length) were opened by a longitudinal ventral incision and the uteri isolated. The uteri were tied off anterior to the nidamental gland and also near the entrance to the cloaca before being transected and removed. The uteri were opened with surgical scissors and the embryos isolated by blunt dissection. Pieces of yolk sac were removed and placed directly into primary fixative. While immersed in fixative, yolk sac tissue was cut into 2 mm square pieces.

For transmission electron microscopy, the tissues were immersed in a primary fixative consisting of 3% glutaraldehyde in 0.1 M phosphate buffer with 0.4 M sucrose and a trace of $CaCl_2$. Fixation was performed at room temperature for 2–6 h. Tissues were washed several times in fresh buffer and transferred to the secondary fixative which was 2.0% osmium tetroxide in 0.1 M phosphate buffer for 2–6 h. Tissues were then washed several times with distilled water and dehydrated by transfer through a graded series of ethanols to 100%. Following dehydration, the tissue went through three changes of propylene oxide of 5 min each at room temperature. Tissues were infiltrated in a 1:1 volumetric ratio of propylene oxide to catalyzed Poly/Bed 812-Araldite (Polysciences, Inc Warrington, Pa.) overnight (Mollenhauer 1964). All samples were then transferred to pure catalyzed Poly/Bed 812-Araldite and embedded. Samples were cured at 30° C for 12 h, 45° C for 12 h, and 60° C for 12 h under vacuum. Blocks of tissue were sectioned with a diamond knife on a Porter-Blum MT-2 ultramicrotome. One-or two-μm thick sections were cut for light microscopy and stained with toluidine blue. Silver or gray sections were picked up on acid-cleaned uncoated 200 mesh copper grids. Sections on grids were stained with uranyl acetate and lead citrate (Venable and Coggeshall 1965). Stained grids were examined in an Hitachi 11-E transmission electron microscope at 80 kV.

Results

General observations

The preimplantation yolk sac of the viviparous placental shark, *R. terraenovae*, is comprised of six layers: (1) ectoderm; (2) somatic mesoderm; (3) a reduced extraembryonic coelom; (4) splanchnic mesoderm; (5) endoderm; and (6) yolk syncytium (Hamlett and Wourms 1983, 1984). As the yolk sac develops, the mesodermal elements differentiate into blood vessels, blood cells, and mesenchymal cells. The greatly reduced extraembryonic coelom separates the splanchnic mesoderm from the somatic mesoderm. Early in development, prior to the establishment of the functional yolk sac placenta, the nutrient and respiratory requirements of the embryo are partially met by the yolk syncytial-endoderm complex (Hamlett et al. 1985a, Hamlett 1986). Yolk is also transported up the ductus vitellointestinalis for digestion in the fetal gut. Therefore, the first membranes active in nutrient transfer are the yolk sac endoderm and the gut epithelium (Hamlett 1986). Transient external gill filaments are capable of uptake of tracer molecules the size of protein and, consequently, may absorb nutrient uterine secretions during the early stages of development (Hamlett et al. 1985). The yolk syncytial-endoderm complex is composed of the central yolk syncytium, the endoderm, connective tissue and mesenchymal cells, and the endothelium of the vitelline vessels (Fig. 1).

The yolk syncytium

Like avian eggs, the large yolky eggs of elasmobranchs are strongly telolecithal. Meroblastic cleavage is restricted to a small disc at one pole of the egg. Cleavage produces two populations of cells, namely (1) blastoderm that will form the embryo and (2) periblast tissue or trophoblast, which borders the yolk peripherally and centrally (Nelsen 1953). Later in development, the periblast tissue is referred to as the yolk syncytium.

The yolk syncytial layer contains many morphologically diverse yolk platelets (Figs. 2–8) as well as cellular organelles. The largest of the yolk platelets are round and present a homogeneous appearance ranging from darkly osmiophilic (Fig. 2) to gray (Figs. 2, 3). The platelets do not appear to be delimited by a membrane (Fig. 3). Indentations occur at the periphery of these large platelets that may represent focal sites of yolk solubilization (Fig. 3). Small yolk droplets presumably derived from the large platelets are visible at the platelet periphery. These droplets become enclosed by membranes that range from single to lamellar (Fig. 3). These membrane-limited packets are then transported and modulated through the Golgi complex of the yolk syncytium (Figs. 7–9). Other profiles representing yolk solubilization are observed in addition to vesiculations at the periphery of the yolk platelet. Some yolk platelets are cleaved into smaller yolk droplets throughout the platelet (Figs. 4–6). Membrane tubules and vesicles occur free in the yolk syncytium (Figs. 2, 7, 8) and within the cleaving platelet. It is postulated that these sequester yolk droplets for transport to the Golgi complex.

The membrane vesicles containing small individual yolk droplets fuse with the cis-face of the Golgi complex (Fig. 9). It is suggested that acid hydrolases are added by the GERL (Golgi-associated endoplasmic reticulum from which lysosomes form). Yolk droplets are budded off the ends of the dilated Golgi cisternae (Figs. 7, 9) as membrane-bounded packets. Packets containing many small yolk droplets fuse with the membrane delimiting the yolk syncytium (Figs. 10–12). Yolk droplets are consequently freed in the yolk syncytial-endoderm interspace (Figs. 10, 11). Occasionally, some platelets are seen to contain an osmiophilic paracrystalline configuration in close association with

Analyses of Hematocrits of Sharks Captured Off North Carolina and the Atlantic Ocean Continental Shelf in Relation to Sex, Size, and Season

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Abstract

Hematocrits (HcT) were compared worldwide for 27 species of sharks, 19 of which were captured during longline fishing off North Carolina and along the western North Atlantic shelf from Cape Cod to Miami. HcT's of four species of sharks, dusky (Carcharhinus obscurus), blacknose (C. acronotus), Atlantic (Rhizoprionodon terraenovae), and smooth dogfish (Mustelus canis), captured off North Carolina were determined in relation to sex, age, and season. HcT's were slightly different only in female blacknose sharks in relation to fork length, male Atlantic sharpnose sharks by fork length and month, male smooth dogfish by fork length and month, and smooth dogfish only by month. A slight significance, by sex, was noted for mature smooth dogfish. Mean HcT's (20%) for North Carolina and shelf caught species were similar to levels reported in the literature. A variety of factors cause or influence the HcT's observed.

Key words: Hematocrits, North Carolina, Continental Shelf, sharks.

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Introduction

The composition of blood reflects the physiological state of an organism, and many techniques have been employed to determine fish blood parameters (Kisch, 1951; Hessler, 1960; Blaxhall and Daisley, 1973, Wedemeyer and Yamatabe, 1977; Zapata and Carrato, 1981). Blood parameters are known to exhibit seasonal variations and are affected by a host of internal and external influences (Martini, 1978; Hardig and Hoglund, 1983; Murru, 1984). Hematological observations, such as hematocrit (HcT), are among the most valued and accurate of all laboratory diagnostic aids (Snieszko et al., 1960; Wells, 1986) used in determining the status and erythrocyte content of fish blood (Snieszko et al., 1960; Strumia and Sample, 1954).

Most of the limited data on elasmobranch blood pertains to smaller, less active species, such as dogfishes, skates, and rays, because large pelagic species are difficult to capture and maintain in captivity (Murru, 1984; Emery 1986). No study has compared HcT values of wild caught sharks to determine variation by sex, size, and season. This report compares HcT Values of four species of sharks captured in 1989 and 1990 in the western Atlantic Ocean off Shackleford Banks, Carteret County, North Carolina, in relation to sex, size, and season. HcT data from 134 sharks, within 16 species, captured during a National Marine Fisheries Service Atlantic Coast Continental Shelf cruise in May 1991 are also reported and compared to HcT's noted in the literature. This study serves as baseline data for further shark physiological studies.

Methods

Four of 13 species of sharks captured off North Carolina, blacknose shark (Carcharhinus acronotus, 36 captured (c), 35 studied (s), dusky shark (C. obscurus, 35 c, 34 s) Atlantic sharpnose shark, (126 c, 102 s), and smooth dogfish (Mustelis canis, 106 c, 63 s) were captured in sufficient numbers to permit HcT determinations by sex, size, and season. Sharks were captured by a 4.8 km longline set 5-12 km south of Shackleford Banks, Onslow Bay, Carteret County, North Carolina, in waters 10-25 m deep. Sampling took place during 15 biweekly periods (April-November) in 1989 and 1990. Longlines were of 7.6 mm braided nylon mainlines and fished with 200, 1.8 m long 2/0 chain gangions fitted with #9 mustad hooks spaced 4.6 m apart. Longlines, during the shelf cruise, were 7.9 mm nylon mainlines fishing 100 #40 Japanese tuna hooks spaced 50 m apart. Occasionally gangions of 157.5 kg test monofilament, fitted with 9/0 mustad hooks, were fished 20-70 m deep. Soak intervals, for each type of gear were one hour per set site. A few additional small sharks were captured using a 12.2 m wide balloon otter trawl towed by the 15.5 m UNC R/V Capricorn. Water temperatures were determined to nearest 0.1^{o}C by either a Taylor pocket thermometer or an electronic Duroc thermometer, the latter mounted on the ship's hull one meter below the water surface. Salinities were determined using an A/O refractometer.

Sharks were kept overboard until removed for identification, sexing, measurement to the nearest millimeter fork length (FL), and blood sample withdrawal. All procedures were accomplished

within several minutes prior to the shark being returned to the sea. Blood samples of all North Carolina samples were taken by direct cardiac puncture, following the methods of Cliff and Thurman (1984) and Schwartz and Maddock (1986); blood of shelf specimens was collected either by cardiac (C) or caudal vein (D) extraction. All blood samples were collected in 3 cc heparinized syringes fitted with 3.8 cm, #23 gauge needles. Occasionally larger diameter or longer, 20 gauge, needles of 5.1-18.2 cm were used to reach hearts of very large sharks. Blood sample volumes ranged 0.5-3.0 ml, depending on shark size. Syringes containing blood were wrapped in aluminum foil and kept on ice until centrifuged. A minimum of two HcT samples/syringe/shark were centrifuged. HcT's were determined on shipboard or in the laboratory by injecting a blood sample into 75 mm long non-heparinized microhematocrit tubes and then spun at 4500 RPM for four minutes in a Clay Adams microhematocrit centrifuge. Blood samples appearing diluted with pericardial fluid or exhibiting hemolysis were discarded. A millimeter ruler was used to measure the erythrocyte layer, buffy layer, and the total blood column height. Each reading was converted to percent volume HcT. The amount of time between drawing blood and HcT determination ranged from several minutes to seven hours (20% of the 1989 North Carolina sampled blood took longer to process because rough sea conditions prevented immediate microhematocrit tube preparation and centrifugation).

Statistical analyses were based on mean sample HcT values and analyzed by a SAS analysis procedure (SAS 1985). An Fmax test analyzed the data for heterogeneity of variance. When

heterogeneity occurred, raw HcT values were transposed using arcsine transformation of analysis of variance procedures (Sokal and Rokolf 1981). A 3-way analysis of variance tested the North Carolina relationships of FL, water temperature, and month of capture to HcT using combined size groups of each species. Smooth dogfish data was also analyzed by sex in relation to mature and immature size groups (Compagno 1984). Dusky, Atlantic sharpnose, and blacknose sharks were not analyzed by age because of an inadequate spread of mature and immature size ranges. One-way analysis of variance was used to test differences between sex by species. Analysis of variance tested HcT differences between males and females of each species, and compared sexually mature and immature smooth dogfish by sex. A linear regression was used to calculate the conversion formula FL = 3.265 + 0.90 TL, where TL = total length when converting TL to FL when distinguishing between mature and immature smooth dogfish (Branstetter and Casey, pers. comm).

Results

HcT means for each of the four North Carolina shark species studied in detail were near 20 while ranges varied from 6.2 in Atlantic sharpnose sharks to 33.4 in smooth dogfish (Table 1). The highest (36.8) and lowest (8.3) HcT's for shelf specimens occurred in male smooth hammerhead sharks. These ranges were similar to those reported in the literature for other sharks (Table 2). A three-way analysis of variance compared HcT's for combined sexes, males, and females, in relation to FL, water temperature, and season (month); no significance was found for most relationships (Table 4). Only a slight significance was

found for blacknose shark female/FL relationships (Table 4). Male Atlantic sharpnose shark HcT's were slightly significant by month but not by FL or water temperature (Table 4). Male smooth dogfish (combined immature and mature specimens) HcT's were slightly significant in relation to FL and month (Table 5). The slight significance between female blacknose and FL could be a reflection of whether the females were carrying young, as this species pups in June in North Carolina (Schwartz 1989). HcT differences between sexes were only noted for combined mature/immature male smooth dogfish (Table 5). None of the shelf caught shark HCT's were tested statistically for effects of sex, size, or season because of inadequate sample sizes per species or between sexes.

Discussion

Tetons and Wells (1984) noted no significant differences in HcT's for carpet sharks, Cephaloscyllium isabella acclimated in warm (15°C) or cold (5°C) waters. Since the Atlantic sharpnose and smooth dogfish HcT's didn't increase with increasing water temperatures, monthly HcT fluctuations may be related to reproductive activity (Siddigui and Naseem 1979) as the Atlantic sharpnose, blacknose, and smooth dogfish sharks pup their young in North Carolina and adjacent waters during the spring and summer (Schwartz 1989). Yamashita (1969) noted blood values may be altered by sexual activity and spawning. Parsons (1983) also found an increase in the gonadosomatic index in male Atlantic sharpnose sharks in late spring and summer as they became reproductively active, a condition that could account for the significance between months noted in North Carolina caught males.

One would expect both sexes of the sharks studied to respond similarly unless reproductive activity, feeding or other factors, were more influential than the parameters examined (Bridges et al., 1976; Pastor, 1983). HcT's of captive starved spiny dogfish were dramatically reduced, along with spleen alterations (Martini, 1978). Lower HcT values are found in sedentary benthic fishes while higher values occur in pelagic species, probably a result of physiological responses to habitat and life stage (Larsson et al., 1976).

The wide HcT ranges observed herein may indicate the effects of captive stress and exercise activity influences (Barham and Schwartz, 1992). Exercise, along with its increased metabolic demand, may increase HcT values (Bushnell et al., 1982). Opdyke and Opdyke, (1971) found the spiny dogfish does not have the capacity of releasing erythrocytes from the spleen in response to stimulation by epinephrine or the sympathetic nervous system, although Nilsson et al., (1977) showed that erythrocytes are released by the in vitro perfused spleen of the spiny dogfish.

Emery (1986) compared blood characteristics between endothermic and ectothermic sharks and found higher levels of hemoglobin and HcT occurred in endothermic sharks such as shortfin mako, Isurus oxyrinchus, and perhaps the common thresher, Alopias vulpinus (Table 2).

Genetic variation may affect the blood composition as differences in HcT within species have been observed (Larsson et al., 1976). Therefore the significant relationships observed in HcT's for North Carolina caught sharks may be the result of a

variety of physiological and environmental conditions which may include hormonal processes related to reproductive activity, food availability, individual variation, growth, stress, and water chemistry.

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Table 1. Combined, male, and female hematocrit data (as percent volume and range) for four species of sharks captured off North Carolina 1989 and 1990.

Species	N	Sex	HcT Mean % vol +S.D.	HcT Range % vol.
Blacknose	36	combined	22.5 ± 0.80	9.3 - 28.7
	19	male	23.1 ± 0.90	13.3 - 28.7
	17	female	21.9 ± 1.38	9.3 - 28.3
Dusky	34	combined	21.2 ± 0.71	11.6 - 28.3
	18	male	21.6 ± 1.03	12.3 - 28.3
	16	female	20.7 ± 0.97	11.6 - 27.5
Atlantic sharpnose	102	combined	21.4 ± 0.50	6.2 - 31.4
	37	male	21.9 ± 1.10	6.2 - 31.4
	65	female	21.1 ± 0.46	11.2 - 29.6
Smooth dogfish	63	combined	20.4 ± 0.72	6.9 - 33.4
	33	male	22.0 ± 0.96	12.3 - 33.4
	30	female	18.5 ± 0.98	6.9 - 27.2
Mature	16	male	24.7 ± 6.27	13.2 - 33.4
	12	female	19.3 ± 4.18	11.7 - 24.7
Immature	17	male	19.5 ± 3.17	12.3 - 23.8
	18	female	18.0 ± 6.08	6.9 - 27.2

Table 2. Mean HcT values ± standard deviation and ranges (as percent volume) recorded during this study (North Carolina and Atlantic Shelf) or reported in the literature for nine families and 27 species of sharks. N = number specimens studied. - = no data, LOC = location, NC = North Carolina, ATL = Atlantic Shelf.

Family and species shark	HcT			Reference
	% vol. + S.D.	N/LOC.	Range	
Ginglymostomatidae				
Ginglymostoma cirratum, nurse	19.5	21	16.0-22.9	Murru 1984
" " captive	11.0	7	_	Stoskopf 1993
" " wild	10.3	5	_	Stoskopf 1993
Odontaspididae				
Carcharias taurus, sand tiger	16.5 ± 1.3	2 ATL	15.5-17.4	This study
" " " "	21.9 ± 3.5	3	-	Filho 1992
Alopidae				
Alopias vulpinus, thresher	37.4 ± 7.8	5	28.5-46.4	Emery 1986
" " "	33.0	1	-	Filho 1992
" " "	29.0	1	28.0-30.0	This study
Lamnidae				
Carcharodon carcharias, white	36.6 ± 9.6	5	22.0-49.0	Emery 1986
Isurus oxyrinchus, shortfin mako	40.8 ± 9.2	21	22.5-60.0	Emery 1986
" " " "	22.6	1 ATL	-	This study
" " " "	28.7 ± 10.6	2	-	Filho 1992
Scyliorhinidae				
Cephaloscyllium isabella, carpet	16.8 ± 4.6 (5^{o}C acclim.)	-	-	Tetons & Wells 1984
" " "	15.0 ± 3.0 (15^{o}C acclim.)	-	-	Tetons & Wells 1984
Triachidae				
Mustelus canis, smooth dogfish	10.5	10	6.2-19.4	Murru 1984
" " " "	20.4 ± 0.7	63 NC	6.9-33.4	This study
" " " "	19.8 ± 3.3	14 ATL	15.2-26.9	" "
Mustelus fasciatus, striped smooth dogfish	23.5 ± 2.1	2	-	Filho 1992
Mustelus schmitti, narrownose smooth dogfish	20.4 ± 8.2	4	-	Filho 1992

Table 2. (continued)

Family and species shark	HcT % vol. + S.E.	N/LOC.	Range	Reference
Carcharinidae				
Carcharhinus altimus, bignose	25.6	1 ATL	-	This study
C. acronotus, blacknose	22.5 ± 0.8	36	9.3-28.7	This study
" " "	17.4	1 ATL	-	This study
C. brevipinna, spinner	25.1 ± 3.4	9	20.4-32.6	This study
" " "	30.1 ± 12.0	5	-	Filho 1992
C. falciformis, silky	20.7 ± 3.8	19 NC	11.8-27.3	This study
" "	22.7 ± 6.4	5 ATL	13.6-28.4	" "
C. isodon, finetooth	25.2 ± 3.7	13 NC	5.0-28.5	" "
C. limbatus, blacktip	21.4 ± 7.6	13 NC	8.9-36.0	" "
" "	17.7 ± 8.3	2 ATL	11.8-23.6	" "
" "	22.3 ± 8.6	3	-	Filho 1992
C. obscurus, dusky	18.2 ± 4.9	12	9.4-25.0	Emery 1986
" "	21.2 ± 0.7	34 NC	11.6-28.3	This study
" "	20.0	1 ATL	-	This study
" "	15.0	1	-	Filho 1992
C. plumbeus, sandbar = (C. milberti)	14.9 ± 5.0	16	9.4-24.0	Emery 1984
" "	16.1 ± 7.0	2	-	Filho 1992
" "	20.0	20	-	Stoskopf 1993
" "	26.2	16	8.8-38.5	Murru 1984
" "	21.5 ± 1.4	6 NC	19.6-23.0	This study
" "	20.0 ± 4.5	22 ATL	12.6-28.1	This study
C. porosus, smalltail	29.9 ± 6.3	7	-	Filho 1992
C. signatus, night	36.0	1 ATL	-	This study
Galeocerdo cuvieri, tiger	28.2	4	26.2-28.9	Murru 1984
" " "	19.8	22	9.4-33.0	Emery 1986
" " "	20.5	1 NC	-	This study
" " "	24.1 ± 2.7	23	19.7-27.4	This study
Negaprion brevirostris, lemon	16.1 ± 1.5	8	13.0-26.0	Bushnell et. al. 1982
" " "	22.6	22	19.4-28.0	Murru 1984
" "	20.0	3	-	Stoskopf 1993
Prionace glauca, blue	15.2 + 4.1	18	9.4-22.5	Emery 1986
" " "	22.3 ± 0.8	14	-	Johnson-Sjobeck and Stevens 1976
" " "	14.3 ± 3.0	9 ATL	11-20.6	This study

Table 2. (continued)

Family and species shark	HcT % vol. + S.E.	N/LOC	Range	Reference
Rhizoprionodon terraenovae, Atlantic sharpnose	21.4 ± 0.5	102 NC	6.2-31.4	This study
" "	19.9 ± 3.5	16 ATL	15.0-26.3	This study
" "	18.5 ± 5.2	18 ATL embryos	8.6-26.4	This study
Sphyrnidae				
Sphyrna lewini, scalloped hammerhead	26.5	1	-	Emery 1986
" " " "	30.4 ± 1.8	3 NC	28.7-32.3	This study
" " " "	27.3 ± 9.8	9 ATL	8.3-36.8	This study
" " " "	27.3 ± 7.4	18	-	Filho 1992
Sphyrna zygaena, smooth hammerhead	25.4	1 NC	-	This study
" " " "	26.6	1 ATL	-	This study
" " " "	25.4 ± 8.8	23	-	Filho 1992
Squalidae				
Centroscymnus coelolepis, Portuguese dogfish	13.0	1	-	Torres et al. 1986
Etmopterus spinosa, velvet belly	18.9 ± 5.6	16	-	Larsson et al. 1976
Somniosus microcephalus, Greenland shark	20.5	2	-	Larsson et al. 1976
Squalus acanthias, spiny dogfish	20.0 ± 2.0 wild pop. 1971	-	-	Martini 1978
" " " "	23.0 ± 2.0 wild pop. 1973	-	-	Martini 1978
" " " "	19.8 ± 5.9	3 NC	13.2-24.3	This study
" " " "	19.0 ± 3.9	6 ATL	13.2-23.4	This study
" " " "	15.3 ± 3.2	4	-	Larsson et al. 1976
" " " "	18.7	21	-	Stoskopf 1993
Squalus cubensis, Cuban dogfish	31.0	1	-	Filho 1992
Squatinidinae				
Squatina argentina, Argentine angelfish	23.1 ± 8.7	14	-	Filho 1992

Table 3. Sizes, numbers, and sexes for which blood HcT's were collected by cardiac (C) and caudal vein (D) extraction from North Carolina (NC) or Atlantic Shelf (ATL) sharks (18 species). See Table 2 for HcT's.

Species	NC				ATL			
	N	Sex	Size Range mm FL	C or D	N	Sex	Size Range mm FL	C or D
Alopias vulpinus	1	M	950	C				
Carcharias taurus					2	1M	1310	D
						1F	2290	D
Isurus oxyrinchus					1	M	1260	D
Sphyrna lewini	1	M	1840	C				
" "	3	2F	1250-1273	C	4	M	1410-1920	C
					4	F	1410-1630	C
S. zygaena	1	F	860	C	1	M	1690	C
Carcharhinus acronotus	19	M	850-1000	C	1	F	780	C
	17	F	290-1175	C				
C. altimus					1	M	1190	C
C. brevipinna	9	4M	905-1175	C				
		5F	850-1000	C				
C. falciformis	19	8M	470-870	C	5	3M	800-1520	C
		11F	730-850	C		2F	1170	C
C. isodon	13	11M	940-1060	C				
		2F	980-1060	C				
C. limbatus	13	10M	920-1280	C	2	1M	1310	C
		3F	920-1658	C		1F	1000	C
C. obscurus	18	M	750-1090	C	1	M	1620	D
	16	F	360-2900	C				

Table 3. (continued)

Species	NC				ATL			
	N	Sex	Size Range mm FL	C or D	N	Sex	Size Range mm FL	C or D
C. plumbeus	6	4M	920-1260	C	22	9M	860-1530	9 C & D
		2F	920-1170	C		13F	600-1650	13 C & D
C. signatus					1	F	2030	C
G. cuvieri	1	F	710	C	23	13M	940-3120	7 C 6D
						10F	840-2260	6 C 4D
Rhizoprionondon terranovae	37	M	460-850	C	35	12M	265-285	9 Emb. C, 3C
	65	F	260-860	C		23F	207-910	9 Emb. C
								14 C & D
Mustelis canis	33	M	310-920	C	14	2M	580-950	C
	30	F	310-1080	C		12F	990-1110	6C 6D
	16	M mature	705-920	C				
	12	F mature	777-1080	C				
	17	M immat.	704-710	C				
	18	F immat.	310-776	C				
Squalus acanthias	3	F	780-900	C	6	6F	580-911	D
Prionace glauca					9	M	1320-1990	D

Table 4. Three-way analyses of variances comparing relationships for combined, male, and female hematocrits (HcT) with fork length mm (FL), water temperature ^{o}C, and month for four species of sharks captured off North Carolina. N.S. = not significant; * $P < 0.05$ significance; r = correlation coefficient.

Species	Sex	N	Range Shark Sizes (FL,mm)	r	FL	^{o}C	Month
Blacknose shark	M	19	850-1000	0.567	N.S.	N.S.	N.S.
Blacknose shark	F	17	290-1175	0.693	*	N.S.	N.S.
Dusky shark	M	18	750-1090	0.399	N.S.	N.S.	N.S.
Dusky shark	F	16	360-2900	0.555	N.S.	N.S.	N.S.
Atlantic sharpnose shark	M	37	460-850	0.639	N.S.	N.S.	*
Atlantic sharpnose shark	F	65	260-860	0.266	N.S.	N.S.	N.S.
Smooth dogfish	M	33	310-920	0.636	*	N.S.	*
Smooth dogfish	F	30	310-1080	0.422	N.S.	N.S.	N.S.
Smooth dogfish, mature	M	16	705-920	0.693	N.S.	N.S.	N.S.
Smooth dogfish, immature	M	17	310-704	0.412	N.S.	N.S.	N.S.
Smooth dogfish, mature	F	12	777-1080	0.583	N.S.	N.S.	N.S.
Smooth dogfish, immature	F	18	310-776	0.600	N.S.	N.S.	N.S.

Table 5. One-way analysis of variance of hematocrit (HcT) values, between sexes, for four species of sharks captured off North Carolina.
r = correlation coefficient; N.S. = not significant

Species	N	r	F	P<0.05
Blacknose shark	36	0.14	0.69	N.S.
Dusky shark	34	0.10	0.32	N.S.
Atlantic sharpnose shark	102	0.03	0.13	N.S.
Smooth dogfish	63	0.31	6.46	*
mature	28	0.44	6.18	*
immature	35	0.18	1.08	N.S.

* 95% significance level