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The Yellow Stingray, *Urobatis jamaicensis* (Chondrichthyes: Urotrygonidae): a synoptic review

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Abstract.—The yellow stingray, *Urobatis jamaicensis* (Cuvier) has been the subject of a multitude of diverse studies on its natural history, morphology, and physiology. We have attempted here to briefly review all the studies on *U. jamaicensis* both published and unpublished with the goal of providing comparative information for researchers working on related species as well as to highlight areas of research requiring further investigation in this one.

Keywords.—Anatomy, Ecology, Elasmobranch, Physiology, Reproduction, Stingray

Introduction

Urobatis jamaicensis (Cuvier), the yellow stingray (Nelson et al. 2004) (Fig. 1), was originally described in 1816 as *Trygon jamaicensis.* It has also been previously classified as *Trygonobatus torpedinus, Urolophus torpedinus, Urobatis sloani*, *Urobatis vermiculatus,* and *Urolophus jamaicensis* (Bigelow and Schroeder 1953); much of the literature refers to the latter synonym. There are several phylogenetic hierarchies currently proposed, the most commonly accepted is: Class Chondrichthyes, Subclass Elasmobranchii, Order Myliobatiformes, Family Urotrygonidae; however, further revision should be expected (Nelson, 2006).

U. jamaicensis is a relatively small ray with an average size of about 335 mm total length (TL) and 160 mm disc width (DW). Typical of elasmobranchs, females grow larger than males. In our studies, with more than 500 animals, the maximum size recorded was a female 480 mm TL (the mean was ≈345 mm); while males reached a maximum size of 398 mm TL (with a mean of ≈ 325 mm). There are multiple publications listing 600 mm and larger TL *U. jamaicensis* (Bigelow and Schroeder 1953; Lieske and Myers 1994; McEachran and Fechhelm 1998; Parsons 2006). However, these appear to be based on an incorrect deduction of an ambiguous estimate ("about 500 mm; tail 190 mm"; Fowler 1945) or a misidentification. It would be a considerably larger *U. jamaicensis* than we have encountered.

Individual rays differ widely in color and pattern; the dorsal side of the disc typically displays a reticulate dark greenish or brown pattern on a pale background, or a close set pattern of minute white, yellow, or golden spots on a dark green or brown background. The ventral side of the disc is lightly colored, uniformly yellowish or brownish-white (Bigelow and Schroeder 1953). However, occasionally the ventral side has the same pattern as the dorsum

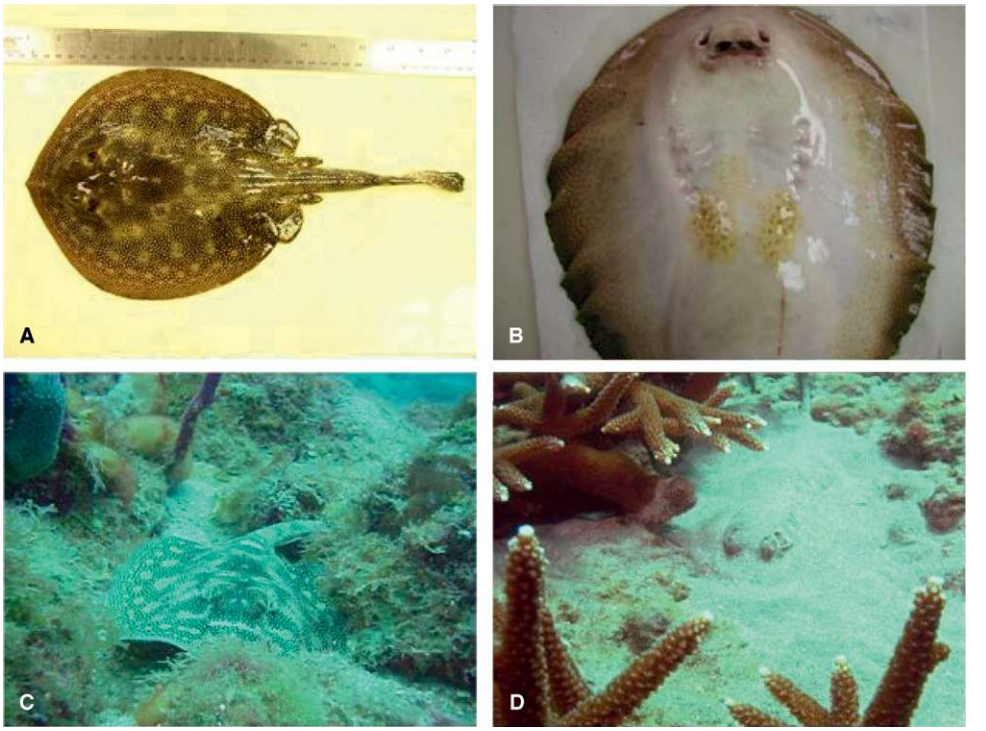

Fig. 1. *Urobatis jamaicensis*: A. dorsal view of male; B. ventral view of female showing uncommon coloration of ventrum; C. on hardbottom; D. partially buried.

either in a patchy distribution or restricted to the outer margins of the wings (Fig. 1).

The animals are found in shallow water (maximum reported depth 30 m) throughout most of the Greater Caribbean. They are patchily distributed throughout their range, but occasionally occur in relatively high abundances (Bigelow and Schroeder 1953). For example, a study off Ft. Lauderdale, Florida, tagged 108 individuals in an area of 2.7 × 0.4 km during 13 months of sampling over a 14 month period without any single recapture of a tagged or tag-site-scarred animal (Sulikowski 1996). Presumably, this is not due to large migratory movements of the animals such as those associated with reproduction in some other elasmobranchs (see Activity Patterns, below).

The geographic range of *U. jamaicensis* has previously been reported to occur from North Carolina to Brazil, including the Gulf of Mexico and widespread throughout the Caribbean Sea (Bigelow and Schroeder 1953; Robins et al. 1986; Böhlke and Chaplin 1993; Hoese and Moore 1998; McEachran and Fechhelm 1998; McEachran and Carvalho 2002; Piercy et al. 2006b). According to the IUCN Redlist report (Piercy et al. 2006b) distribution is listed for all countries within the northern and southern limits of the species range. However, reports on abundance or even presence in many of these regions are typically unverified and open to question. Although the presumed range of *U. jamaicensis* is quite extensive, available data on distribution indicates that a complete absence or rare occurrence is associated with several regions. Thus, a clear distribution pattern remains uncertain. Populations of *U. jamaicensis* are most prevalent in South Florida (including Florida Bay and the Keys), Bahamas (north and central islands), Greater Antilles (west of Mona Passage, including the Cayman Islands), and Caribbean Mexico (Campeche, Yucatan, Quintana Roo, Cozumel) through Belize. However, north of Jupiter Inlet on the east coast of Florida and in waters of the

northern and western Gulf of Mexico *U. jamaicensis* is considered a rare tropical stray (Robinson 1969; Gilmore et al. 1981; Snelson and Williams 1981; Hoese and Moore 1998; Schmid et al. 1988; REEF 2009). In the Greater Antilles, reports are lacking for east of Mona Island across the Puerto Rican Plateau (Puerto Rico, Vieques, Culebra, St. John, St. Thomas, Tortola, Virgin Gorda, and Anegada). Likewise, records from St. Croix, Lesser Antilles (with the possible exception of Grenada, Trinidad, and Tobago) and south of Venezuela (Guyane, Suriname, Guyana, and Brazil) are either nonexistent or questionable (Lowe-McConnell 1962; Dennis et al. 2004, 2005; Menni and Stehmann 2000; Lasso et al. 2004; Nunes et al. 2005; Acevedo et al. 2007; Grijalba-Bendeck et al. 2007a, b; REEF 2009). Further, there are few studies on temporal variation in abundance from areas where the animals are prevalent. There has been one report of a dramatic decrease in sightings of yellow stingrays in the greater Caribbean area over a 14 year period (from sightings in 20.5% of dives to 4.7%); however, the trend was not consistent across all surveyed regions (Ward-Paige et al. 2010). In some, *U. jamaicensis'* distribution throughout the Caribbean basin appears more restrictive than previously considered and the patterns of biogeography and connectivity of this animal remain to be elucidated.

U. jamaicensis has been the subject of a multitude of diverse studies on its natural history, morphology and physiology. We have attempted here to review all the studies on this animal of which we are aware, both published and unpublished. Our goal is to summarize current knowledge of *U. jamaicensis* in order to provide comparative information for researchers working on related species as well as highlight areas of research requiring further investigation in this one.

Anatomy and Physiology

Integument

The integument of *U. jamaicensis*, as in other batoids, is relatively thick and covered, in part, with placoid scales or denticles (Bigelow and Schroeder 1953; Kemp 1999). At parturition, the skin is devoid of denticles. However, shortly thereafter, development begins of low blunt tubercles on the mid-dorsum and re-curved thorns along dorsal margins of the caudal fin. Larger adults have the mid-dorsal tubercles to the orbits and a lateral band of thorns over each shoulder. The ventrum remains smooth throughout life (Bigelow and Schroeder 1953).

The teeth of *U. jamaicensis*, apparently evolutionarily derived from denticles (Kemp 1999), number about 30 per row on both the upper and lower jaws in about 5 and 8 rows respectively. All rows are simultaneously functional. In females and immature males, the teeth are closely arranged and oval in shape with low cusps. In mature males the upper teeth are more loosely spaced with high conical cusps that are slightly blunt at the end (Bigelow and Schroeder 1953). This sexually dimorphic trait is associated with reproductive behaviors and likely functions to allow the male to maintain a grasp on the female during copulation (see below). Sexually dimorphic dentition is a common trait observed among batoids with females exhibiting a smooth, molariform shape, whereas male dentition consists of sharp, recurved cusps (Bigelow and Schroeder 1953; Feduccia and Slaughter 1974; McCourt and Kerstitch 1980; Taniuchi and Shimizu 1993; Nordell 1994; Kajiura and Tricas 1996). Male *Dasyatis sabina* exhibit a seasonal transition in dentition; feminine-like teeth during non-reproductive periods are replaced by sharp cusps during the protracted mating season (Kajiura and Tricas 1996). The re-curved condition of male *U. jamaicensis* dentition is static throughout the year; however, preliminary gross observations indicate sharp cusps are more prominent during periods of active breeding (Fahy unpublished). Additionally, increased incidence of dermal bite wounds on females has been correlated to male dentition and seasonal mating activity in *D. sabina* (Kajiura et al. 2000).

Caudal Spine

Urobatis jamaicensis typically has a single venomous caudal spine (Fig. 2) which, like many other stingrays, is shed periodically (Johansson et al. 2004; authors unpublished). In a study off Seal Beach, California, natural spine replacement occurred in *U. halleri*

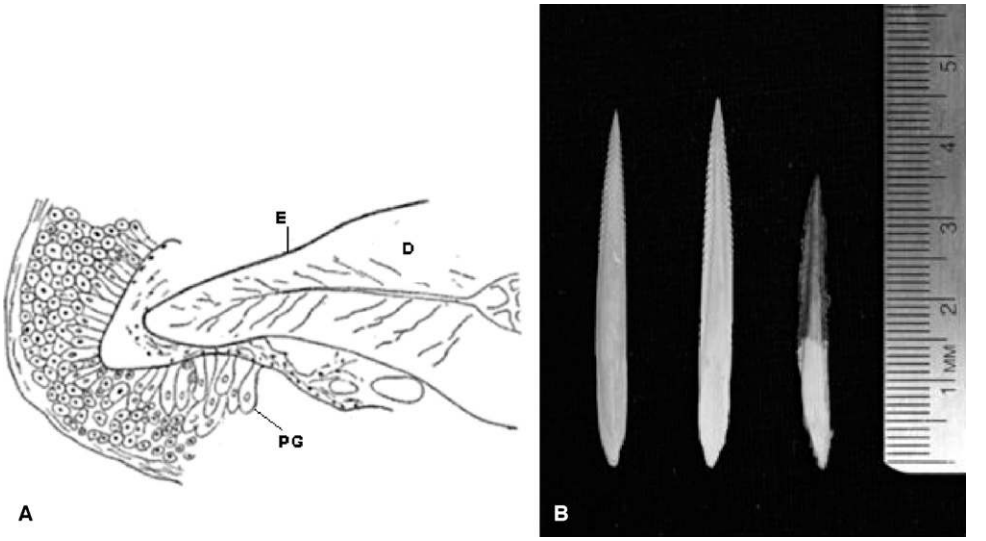

FIG. 2. A) Transverse section of caudal spine of *Urobatus halleri*, illustrating enamel (E), dentine (D) and "poison gland" cell (PG) (minor modification of original by A. Paden from Daniel 1934). B) Three spines of *U. jamaicensis,* dorsal and ventral views of cleaned spines (left and center, respectively) and uncleaned spine with dried epidermal sheath (right).

between August and October (Lowe et al. 2007). During the period when the new spine is growing, the animal carries two spines and rarely three. Through most of the year, the spine has a strong attachment to the vertebral column and is not readily removed from the tail. During these times, the spine will bear the entire weight of the animal out of water and entanglements in nets are more likely to break the spine than pull it out. During periods when the spine is being shed, it is released with relative ease. The spine is normally used in a stabbing motion that produces a puncture wound, although, if the ray is lashing its tail about, a scalpel-like slash can be inflicted. This normally deceptively docile animal can stab its spine with surprising speed, a fact which most researchers working with it can attest to. We are unaware of studies on the toxin of the *U. jamaicensis* spine but it is likely similar to other stingrays. The toxin is a protein produced in glandular tissue of the sheath, within the ventrolateral grooves, that remains behind in the wound rather than an injected venom (Fig. 2) (Russell 1959; Pedroso et al. 2007). The pain produced by the toxin depends on the wound, and individual-specific responses to the envenomation, and ranges from an itch to severe pain requiring medical treatment; again we write from experience here.

NERVOUS SYSTEM

Brain Morphology

There has been little work on the nervous system of *U. jamaicensis*. Walker and Sherman (2001) looked at gross morphology and there has been some abstracted, and unpublished, work on cerebellar function (Sherman et al. 2003). Like other stingrays, *U. jamaicensis* has a brain 3 to 10 times the size of their sister groups, the electric rays, guitarfish, and skates. The brain is well developed and, relative to fishes, quite large in proportion to body weight, rivaling mammals in size (≈1–2% bw) (Northcutt 1989; Walker and Sherman 2001).

Gross morphology of the *U. jamaicensis* brain is similar to the closely related Dasyatids, including the presence of an asymmetric cerebellum (Fig. 3). Like mammals, they also have a large, complex, three-lobed cerebellum. However, in *U. jamaicensis*, these lobes are completely separated. Thus, the lobes can be individually manipulated to examine behavioral correlates of specific

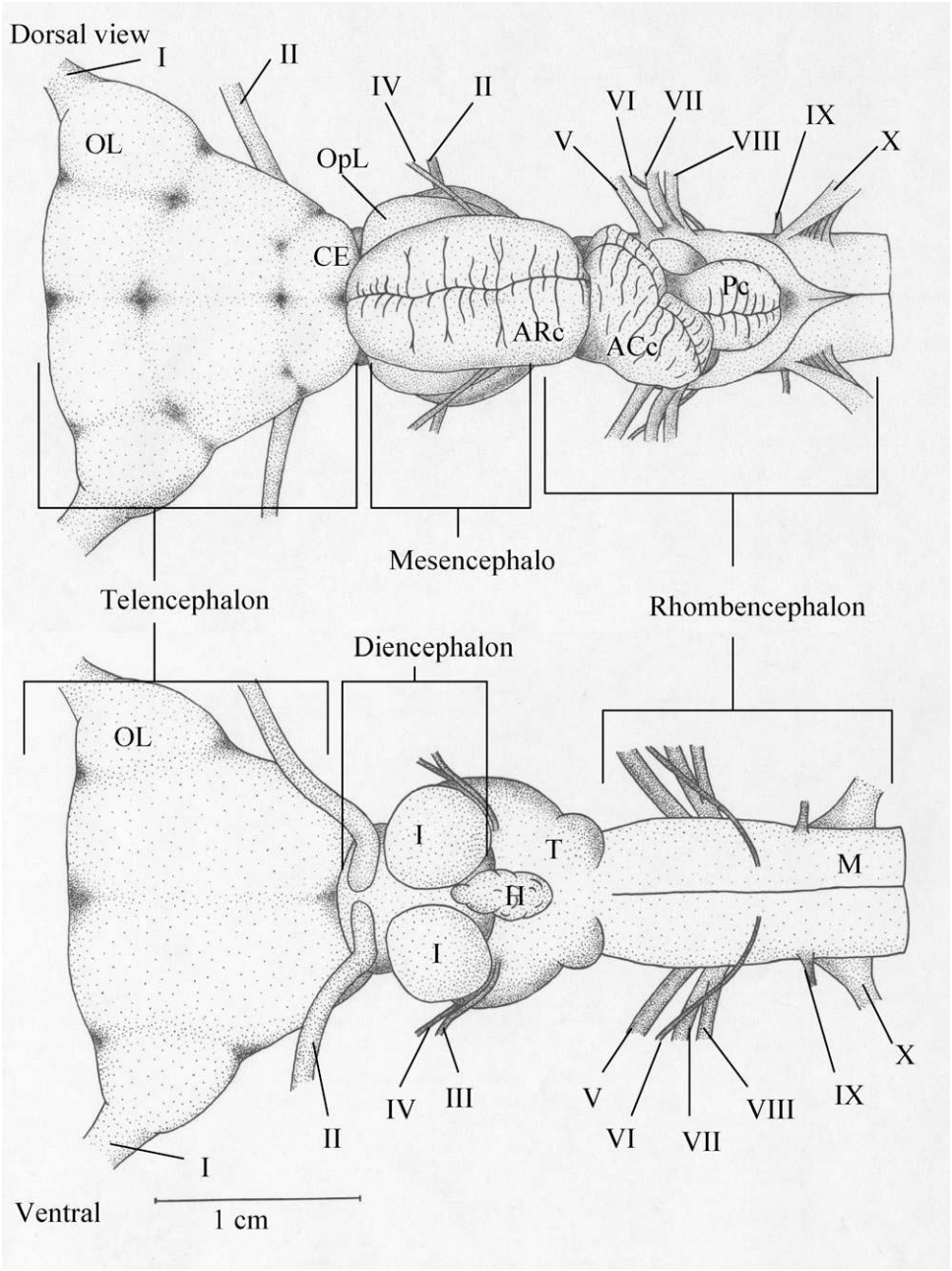

FIG. 3. Dorsal and ventral view of brain with cranial nerves and major topography of *Urobatis jamaicensis*. Cranial Nerves: I-Olfactory, II-Optic, III-Oculomotor, IV-Trochlear, V-Trigeminal, VI-Abducens, VII-Facial, VIII-Auditory, IX-Glossopharyngeal, X-Vagus. Major Topography: ACc-Anterior caudal cerebellum, ARc-Anterior rostral cerebellum, CE-Cerebrum, H-Hypophysis, I-Inferior lobes of infundibulum, MO-Medulla oblongata, OL-Olfactory lobe, OpL-Optic Lobe, Pc-Posterior cerebellum, T-Tegmentum (from Walker and Sherman 2001).

lobes. Some preliminary work examined the function of these lobes. Cerebellar ablation was performed on anesthetized animals by first creating a hinged window in the dorsal portion of the chondrocranium, using an electric drill with a thin (0.1 mm) circular saw blade, exposing the midbrain. The three lobes of the cerebellum were identified and either the center lobe (n = 7) or caudal lobe (n = 3) was removed. Following removal of the cerebellar lobe, the cartilaginous flap over the window was closed with a single suture and surgical adhesive, paraffin, or liquid Band-Aid® used to seal the cut edges. The entire procedure, from anesthesia induction until completion of the surgery and resuscitation, took approximately 30 min. As controls, four animals were subjected to all the surgical procedures, but no brain tissue was removed.

Gross, reproducible behaviors were readily noted one day after surgery and did not improve over 3 weeks time (the longest period an animal survived following lobe ablation). As noted in mammals, there appears to be a relationship between the cerebellum and voluntary coordination and behavior in *U. jamaicensis*. Ablation of the center lobe caused a generalized pattern of uncoordinated hyperactivity. When disturbed by gentle prodding, the animals responded with an atypical rapid swimming to the surface, spinning, and often swimming, momentarily, upside down and backwards (Sherman et al. 2003). These results, of uncoordinated hyperactivity, would support an inhibitory role for the center lobe of the cerebellum of *U. jamaicensis* similar to that reported for the mammalian cerebellum (Ito et al. 1964). In sharp contrast, however, ablation of the caudal lobe caused extreme lethargy. The animals were unresponsive to prodding; even lifting by hand did not elicit an escape response. Sham controls did not show any detectable difference in behavior from non-operated controls. Both sham and non-operated controls spent most of the day buried in the sand substrate of the holding tanks. None of the ablated animals buried despite apparent attempts (i.e., forming shallow depressions). The study was ended prematurely due to technical difficulties with the aquarium facilities. As a caution to future researchers, although the brain is readily accessed, the chondrocranium never repaired itself, and neither cements nor sutures adequately reattached an opened window. Nonetheless, the large brain should make *U. jamaicensis* an interesting model for neurophysiologists interested in fishes and the large cerebellum in this sedentary animal begs further investigation.

Sensory Systems

Vision

Urobatis jamaicensis has the eyes located well up on the dorsum and somewhat protruding and periscopic in comparison to other batoids. Presumably this protrusion allows the eyes to stay slightly above the surface and provide vision when the animals are buried (McComb and Kajiura 2008). Like many other batoids, *U. jamaicensis* has crescent shaped pupils and a pupillary operculum, a complex flap of iris tissue hanging over and partially covering the pupil. The crescent-shaped pupil preserves a small depth of field, limits light flux to the retina and decreases the effects of spherical aberration inherent to the globular lens. The pupillary operculum effectively creates multiple apertures, and thus multiple images, of objects lying either in front or behind the plane of optical focus. This provides the ray with enhanced sensitivity to movement. In addition, the pupillary operculum may provide a larger visual field than a circular pupil of identical area and may also diminish the effects of lens-induced spherical aberration (Murphy and Howland 1990).

McComb and Kajiura (2008) conducted an ecophysiology study on the visual field of four batoids, including *U. jamaicensis*. They found that *U. jamaicensis* had a horizontal visual field of 360° and a vertical field of 264°, thus the animals can see in all directions with virtually no blind spots except directly on top of their head (Fig. 4). However, horizontal binocular vision in front of the animal was only 34°. The authors deduced that given food acquisition is primarily blind foraging in the substrate, and likely not requiring great visual acuity, the binocular vision was adequate for forward swimming. Further, they

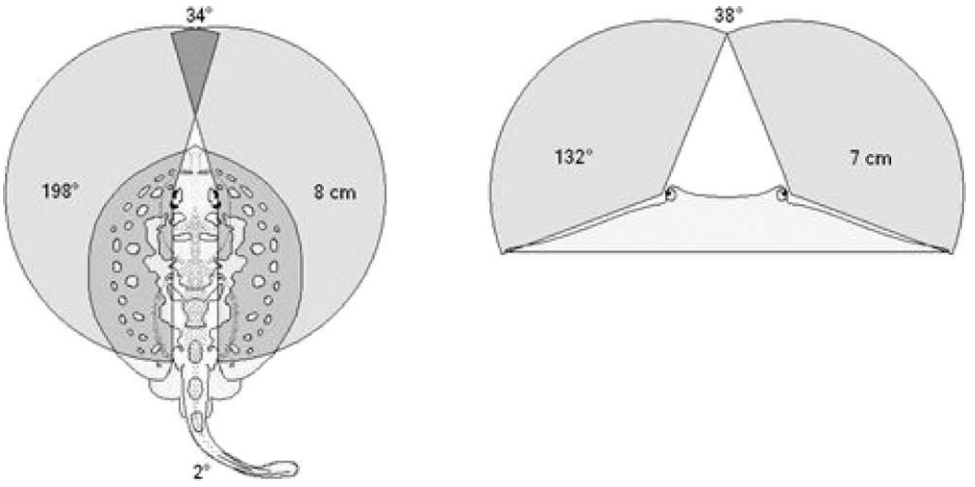

FIG. 4. Horizontal and vertical visual fields and standardized convergence distance (cm) of *Urobatis jamaicensis*. Monocular and binocular visual fields are lightly and darkly shaded respectively (after McComb and Kajiura 2008).

suggested the large horizontal and vertical visual fields of this animal are associated with a sedentary lifestyle and, likely, high predatory pressure.

Hearing

Casper and Mann (2006) examined hearing thresholds of *U. jamaicensis* using auditory evoked potentials (AEP), essentially recording acoustic-stimuli-evoked potentials from the brain. Test frequencies ranged from 100 to 2000 Hz. However, AEP were only obtained up to 1000 Hz. The animals appeared to be most sensitive at 300 and 600 Hz with a threshold of 139.45 dB and 140.23 dB re 1 μPa respectively. Like other elasmobranchs, or teleosts lacking a swim bladder, *U. jamaicensis* appears to have poor hearing abilities and is limited to detecting particle motion and not sound pressure.

RESPIRATORY SYSTEM

Gross examination of the gills confirms the basic structure of the gill arches in *U. jamaicensis* is similar to those of other elasmobranchs. The hyoid arch supports a single hemibranch. This single, anterior gill is the first hemibranch. The posterior gill arches support the first, second, third and fourth holobranchs, respectively. The filaments of each holobranch are attached to an interbranchial septum, which is attached to both the dorsal and ventral surfaces of the pharyngeal cavity. The interbranchial septa separate the gill pouches and are formed of skeletal (striated) muscle supported by cartilaginous rays. The gill arches contain a number of small, coarse gill rakers that prevent large particles from entering the gill pouch and possibly damaging the gill filaments.

Sherman et al. (1995) examined two other species of stingrays, in which the lamellar surface area utilized for gas exchange ranged from two to seven times the animal's body surface area. They suggested that in batoids, like other fishes, the ratio of gill surface area to body surface area appears to be a function of the normal activity level of the animal being examined (Satchell 1962). For example, a species that feeds high in the water column or migrates long distances will have a higher gill surface area to body surface area ratio than a more sedentary animal.

As in other batoid elasmobranchs, it appears *U. jamaicensis*' water for respiration is primarily pumped through dorsally located spiracles and, presumably, may secondarily also be taken in through the mouth. The water flows into each gill pouch, across the lamellar surface, down a water channel at the base of each filament, and out through the gill slit on the ventral surface.

Respiratory water flow may be increased or decreased, as needed, by muscular pumping (Donald 1988; Sherman 1998; Butler 1999). Constrictor muscles in the yellow ray cover most of the head and gill region. They consist of dorsal superficial constrictors that lie dorsal to the gill pouches, and ventral superficial constrictors that lie ventrally between the gill slits. The superficial constrictors in sharks compress the pharyngeal chamber, eject the water, and close the gill slits (Gilbert 1993; Ashley and Chiasson 1988). The similarity in these structures in stingrays suggests that they perform the same function. We are not aware of any work discussing a tidal respiratory water-flow, in and out through the spiracles. However, such an exchange would appear to be advantageous to an animal with ventral gill slits when buried in sand and might be an interesting topic for future research.

Cardiovascular System

Blood flow in elasmobranchs is a single circuit, flowing sequentially from the *sinus venosus* to the atrium, the ventricle, the *conus arteriosus,* the ventral aorta, the gills, then to systemic tissues and return (Tota 1999). Hamlett et al. (1996c) examined the anatomy, histology, and development of the three sets of cardiac valves in embryonic and adult elasmobranchs, including *U. jamaicensis*. The *sinus venosus* is the first heart chamber to receive venous blood, and one-way flow is aided by a pair of sinoatrial valves, which prohibit return flow of blood from the atrium into the *sinus venosus*. These valves are simple flaps of tissue lacking papillary muscles or *chordae tendineae*. In contrast, as in higher vertebrates, the atrioventricular valves, located between the atrium and the ventricle, have *chordae tendineae*, are composed of linear arrays of collagen, and link valve tissue to papillary muscles in the ventricle. There are multiple rows of conal valves in the *conus arteriosus* which prevent blood from reentering the ventricle. The conal valves have *chordae tendineae,* but lack papillary muscles. Preliminary work using mercox perfusion indicates the arterial blood supply to the heart of *U. jamaicensis* is similar to other batoids (Prior and Marples 1945) with the coronary arteries arising from the hypobrachial arteries (Rogers et al. unpublished). Interestingly, Olson et al. (2000) reported spontaneous contractions in the blood vessels from four elasmobranchs, two sharks and two batoids, including *U. jamaicensis.* The authors noted that, in general, these contractions were more prevalent in the sedentary batoids than in the sharks and speculated that this might be due to a decreased utility of muscle pumps associated with this lifestyle.

The *conus arteriosus* extends from the heart anteriorly to the end of the pericardial cavity. Beyond this point the vessel continues as the ventral aorta, a median vessel which gives off five pairs of afferent branchial arteries leading to the gills. The fourth and fifth branchial arteries arise simultaneously just anterior to the pericardial cavity at the point where the *conus arteriosus* joins the ventral aorta and serve the third and fourth holobranchs. The third afferent branchial artery serves the second holobranch. The ventral aorta then extends without further branching to the level of the hyoid arch where it bifurcates, forming two stems which turn posteriorly. Each stem divides into two arteries, the first and second afferent branchials which lie on either side of the first gill pouch, the posterior branch serving the first holobranch, and the anterior branch serving the single hemibranch. Sherman and colleagues have done several studies on the vascular structure of *U. jamaicensis'* gills using corrosion casting. In general, this animal's gill structure resembles that noted in other elasmobranchs (Donald 1988; Sherman 1998; Sherman and Spieler 1998; Sherman et al. 2001). However, some aspects of the arterio-arterial pathways in *Urolophus* and *Urobatis* spp. gills differ from that of teleosts and other elasmobranchs (Donald 1988; Sherman 1998). There is a more extensive *corpus cavernosum* in the afferent circulation of *Urobatis* than that found in other groups. This *corpus cavernosum* is a well developed structure into which blood flows from the afferent filament artery. From there, blood enters the lamellae through afferent lamellar arterioles. Although the function of the cavernous tissue has not been fully established, it may have a storage function, act to dampen the blood pressure pulse, or

serve as a hydrostatic skeletal structure. In addition to an enlarged *corpus cavernosum*, additional, unique structural differences from other elasmobranchs include: 1) the lack of a septal *corpus cavernosum*; 2) the existence of a vessel, or vascular arcade, which connects the afferent filament arteries near the tip of the filament; 3) a channel, possibly an extension of the afferent filament artery, at the top of the filament *corpus cavernosum* (Donald 1988; Sherman 1998). Donald (1988) suggests the vascular arcade may be homologous to the septal *corpora cavernosa* found in other elasmobranchs. Evidently, this arrangement of vessels is not found in all batoids because the vascular anatomy of some skates lacks the vascular arcade; in *Raja erinacea*, and *R. clavata* gill filament vasculature is similar to that of selachians (Sherman et al. 2001).

A non-gill secondary circulation has only been identified in teleosts (Satchell 1991). However, there are interlamellar vessels in the gills of *U. jamaicensis* that have been speculated to be part of a secondary,

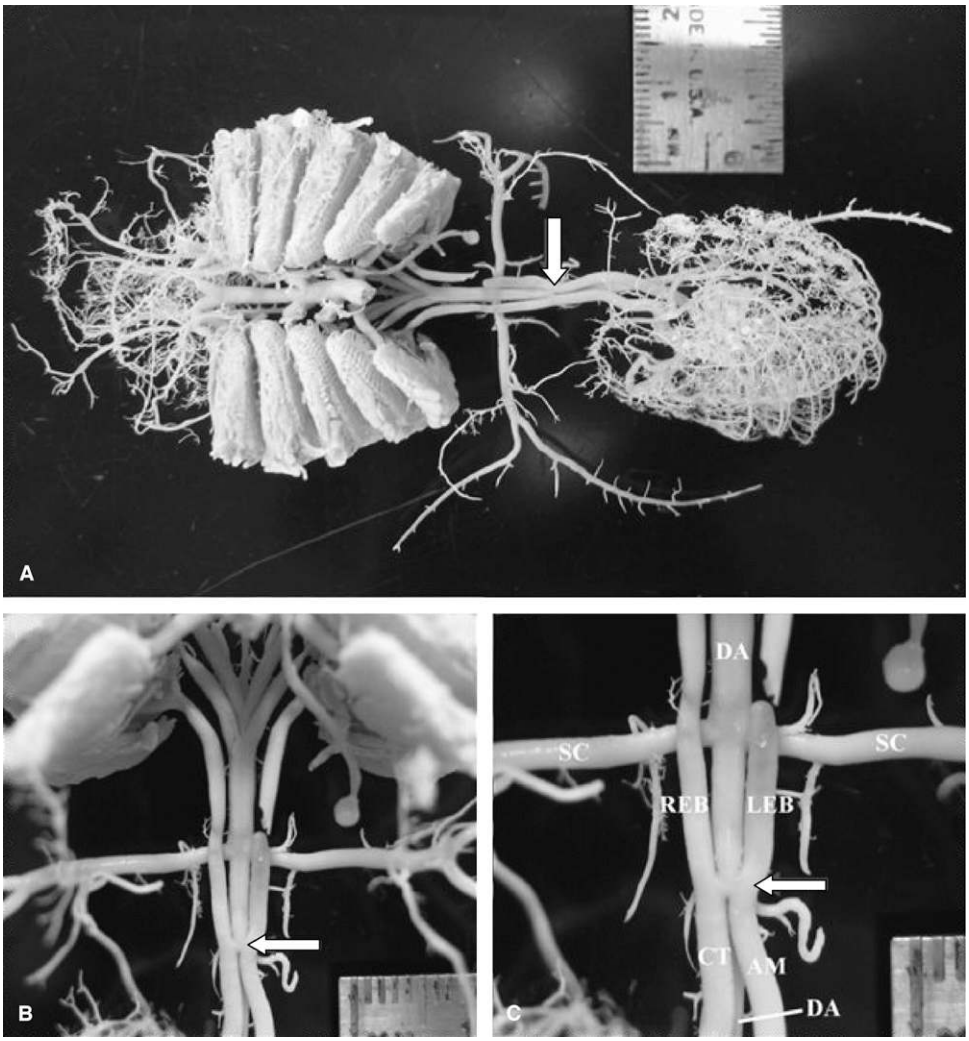

FIG. 5. Example of an arterial cast of a yellow stingray, *Urobatis jamaicensis* (ventral view, in successive increasing magnification). Anastomosis between the fourth epibranchial arteries and the dorsal aorta is indicated by the arrow. DA-dorsal aorta; SC-subclavian; REB-right fourth epibranchial artery; LEB-left fourth epibranchial artery; CT-celiac trunk; AM-anterior mesenteric artery (from Basten et al. 2007).

arterio-venous, circulatory system (Sherman 1998). Presumably, these secondary vessels empty into central veins of the head such as the branchial and inferior jugular through which the blood/plasma is transported back to the heart. In *U. jamaicensis,* this system includes a series of interconnecting vessels originating at arteriovenous anastomoses from the efferent filament artery and from some of the efferent lamellar arterioles. These post-lamellar arteriovenous anastomoses supply blood to the central venous sinus, a network of interconnecting vessels that occupy the core of the filament located between the *corpus cavernosum* and the efferent filament artery. This sinus is connected to afferent and efferent companion vessels that run parallel to the afferent and efferent filament arteries (Sherman 1998). These companion vessels are named for their positions, not their functions, as both vessels serve to drain the blood and, possibly, lymphatic fluid from the central venous sinus to venous sinuses in the gill arch (Metcalfe and Butler 1986). In teleosts, this system was regarded as primarily lymphatic until it was determined that its source of blood is arterial and that red blood cells are sometimes passed through its vessels (Satchell 1991). To conclude, most of the arterio-arterial gill anatomical structure in *U. jamaicensis* has been worked out while much of the arterio-venous structure has not. The physiological significance of many of the structures of both systems remains to be elucidated.

Oxygenated blood flows from the gills via epibranchial arteries to systemic circulation. In most teleosts and elasmobranchs studies, the epibranchials join to form the dorsal aorta which gives rise to the subclavian, anterior mesenteric, and gastric arteries. However, with light and scanning electron microscopy of vascular corrosion casts, Basten et al. (2007; 2009) observed that the fourth epibranchial arteries do not merge completely with the dorsal aorta in *U. jamaicensis*. Instead, they form a brief anastomosis with a short vessel projecting ventrally from the dorsal aorta and maintain their integrity as separately distinct vessels. Posterior to the anastomosis, the right epibranchial becomes the celiac trunk and left epibranchial becomes the anterior mesenteric artery/posterior intestinal artery. This vascular configuration appears to be unique in elasmobranchs; the physiologic function of this configuration is unclear, but it has been hypothesized to prevent a large decrease in blood pressure that might occur at the juncture of the dorsal aorta and the subclavian arteries (Basten et al. 2007; 2009) (Fig. 5).

Blood to the spiral valve arises from the anterior mesenteric artery which feeds the spiral valve externally and from the anterior intestinal artery which feed the spiral valve internally. Each of the 13 valves receives a direct arterial blood supply from the anterior mesenteric artery. Venous vessels lie above the arteries at each valve and anastomose, as do, apparently, all vessels of the digestive tract in elasmobranchs, into the hepatic portal vein (Daniel 1934; Muñoz-Chápuli 1999; Maroni et. al. 2009).

Other than some scattered work on reproductive organs (see below), little work has been done on arterial perfusion, or venous return, of the remaining organs of *U. jamaicensis.*

Digestive System

Gut

Like many elasmobranchs, *U. jamaicensis* has a U-shaped stomach with a pyloric end that enters a proximal (anterior) intestine then a spiral valve to a distal (posterior) intestine, rectum, and cloaca (Fig. 6). In extant fishes, the spiral valve is found in elasmobranchs and some primitive families of Subclasses Cladistia and Chondrostei. It functions in lieu of a small intestine and, by the addition of internal structure, increases the surface area allowing for increased area for digestion and absorption of nutrients. The spiral valve in *U. jamaicensis* has 13 turns in an anterior oriented conicospiral configuration (Holmgren and Nilsson 1999). Cestodes are routinely found in the spiral valves of elasmobranchs, including batoids, and *U. jamaicensis* is no exception. At least four species of tapeworms have been described from the spiral valves of *U. jamaicensis* taken in Jamaica (Kovacs and Schmidt 1980; Gardner and Schmidt 1984;

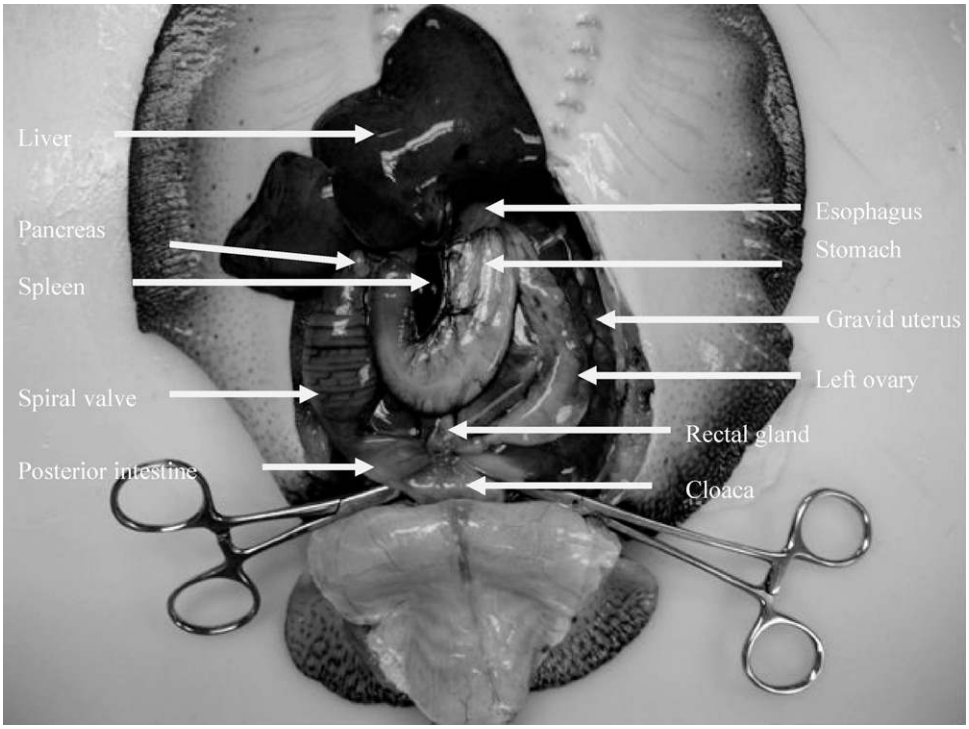

FIG. 6. Abdominal cavity of female *Urobatis jamaicensis,* with liver reflected.

Huber and Schmidt 1985). Additionally, the digestive tract from specimens collected in South Florida is often heavily invested with un-identified nematodes (Quinn 1996; Fahy unpublished).

Liver

Hepatosomatic indices (HSI; liver weight/ body weight × 100) of *U. jamaicensis* are smaller than many other elasmobranchs including some other batoids. Sherman and Gilliam (1996) reported a mean HSI from 16 *U. jamaicensis* of 3.40 ± 0.31 (mean ± SE) This was lower than free-swimming rays (i.e., *Aetobatus narinari*, *Rhinoptera bonasus*) and is dramatically lower than the 20+% HSIs noted in some sharks (Kohler et al. 1996). The large HSI in elasmobrachs has been attributed to using the liver as a buoyancy organ as well as for food storage (Bone and Marshall 1992). We suspect *U. jamaicensis* is a sedentary animal with access to a relatively constant food supply and does not require high levels of lipid storage for periodic events (e.g., reproduction, migration) and thus has little need for a large liver.

Osmotic Regulation

In its natural habitat, *U. jamaicensis* has been collected in seawater (SW) that ranges from 26‰ to 40‰ salinity (Yañez-Arancibia and Amezcua-Linares 1979). In order to test the osmoregulatory capacity of this potentially euryhaline species, Sulikowski and Maginniss (2001) characterized the water and solute composition for plasma and a single intracellular compartment (erythrocytes) as a function of environmental salinity. In the laboratory, stingrays exhibited rapid and significant increases in body mass upon exposure to stepwise seawater (33‰) dilutions (82%, 74%, 66% SW). Average weight increases of 7-10% were recorded within 24 h of exposure to the three dilution steps. However, body fluid recovery was generally achieved within 2-6 days for each of the three experimental

groups. Likewise, changes in red blood cell (RBC) water content and mean corpuscular Hb, indicative of erythrocyte swelling, suggested the stingray erythrocytes are regulated at a volume substantially less than a passive RBC osmometer. Together, these data suggest that *U. jamaicensis* are capable of extracellular and intracellular volume regulation during hypo-osmotic exposure, especially at lower salinities.

In 100% SW, stingray plasma was slightly hypo-osmotic to the external medium. Although plasma osmolality decreased with hypo-osmotic exposure, the reductions were not in proportion to the medium dilution. The measured plasma solutes also exhibited significant dilution-induced changes in concentration, consistent with the corresponding osmolality values. However, the relative variations in plasma solutes were generally disproportionate and suggested regulation of the individual plasma solutes. For example, in 82% SW, plasma Na, Cl, and urea were reduced 13%, 13%, and 21% below control levels, respectively; in 74% SW, the corresponding values were 22%, 23%, and 25%, respectively. In the most dilute medium (66% SW), further losses of the two primary electrolytes were curtailed. In fact, plasma concentrations of Na and Cl were reduced only 17% and 15%, respectively, below control levels. The animal's lower limit of tolerance for extracellular ionic dilution may occur within this concentration range. Solute compensation for the transition from 74% to 66% SW was therefore achieved largely by further, and substantial, reductions of extracellular urea. In 66% SW, the plasma [urea] of acclimated stingrays was reduced by 59% below control levels. Changes in plasma [K] and [Ca] were minor at each dilution.

The three measured RBC cations (K, Na and Ca) exhibited similar responses to environmental dilution and were reduced by 12-16% in 82% SW and 32-37% in 74% SW, while in 66% SW, the electrolytes revealed a leveling-off effect which may reflect the animal's lower limit of tolerance for intracellular ionic concentration. Intracellular concentrations of urea have not been reported for the yellow stingray. However, the literature provides considerable support for the uniform distribution of urea across the RBC membrane of elasmobranchs, and it is most likely that urea levels for erythrocytes and plasma in *U. jamaicensis* were nearly identical and exhibited comparable declines with environmental dilution (Walsh et al. 1994; Carlson and Goldstein 1997).

Based on these results it would appear that when exposed to mild or moderate dilutions (82% and 74% SW), *U. jamaicensis* regulate their body fluid compartments slightly hyperosmotic to the external milieu by comparable reductions of the major electrolytes and urea. With greater dilution (66% SW), these elasmobranchs maintained their hyperosmotic state by eliminating additional urea, while resisting further reductions of electrolytes (Sulikowski and Maginniss 2001). Like many other marine elasmobranchs, the yellow stingray has a demonstrated capacity for survival and acclimation in reduced salinity environments (Lacy and Reale 1999).

Reproductive System

General

The gross and microscopic structure of the reproductive anatomy of *U. jamaicensis* was originally described by LaMarca (1961; 1964) (gross structure: Figs. 7-10). More recently, several histological and ultrastructural examinations of specific reproductive structures (ovary, oviducal gland, uterus, and testis) have been conducted (Hamlett and Hysell 1998; Hamlett and Koob 1999; Hamlett et al. 1996a; 1998; 1999a, b; 2005a, c). However, details on developmental patterns of these structures throughout the reproductive cycle are incomplete. Typical among elasmobranchs, gonadal tissue is intimately associated with lymphomyeloid tissue, forming the epigonal organs (LaMarca 1961; Hamlett et al. 1999c). In *U. jamaicensis*, this gonadal-epigonal complex forms paired, dorsoventrally flattened and elongated organs with morphological compensation due, presumably, to physical constraints of the visceral anatomy within the coelomic cavity. At present, no studies have been conducted on steroidogenesis in *U. jamaicensis*; although, photoperiod, temperature, and the reproductive cycle have been correlated with circulating levels of sex steroids in *U. halleri*.

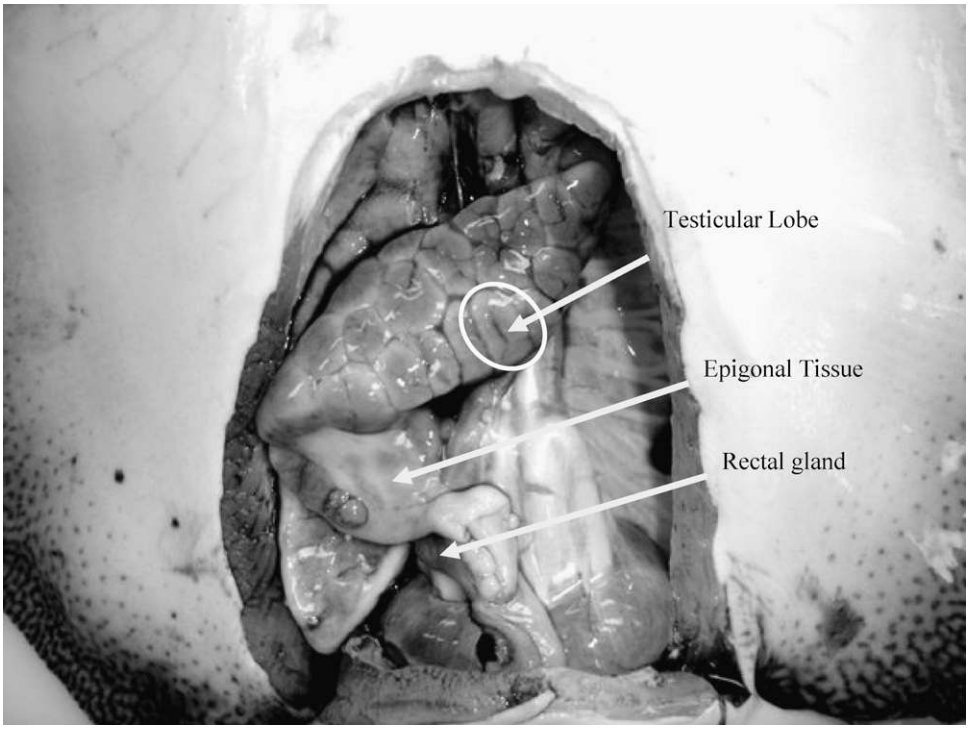

FIG. 7. Reproductive organs of mature male *Urobatis jamaicensis*, with the left testis reflected to provide dorsal view of testicular lobes.

Androgens (testosterone and 11-ketotestosterone) were positively correlated with recrudescence, with peaks at final sperm maturation and the onset of copulatory activity and negatively correlated with the photophase and water temperature. Progesterone peaked at the time of ovulation, remained elevated through embryogenesis, and was positively correlated with water temperature (Mull 2007; Mull et al. 2008).

Male Reproductive System

The reproductive anatomy of male chondrichthyans (Figs. 7, 8) is structurally more conserved than females (Hamlett 1999). However, some variation exists in testicular structure and accessory glands, with only minor differences in the extratesticular tract among species. Both testes are equally developed and functional in males; however the left testis is posteriorly folded conforming to the contours of the U-shaped stomach (LaMarca 1961). The paired testes of *U. jamaicensis* are consistent with the compound testis type described by Pratt (1988), with spermatocysts radiating both outward from the germinal zone on the ventral surface of each lobe and dorsally across the diameter of the gonad (LaMarca 1961; Babel 1967). In *U. jamaicensis*, the germinal zone consists of a testicular appendage that may be an exclusive structure of myliobatiform testicular morphology (LaMarca 1961, Lewis 1984). A condensed description of spermatogenesis (7 stages) has been reported with typical patterns of elasmobranch spermatocyst/Sertoli cell development (Hamlett 1999).

Variations have been observed in testicular lobate structure and efferent ductule development between conspecifics (LaMarca 1961; Babel 1967; Lewis 1984). In *U. halleri,* each lobe consists of a permanent primary lobule and a transient secondary lobule (not present during the quiescent phase of the reproductive cycle), with further subdivision of the secondary lobule by connective tissue septae that contain intermediate collecting ducts (Babel 1967; Mull 2007; Mull et al. 2008).

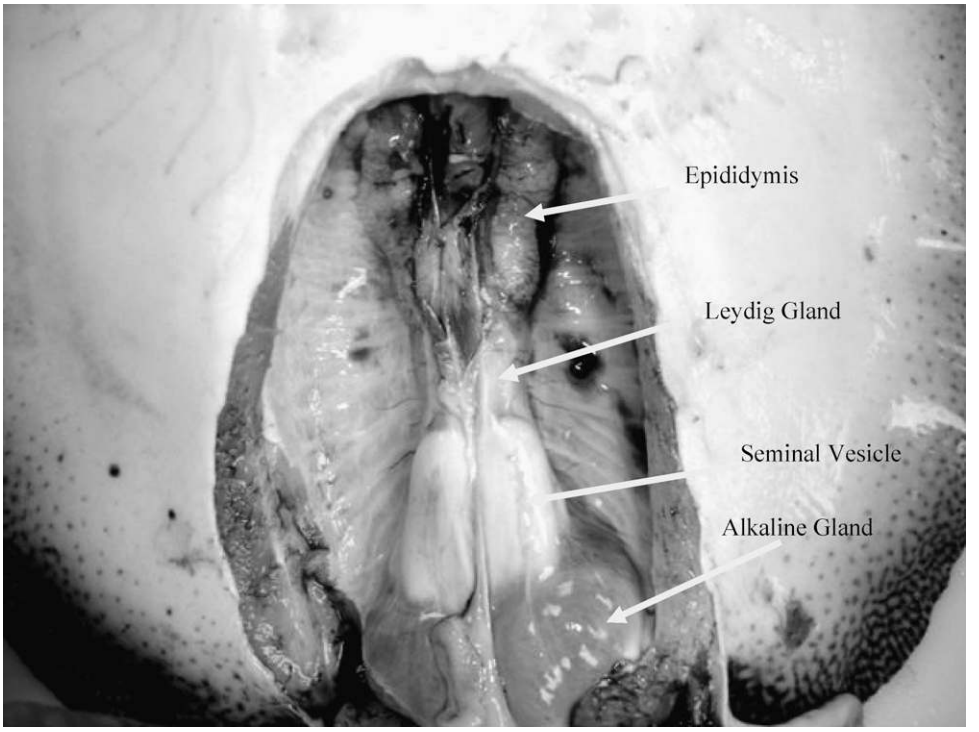

FIG. 8. Reproductive organs of mature male *Urobatis jamaicensis,* with testes removed.

In *U. jamaicensis,* testicular lobes persist throughout the year (lacking a quiescent phase) with no indication of distinct primary and secondary zonation (LaMarca 1961; W. Hamlett personal communication) possibly due to the biannual reproductive cycle (see below). Seasonal patterns of testicular development occur (indicating periods of degeneration and recrudescence); however, monthly histological examination of the testes and reproductive tract is still required to determine production and storage of spermatozoa throughout the year (LaMarca 1961; W. Hamlett personal communication). *U. jamaicensis* exhibits a single longitudinal collecting duct supplied by interlobar collecting ducts, whereas *U. halleri* displays individual longitudinal ducts associated with each testicular lobe (LaMarca 1961; Babel 1967). These ventrally-located longitudinal ducts course through connective tissue embedded within the testis-epigonal interface in both species (LaMarca 1961; Babel 1967; Lewis 1984). LaMarca (1961) reported that these smaller collecting branches of *U. jamaicensis* are confluent with degenerating spermatocysts during spermiation. The luminal epithelium of both collecting and efferent ducts is identical, consisting of a simple columnar epithelium with elongated cilia. In *U. jamaicensis,* the longitudinal ducts coalesce into a single efferent duct that subsequently divides into 2-3 smaller branches, each branch separately entering into the initial segment of the epididymis (LaMarca 1961). LaMarca (1961) noted connective tissue septa that partition the epididymis into two or three rounded segments and identified two zones (anterior and posterior) that vary in diameter and epithelia. The narrow diameter and reduced lumen of the initial segment displays a high, irregular ciliated columnar epithelium. The luminal diameter increases as the epididymis transitions into the terminal segment, which is composed of a uniform, low ciliated cuboidal epithelium. The external diameter of the epididymis gradually increases as the convoluted tubule progresses towards the terminal segment, and

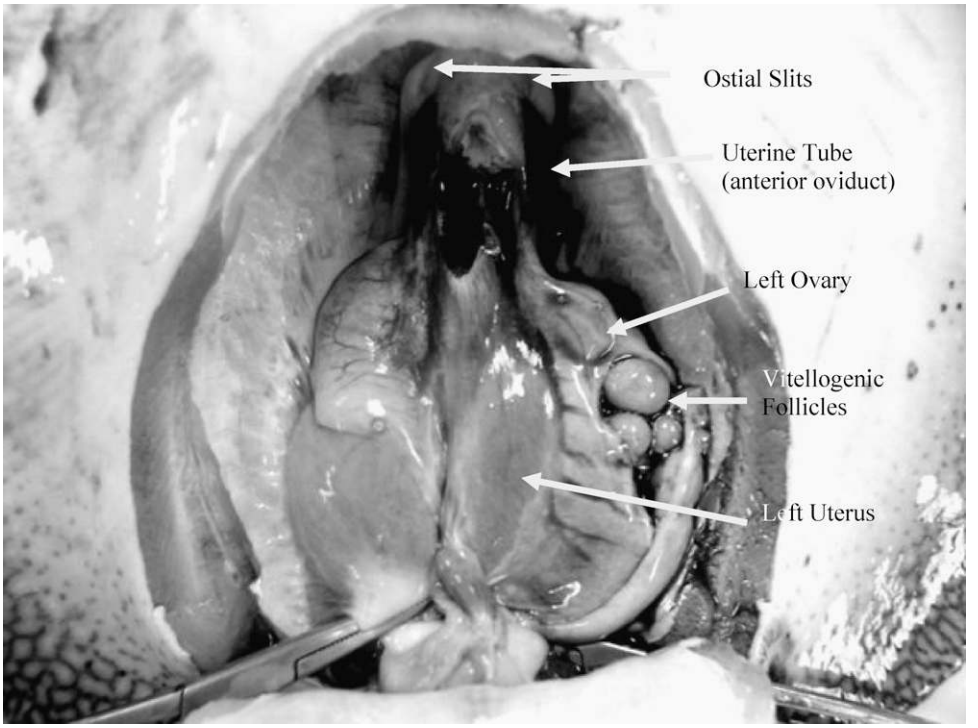

FIG. 9. Reproductive organs of mature female *Urobatis jamaicensis*, with distended uteri and enlarged ova.

eventually transitions into the larger and more sinuous *ductus deferens*. The anterior *ductus deferens* has a uniformly high, ciliated columnar epithelium and is partially embedded within the ventral tissue of Leydig's gland (LaMarca 1961). Currently it is unclear if Leydig's gland tissue merely surrounds portions of terminal segment or if excretory ducts actually empty into the epididymal tract. LaMarca (1961) and Babel (1967) have reported secretions from Leydig glands empty solely into the *ductus deferens* proper in *U. jamaicensis* and *U. halleri*, respectively. Leydig glands consist of a series of convoluted tubules with uniform columnar secretory epithelium and elongated cilia, similar to the upper epididymis. The tubules empty into non-secretory collecting ducts prior to discharging their contents into the extratesticular tract. LaMarca (1961) referred to the enlarged S-shaped seminal vesicle as the posterior *ductus deferens* or ampulla, and described low irregular folds of the mucosa that form nearly transverse septa with ciliated columnar epithelium. He also remarked on the development of smooth muscle into mixed circular and longitudinal fibers that extend up into the connective tissue septa. Each transverse septum has an eccentric perforation with radially aligned smooth muscle that may regulate the spiraling luminal aperture throughout the seminal vesicle. The seminal vesicle is considered a male sperm storage site, and LaMarca (1961) has suggested the arrangement of smooth muscle represents an ejaculatory mechanism during copulation.

Although luminal fluids have not been characterized throughout the genital ducts of *U. jamaicensis*, continual absorption and seminal fluid modification has been reported for *Heterodontus portusjacksoni* (Jones et al. 1984; Jones and Lin 1993; Hamlett et al. 1999b). Additionally, motility is enhanced in stepwise progression through the genital tract with further transitions in sperm luminal arrangement (Hamlett et al. 1999b). LaMarca (1961) described varying columnar cell characteristics of luminal epithelia in *U. jamaicensis* that are consistent with more

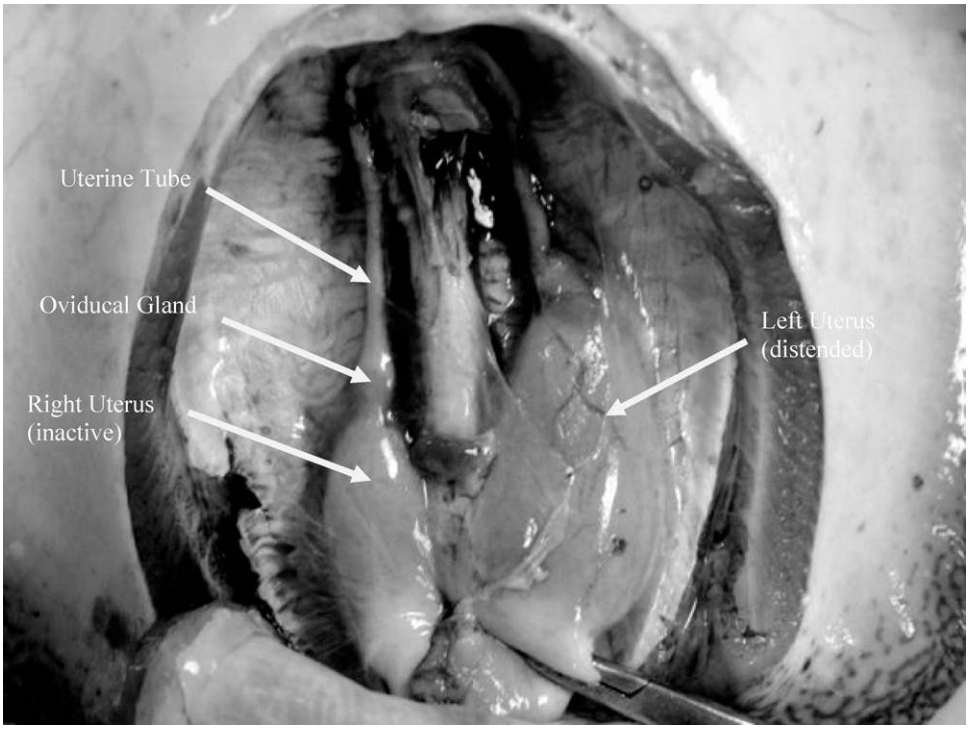

FIG. 10. Reproductive organs of a mature female *Urobatis jamaicensis,* with distended uteri (ovaries have been removed).

recent descriptions of 2-3 cell populations with varying distributions and functions (i.e. protein synthesis and secretion, absorption, and transport) (Botte et al. 1963; Jones and Jones 1982; Jones and Lin 1993; Jones and Hamlett 2003; 2006; Jones et al. 2005). Accessory glands in batoids have been variably termed over the years and research directed at morphological and functional characteristics is lacking. The alkaline glands (formerly sperm sac) and clasper gland/sac (formerly siphon gland/sac) are paired organs and presumably assist in the transfer of spermatozoa during coitus (LaMarca 1961; Babel 1967; Lacy 2005). Alkaline glands are ventrally situated on the posterior aspect of each kidney and in stingrays the excretory duct is confluent with the terminal portion of the seminal vesicle (LaMarca 1961; Grabowski et al. 1999; Lacy 2005). Alkaline glands in *U. jamaicensis* are observed as small protuberances in immature specimens (LaMarca 1961) and are variably distended throughout the year in mature males (Fahy unpublished). The gland lumen consists of complex folds lined with simple columnar epithelium and a surrounding layer of smooth muscle that extends into mucosal folds (LaMarca 1961). Alkaline gland secretions are considered to act directly on sperm motility and longevity with a potential function in the female reproductive tract correlated with synthesis of a relaxin-like molecule (Grabowski, et al. 1999; Lacy 2005).

LaMarca (1961; 1964) examined the structure of claspers and clasper glands of *U. jamaicensis* including some histochemical analyses of clasper gland secretions. Claspers are intromittent organs for internal fertilization formed by developmental modifications of pelvic fin cartilages. In *U. jamaicensis,* these modifications consist of three connecting pieces, an appendix stem and five fully-calcified segments (LaMarca 1964). The diameter of the clasper tip is increased during copulation by flexion of a dilatator muscle to separate the terminal cartilages and expand the hypopyle, thus

anchoring the clasper within the female cloaca. In *U. jamaicensis*, claspers are short and stout, continually growing at an even rate throughout sexual maturation. A viscous white glycoprotein/phospholipid secretion is produced within simple tubular glands, which radiate dorsally or dorso-laterally from the secretory ridge (LaMarca 1964; Lacy 2005). Contraction of striated muscle that surrounds the organ expels secretory products from the gland through a series of papillae (secretory openings) into the clasper sac (Lacy 2005; Piercy et al. 2006a). Each clasper gland papilla drains a series of tubules which are lined with simple columnar epithelium via collecting ducts with pseudostratified epithelium (LaMarca 1964; Lacy 2005; Piercy et al. 2006a). The secretory openings are situated within the central longitudinal groove of the organ with further muscular contractions delivering secretions into the clasper groove via an elongated slit in the apopyle clasper segment (Lacy 2005). Clasper gland secretions mix with spermatozoa emitted from the cloaca once inside the clasper groove (LaMarca 1964; Lacy 2005). In *U. jamaicensis,* the mixture of spermatozoa with clasper gland secretions produced hyperactivity with motility persisting for over 3 hours, whereas seawater mixing entailed much lower activity for periods lasting only 15-20 minutes (LaMarca 1961; 1964). LaMarca (1964) proposed that clasper gland secretions seal the clasper groove into a watertight closed tube and also act as a medium for sperm suspension and transport.

Female Reproductive System

Females have two ovaries (Fig. 10) but the right ovary is significantly reduced and production of mature ova is generally considered a sole function of the left ovary (LaMarca, 1961; Fahy et al. 2007). However, Fahy et al. (2007) have reported enlarged vitellogenic oocytes from the right ovary of two large females (single ovum ≈10 mm or larger). The germinal epithelium of the ovary is simple cuboidal with rounded apices and microvilli, overlying a moderately dense layer of connective tissue (*tunica albuginea*) (Hamlett et al. 1999c). Numerous primordial follicles are peripherally located (subjacent to *tunica albuginea*) with simple squamous epithelium and abundant lipid-like cells in the follicular wall. As follicles grow, a typical transitional gradient is observed for simple cuboidal (unilaminar) tissue in primary follicles (pre-vitellogenic), followed by stratification (multilaminar) and further development of columnar follicle cells. During initial stages of folliculogenesis, round lipid-like cells attain large sizes, but eventually dissipate and vanish prior to ovulation. A distinct *zona pellicuda* is evident between the oocyte and follicle cells. Follicular extensions extend across the *zona pellucida*, indent the oolemma and form definitive transosomes during multilaminar stages of follicle development (Hamlett et al. 1999c).

Ultrastructural observations of ovarian folliculogenesis have described elaborate invaginations of the follicular epithelium along with subjacent portions of highly vascularized thecal tissue (Hamlett et al. 1999c). These inward folds initiate once ova attain diameters of 1.5 to 2.0 mm and are considered to increase surface area for a rapid and efficient transport of hepatically derived yolk proteins during vitellogenesis. These structures have also been described for other species of myliobatiform stingrays (Babel 1967; Lewis 1984; Teshima and Takeshita 1992; Mull 2007) and are likely characteristic of the order. Although Babel (1967) reports ~24 months for egg development in *U. halleri*, a rapid onset of growth in the latter stages of gestation appears more characteristic of *U. jamaicensis* (Hamlett and Koob 1999; Hamlett et al. 1999c).

LaMarca (1961) reported that specimens collected during March and July displayed all stages of oogenesis, including *corpora lutea, corpora albicans*, and atretic follicles in the left ovary. *Corpora albicans* and atretic follicles were often deeply embedded within epigonal tissue, whereas *corpora lutea* were peripheral and described as large hollow structures with inward folded walls. Lewis (1984) noted these observations were from misidentified vitellogenic follicles, exhibiting the above mentioned follicular epithelial folds. LaMarca (1961) also mentions small ova were present in the right ovary, but did not observe any glandular activity of atretic

follicles as noted by Babel (1967) for *U. halleri*. Hamlett et al. (1999c) reported both degeneration of atretic preovulatory follicles and *corpus luteum* formation are observed with an outer layer of vascularized thecal cells surrounding a collapsed layer of lipid-rich granulosa cells. Babel (1967) mentioned that large degenerate ova are often mistaken for *corpora lutea*. He proposed that *corpora lutea* are derived solely from hypertrophy of *theca externa* cells within the collapsed follicle, whereas follicular folds and *theca interna* tissue remain with the ovulated ovum. Thus, two distinct thecal layers (*theca interna* and *theca externa*) are observed for *U. halleri,* in contrast to the uniform layer of vascularized thecal cells reported for *U. jamaicensis* (Hamlett et al. 1999c). The remaining female reproductive tract (anteriad to posteriad) consists of paired ostia, uterine tubes, oviducal glands, and uteri (Hamlett and Koob 1999; Fahy et al. 2007). A common ostium is fused ventrally over the esophagus, with two laterally distinct ostial openings (longitudinal slits) corresponding to individual uterine tubes (anterior oviducts). Each uterine tube lumen is continuously disrupted into extensive longitudinal folds with ciliated columnar epithelium, interspersed with secretory cells that often form basal secretory acini (Fahy, unpublished). Posteriorly, uterine tubes eventually transition into slightly enlarged, bell-shaped oviducal glands (LaMarca 1961; Hamlett and Koob 1999; Fahy et al. 2007). Typically, four histologically distinct zones (club, papillary, baffle, and terminal zones) characterize oviducal gland (OG) structure of elasmobranchs. However, two visually discrete zones are grossly discernable from OG in *U. jamaicensis* with further corroboration of zonation from histochemical analyses (secretory granules are PAS (+) in anterior tubules and PAS (-) in posterior tubules) (LaMarca 1961). The simplified OG of *U. jamaicensis* is composed of a series of parallel tubular glands with secretory activity increasing adluminal and posteriad within the organ (Hamlett et al. 1996a; 1998; 1999a; 2005a). Recently, Hamlett et al. (2005a) have reported that the highly modified OG of *U. jamaicensis* does not have club or papillary zones, thus the ability to produce egg jelly is lost. Likewise, there is no egg-envelope produced due to the lack of baffle plates associated with egg investment (this region of the OG in *U. jamaicensis* has been referred to as baffle zone equivalent) and a terminal zone is entirely absent (Hamlett et al. 1996a; 1998; 1999a). However, Fahy (unpublished) has repeatedly observed the presence of an isolated thin membranous casing from uteri with recently ovulated eggs. Therefore, some form of a short-lived egg covering is likely produced and warrants further investigation of OG structure and function in *Urobatis*. The OG is typically considered the site of fertilization (upper OG or uterine tube) and sperm storage (terminal zone) in elasmobranchs; however, the unconfirmed egg investiture and lack of terminal zone storage tubules in *U. jamaicensis* are unique features.

Maternal Anatomy and Fetal Development

In *Urobatis*, both uteri are functional, but with a unilateral dominance of the left uterus (LaMarca 1961; Babel 1967; Fahy et al. 2007). Uterine morphology corresponds with mode of reproduction and the most significant modification observed is the endometrial proliferation of villous extensions, termed trophonemata. Like all myliobatiforms, in *U. jamaicensis* matrotrophic input of histotroph is supplied via trophonemata (termed, lipid histotrophy) that provisions developing embryos beyond the initial egg investiture (Hamlett 1986; Hamlett and Koob 1999; Hamlett et al 2005b, c). Corrosion casting (Basten 2007) confirmed the basic vascular structure noted with previous histological observations (LaMarca 1961; Hamlett and Hysell 1998; Hamlett et al. 2005b). A central artery bifurcates into two arterioles that run parallel to each other down the edges of each villus and ramify into a capillary bed at the distal end of the villus. The villus is comprised of a network of web-like capillaries that wrap around the peripheral arterioles and throughout the center of the villus. The arterioles feed these capillaries through a series of connections along their length. Venous blood passes from capillaries into collecting venules that channel blood into the axial vein. While there does appear to be some variation in the density of the capillaries among trophonemata, no correlation

has been found between capillary density or vessel shape and gestational stage (Basten 2007). These observations may be indicative of consistent development of trophonemata in *U. jamaicensis*, associated with repetitive pregnancies throughout a female's entire adult life. *Dasyatis americana* trophonemata, have a transition from small capillaries with overlying cuboidal epithelium during early gestation to enlarged sinusoidal capillaries with simple squamous epithelium during term stages (Hamlett et al. 1996b). The enhanced vascularization combined with decreasing gas diffusion distances, were correlated with increased oxygen demands of developing fetuses. Trophonemata secrete uterine fluids (histotroph) composed of a high organic content as nourishment for developing embryos (Hamlett et al. 1993; 1996b; 2005c). However, ultrastructural comparisons of secretory crypts of trophonemata between near term *D. americana* and *U. jamaicensis* displayed dramatically fewer lipid droplets in *Urobatis* (Hamlett et al. 2005c). Additional comparisons of the biochemical composition of histotroph also demonstrated considerable differences: protein size (56.2 kDa and 85.6 kDa), protein concentration (20.6 mg/ml and 9.5 mg/ml), total lipid content (3 mg/g and <0.5 mg/g), lipid composition (primarily triglycerides vs. primarily phospholipids), and fatty acid content (ratio of saturated to unsaturated fatty acids, 1: 1.5 and 12.5: 1) in *D. americana* and *U. jamaicensis*, respectively (Hamlett et al. 2005c). The lesser degree of lipid histotrophy demonstrated by *U. jamaicensis* in comparison with *D. americana* is noteworthy, since comparable levels of embryonic development are reported for both species (Hamlett et al. 1996a; Hamlett et al. 2005c; Fahy et al. 2007). Preliminary wet weight determinations indicated *U. jamaicensis* is highly matrotrophic with an approximate 4,600% increase in weight from mature ova to term fetus. This increase exceeds that reported for *D. americana* (3,750%) (Hamlett et al. 1996b; Fahy et al. 2007). Ongoing research is currently examining the histotroph composition and structure of trophonemata throughout gestation to clarify how *U. jamaicensis* achieves these results with a seemingly dilute histotroph.

Reproductive Cycle

The reproductive cycle of *U. jamaicensis* in coastal waters of South Florida has been examined with field observations and monthly collections (Fahy 2004; Fahy et al. 2007; Fahy unpublished). Gravid females are visually conspicuous, displaying a convex dorsum often with apparent movement of term-stage young. For short periods postpartum there is an obvious depression or dorsal concavity with the skin stretched and loose in appearance. Gravid females were observed year round, with two consecutive peaks in reproductive activity. Examination of the reproductive tract indicated a protracted period of ovulation from January to April, and a second, more restricted, period of ovulation during August/September. The mean monthly peaks in maximum ovum diameter (MOD) corresponded with both periods of peak ovulation (Fahy unpublished). Additionally, all females observed midway through both gestation periods (May and October, respectively) were pregnant with subsequent periods of parturition between June and September (with a late July/early August peak) and again between November and January. The bimodal overlap in embryonic development with concurrent vitellogenesis is further supportive of a biannual reproductive cycle (Fahy et al. 2007). Male stingrays exhibited maximal testicular development (i.e., elevated GSI and prominent testicular lobes) 1-2 months prior to each ovulatory peak. This timing also corresponded with an increased occurrence of female copulatory bite marks. The increased prevalence of bite marks on postpartum females is suggestive of mating events closely following parturition similar to *D. americana* (Henningsen 2000; Chapman et al. 2003).

A gestation rate of 5-6 months was observed for *U. jamaicensis* in South Florida with a transitional overlap occurring between both cycles (i.e. ovulation and gestation) (Fahy et al. 2007). There has been a previous estimate of a 3-month gestation rate for *U. jamaicensis*; however, this was based upon Babel's (1967) observed patterns for the congener *U. halleri* (Hamlett 1999). Variable reports of maximum fecundity (3-5) for

U. jamaicensis have persisted throughout the literature (Bigelow and Schroeder 1953; Hamlett 1999; McEachran and de Carvahlo 2002, Piercy et al. 2006b). Recently, Fahy et al. (2007) reported a maximum uterine fecundity (combined contents of both functional uteri) of seven offspring. Brood size increased with maternal size and was significantly higher during the spring/summer reproductive cycle ($\bar{X} = 3.1 \pm 0.179$ SE, range 1-7) compared to the autumn/winter cycle ($\bar{X} = 1.4 \pm 0.110$, range 1-3) (Fahy et al. 2007). This seasonal variation in uterine fecundity is further supportive of a biannual cycle, rather than differences in the reproductive cycles of separate breeding populations. The transition from the initial cycle (both uteri typically active) to the second, less fecund cycle (only left uterus typically active) is often represented by presence of ova in the left uterus and the right uterus distended from recent parturition (D. Fahy unpublished).

Although both male and female *U. jamaicensis* exhibit biannual cycles of gametogenesis and breeding activity in South Florida, reproductive cycles among stingrays vary with geographic location. Likely, annual cycles involve various environmental signals (i.e., temperature, salinity) as suggested for other species, to establish steroidogenic regulation of vitellogenesis, folliculogenesis, and gametogenesis and the associated behavioral characteristics (Babel 1967; Thorson 1983; Charvet-Almeida et al. 2005; White and Dharmadi 2007; Mull et al. 2008; Pierce et al. 2009). Reproductive periodicity of the congener *U. halleri* is a well defined annual cycle among male stingrays with conflicting reports of synchronous and asynchronous annual ovulatory cycles among females (Babel 1967; Mull et al. 2008). Closely related species (*Urotrygon* spp.) with a more tropical distribution have not displayed well-defined cycles (Tellez et al. 2006; Mejía-Falla and Navia 2007). Studies in South Florida on *U. jamaicensis* (Fahy et al. 2007) were accomplished near the northern extent of the species range. Additional observations from several locales have also indicated that the primary reproductive season occurs from February to July; however, data collections from these studies appear biased towards summer months (LaMarca 1961; Yañez-Arancibia and Amezcua-Linares. 1979; Young 1993; Piercy et al. 2006b). LaMarca (1961) reported that ovulation of *U. jamaicensis* in Bimini, Bahamas, occurs over a wide period during "early months of the year" (based upon ovarian condition and uterine embryo sizes), with parturition occurring during summer months (with mention of a single term pup delivered during the month of March). Likewise, Piercy et al. (2006b) reported parturition during the months of June through August in the Bahamas. Young (1993) proposed peak mating occurs during February/March in Belize, based on copulatory observations. Yañez-Arancibia and Amezcua-Linares (1979) reported parturition in the southern Gulf of Mexico occurred from May to October. Thus, most studies are in agreement on the timing of the initial reproductive cycle of *U. jamaicensis*. However, additional work is required to verify the occurrence of a second cycle in other portions of the species range.

Natural History

Activity Patterns

In general, *U. jamaicensis* have a demersal lifestyle. They are most often seen in stationary positions and when seen moving it is for short distances and less than a meter above the substrate (authors unpublished). Swimming appears to be done primarily by undulation of their pectoral fins, a locomotory style displayed by other demersal batoids (Rosenberger 2001; Schaefer and Summers 2005; McComb and Kajiura 2008). Because the animals display nocturnal activity (see below), and most diving (and thus most sightings) is during the daylight hours, it may be that animals exhibit a pelagic behavior at night. However, all observations at nighttime are also consistent with a demersal lifestyle (Fahy 2004). In addition, *U. jamaicensis* have a lower hepato-somatic index than a pelagic stingray, a relatively low binocular overlap in the horizontal visual field, and low lipid content in the chondocranium; all of these are adaptations associated with a demersal lifestyle (Phleger 1988; Sherman and Gilliam 1996; McComb and Kajiura 2008).

Several recent studies, of other batoids, using active tracking, passive monitoring techniques and archival tags have established long-term site fidelity, repetitive seasonal movements or extensive periods of residency within limited areas (Hunter et al. 2005; Collins et al. 2007; Dewar et al. 2008; Le Port et al. 2008). However, short-term movements and seasonal patterns of *U. jamaicensis* distribution have only been examined in a limited portion of the species range (Sulikowski 1996; Fahy 2004). In South Florida, *U. jamaicensis* are permanent residents throughout the year and primarily associated with hardbottom and reef habitats (Sulikowski 1996; Fahy 2004). Movements over open sandy bottoms are highly directed transitions between adjacent reef sites or brief forays with a subsequent return to previous hardbottom habitats (Fahy unpublished). However, literature from other locations has emphasized the importance of seagrass habitats for pupping (Yanez-Arancibia and Amezcua-Linares 1979; Piercy et al. 2006*b*).

Fahy (2004) examined the activity patterns and space utilization of *U. jamaicensis* in coastal waters of southeast Florida via active tracking of 17 adult stingrays. Stingrays were captured with handnets via SCUBA from shallow inshore hardbottom communities in water ranging from 3-15 m of depth. Animals were anesthetized and tagged with external telemetry transmitters attached by sutures to the epaxial musculature. After revival the stingrays were immediately returned to capture locations and monitored with a tracking receiver and directional hydrophone. Animals were tracked continuously for periods ranging from (2-28 h); eight individuals were tracked for a full diel cycle (24 h). Activity spaces for both 95% Kernel Utilization Distributions (KUD) and 50% KUD core areas were significantly larger during nocturnal periods. Total (24 h) KUD were representative of confined activity spaces (mean = 0.02 km^2 +/− 0.01 SE) with linearity indices and random walk analyses further demonstrating strong site attachment. Similarly, active tracking conducted in Belize demonstrated short-range movements with further evidence of a high degree of site attachment to shallow water habitats (P. Lobel, personal communication). However, intermittent tracking (over 2-7 days) of several animals indicates *U. jamaicensis* activity spaces may be larger with animals only using portions of their full range on a daily basis (Fahy 2004). Similarly, for *U. halleri* in Southern California, patterns of sedentary behavior, with little movement, interspersed with periods of elevated activity were observed throughout the day. However, at night this activity was correlated with ebbing tides and the influence of a heated effluent (Vaudo and Lowe 2006). Additionally, *U. halleri* has been reported to move substantial distances (>30 km in 3 months) after release (Russell 1955; Babel 1967; Vaudo and Lowe 2006).

In the Fahy (2004) study, bottom topography had considerable influence on the space utilization of *U. jamaicensis*, and movements varied with location in relation to proximity from the reef edge/sand interface. Animals centrally located within consistent hardbottom displayed meandering movement patterns and continually returned to core areas. In contrast, stingrays situated along the reef/sand interface traveled along more linear pathways as defined by reef characteristics. Although detailed analysis of habitat selection was not conducted, an apparent preference for hardbottom substrate was observed from tracking data locations and by direct observations during extended periods of inactivity (Fahy 2004). However, longer term studies are necessary to determine the repeatability of diel movements across multiple days to verify patterns of residency and habitat utilization. Future active tracking, coupled with passive monitoring techniques, would better establish the level of site fidelity displayed by *U. jamaicensis* and potentially characterize the existence of a home range.

Seasonal distribution was assessed to determine population residency within the study site and ascertain the occurrence and temporal patterns of onshore/offshore movements (Fahy 2004). Data on *U. jamaicensis* were extracted from several stationary visual fish count studies (over 700 point counts) in Broward County, Florida, from January 1998

to December 2003 and combined to determine abundance on each of the three coral-reef tracts (Baron et al. 2004; Ferro et al. 2005). The tracts lie parallel to the coast in progressively deeper water with increasing distances from the shoreline. Data from these studies were tested for monthly and seasonal differences as well as differences among reef tracts. Analysis of seasonal distribution established population residency was year-round with no indication of offshore emigration associated with water temperature or other environmental factors. However, this conclusion requires further study as the Baron et al. (2004) and Ferro et al. (2005) studies were concentrated on fish assemblages at hardbottom areas and were not designed specifically for addressing inshore/offshore movement. Thus, adjacent sand habitats were not sampled and may have been preferred at different times of the year.

Datasets on population structure from several studies (Baron et al. 2004; Ferro et al. 2005) and chance encounter/collecting data (Fahy unpublished) were analyzed in order to examine sexual segregation and ontogenetic partitioning. The sex ratio was compared for differences monthly, seasonally, and between reef tracts. Only spring observations (March through May) evidenced a statistically significant difference from a 1:1 ratio when females dominated the inshore visual observations (2.5F:1M; n=28). This observation of seasonal segregation was likely associated with the reproductive cycle (see below), as most females recorded during this period (15/20) were actively gestating. Although few neonates were recorded in the datasets, most observations occurred in shallow inshore water (< 6 m depth), suggesting a nearshore pupping area with no indication of an established nursery area as defined by Heupel et al. (2007). Increased abundance and presence on the offshore reef among intermediate size classes (250-299 mm to 300-349 mm) suggests a potential ontogenetic shift to deeper water by sub-adults (Fahy 2004).

Refuge

Cryptic coloration makes the animals difficult to see in their natural habitats of coral reef, hardbottom, and sea grass. They will also bury themselves completely on sandy bottoms and may lie concealed under rock ledges (Fig. 1). When on the substrate they often sit with the rostral portion of the disk raised forming a cave-like area. It has been suggested this behavior is related to feeding and is used to attract invertebrates seeking refuge (Robins et al. 1986). However, we are unaware of any reports documenting feeding from this position and startled rays will often swim away from a stimulus (e.g., diver) and assume the caving posture immediately on alighting to the substrate. This might indicate the behavior is related to respiration, but this requires further studies (Summers and Ferry-Graham 2001).

Trophic Position

U. jamaicensis, like its congener *U. halleri,* apparently obtains buried prey by burrowing with its pectoral fins (Bigelow and Schroeder 1953; Babel 1967). Mulvany and Motta (2009) found *U. jamaicensis* and *D. sabina* would swim over presumably exposed live or dead prey and, using the anterior pectoral fin margin, trap and reposition prey between the substrate and their body. Once the prey was near the mouth, ingestion was accomplished using suction and biting.

Bigelow and Schroeder (1953) reported that the stomach of one specimen of *U. jamaicensis* contained shrimp (*Penaeus brasiliensis*) and the stomach of another contained bottom detritus. Yanez-Arancibia and Amezcua-Linares (1979), working in the Terminos Lagoon system in the Mexican province of Campeche, examined the stomachs of 16 adult *U. jamaicensis;* 11 (68.8%) had contents; the remainder had empty stomachs. They reported yellow stingrays consume different types of crustaceans, polychaetes, mollusks, amphipods, and stomatopods. The primary food consisted of polychaetes, crustaceans, and mollusks, with these three groups representing up to 82% of the diet.

Quinn (1996) examined 31 *U. jamaicensis* throughout the year in South Florida. Their diet consisted primarily of polychaetes, crustaceans, nemerteans, sipunculids, nematodes,

and chaetognaths, with polychaetes and crustaceans comprising 67% of the stomach contents by volume. Most of the remaining stomach content volume consisted of digested organic matter and unidentified vermiforms. There was no apparent difference in diet between sexes, and seasonal changes in diet appeared to be limited to an increase in the proportion of polychaetes found in the stomach during spring compared to fall. At the present, we are not aware of any studies on seasonal polychaete abundances in South Florida. However, there are reports, from other areas, that suggested changes in polychaete abundance were correlated with changes in the diet of demersal fishes (Nishikawa et al. 2000). In conjunction with other, non-feeding-related, studies it has been noted that *U. jamaicensis* have also ingested dusky jawfish (*Opistognathus whitehursti*), a small (< 10 cm) tunnel/cave dweller (Fahy unpublished). Similarly, Babel (1967) reported that bivalves, polychaetes, and crustaceans composed over 94 % of the total food content, by volume, for *U. halleri*; however, bivalves were the most important single food class. In contrast, Valadez-González et al. (2001) reported *U. halleri* fed primarily on stomatopods, crustaceans, and to a lesser extent on polychaetes and fishes. The samples sizes for the stomach content data of *U. jamaicensis* are small and caution should be taken in their interpretation. Nor are we aware of any studies on ontogenetic shifts in diet in these animals. Nonetheless, the differences among the diets in these studies lead us to conclude that at least these two urotrygonids are generalists and likely opportunistic feeders.

Information on the predators of *U. jamaicensis* is sparse. Nassau grouper, *Epinephelus striatus,* and lemon sharks, *Negaprion brevirostris*, are mentioned in the literature (Silva Lee 1974; Cortes and Gruber 1990) and they have been found among the gut contents of other fishes (i.e., black grouper, *Mycteroperca bonaci*; B. Buskirk, personal communication). *U. jamaicensis* has been observed in the stomach contents of a *Centrophorus* sp. in deep waters off the northern coast of Jamaica. This is intriguing as *Centrophorus* sp. were only collected at depths of 450 m or greater (J. Morrissey personal communication). Although there are apparently no predators specializing on yellow stingrays we suspect they are commonly taken by generalist fish, and possibly bird, piscivores (Banks and Bostic 1966).

Age and Growth

Sulikowski (1996) did some preliminary age and growth determinations on *U. jamaicensis*. He looked at alizarin red stained vertebral centra of 20 yellow stingrays and examined opaque and translucent bands of the *corpus calcareum*. He found a linear relationship exists between centrum diameter and total length making this structure useful for age estimation. Using marginal increment analysis and the von Bertalanffy growth equation he concluded the animals are relatively short-lived, 7-8 years maximum, and achieve most (80%) of their annual growth during late spring through summer months. A study currently underway with a larger sample size (100+ animals) likewise draws the conclusion of a maximum lifespan of 7-8 years (B. Buskirk unpublished). A similar conclusion of an 8-year lifespan was reached for congener *U. halleri* (Babel 1967); but other studies on that animal assessed the maximum age at 13-14 years (Hale et al. 2006; Hale and Lowe 2008). Not surprisingly for a short-lived animal, *U. jamaicensis* grow rapidly during the first year of life. Approximately 150 mm TL at birth, they attain 200 mm TL by the second year (Yanez-Arancibia and Amezcua-Linares 1979; Sulikowski 1996; Basten 2007). Yanez-Arancibia and Amezcua-Linares (1979) have estimated *U. jamaicensis* is mature at 200 mm TL. However, LaMarca (1964) found the smallest male with masses of spermatozoa in the intra-septal spaces of the seminal vesicle was 137 mm disk width (DW) (about 265 mm TL), and it was unclear if males were reproductively active until slightly larger. In females, size at maturity still needs to be confirmed by histological analysis of the reproductive tract (e.g. developed trophonemata) as maternal indices are better estimates of the female reproductive state than maturity determined solely by ovarian development (Walker 2005). For example, in our studies the smallest female observed in maternal condition measured 158 mm DW with a

single 158 mm TL male embryo (Fahy et al. 2007). This is comparable in size to the smallest gravid female (149 mm DW) of *U. halleri* in Babel's (1967) study.

Courtship

There is apparently little written about courtship behavior in *U. jamaicensis*. Issues of attraction, rejection, or acceptance are obviously dealt with by this species, but it is unclear how. We have observed females fleeing from males, as well as ganging behavior, where multiple males attempt to mate with a single female. It is also apparent that there is some attractant, likely pheromonal, emitted by the females, as males will converge from a distance on a female. Equally likely, electroreception is used for short-distance orientation as it is in *U. halleri* (Sisneros and Tricas 2002). We assume the mating drive in males is strong, as we have noted, on several occasions, a recently captured male attempting to copulate with a female while both were contained in a small mesh dive bag carried by a diver. However, other than what can be inferred from these anecdotal observations, nothing is known about the proximal physiological mechanisms involved in copulation.

Copulatory Behavior

The copulatory behavior of *U. jamaicensis* is typical of most stingrays (McCourt and Kerstitch 1980; Dugger 1987; Young 1993; Nordell 1994; Chapman et al. 2003). Male individuals orally grasp a female's pectoral margin and rotate to a ventrum to ventrum position and insert the ipsilateral clasper into the female's cloaca. The male bite and hold is forceful and mating wounds and scars are common on the pectoral margin of females. Multiple males are often seen crowding mated pairs or exhibiting following behavior (Dugger 1987; Young 1993; authors unpublished), suggestive of the polyandrous breeding strategy exhibited by *D. americana* (DeLoach 1999; Chapman et al. 2003). Young (1993) reported copulation is brief (~4 min) with similar reports for congeners *U. concentricus* (McCourt and Kerstitch 1980) and *U. halleri* (Nordell 1994). Female *U. jamaicensis* have also been reported to simultaneously bite males during copulation (Dugger 1987); however, due to Dugger's (1987) initial misidentification of the sexes this behavior requires additional confirmation. Furthermore, the female's need to bite and to effectively maintain a grasp during coitus is questionable due to sex-specific tooth morphology. We found no reports of studies examining the possible effects of male biting on female reproductive behavior (i.e., enhancing receptivity) or physiology (i.e., stimulating reproductive processes). Because biting appears to invariably be associated with copulation, this may be a fertile area for research.

Pupping and Nursery Habitat

Specific requirements of the nursery habitat of *U. jamaicensis* are unclear. Nearshore pupping is apparent, but the cryptic nature and small size of neonates has made for few field observations. In the Terminos Lagoon (Campeche, Mexico), *U. jamaicensis* is considered rare throughout most of the year; however increased prevalence of gestating females and neonates during the rainy season (May–October) in seagrass has suggested the importance of this habitat as a primary pupping area (Yañez-Arancibia and Amezcua-Linares 1979). Parturition has also been observed in seagrass beds in the Bahamas (Piercy et al. 2006b). Interestingly, small aggregations of predominantly gestating females have also been observed beneath mangrove trees (apparently only those occupied by nesting egrets) during summer months in Jamaica (J. Morrissey personal communication). In Broward County, Florida, where there is minimal seagrass or mangroves at the shoreline, pregnant females and neonates of *U. jamaicensis* are found on hardbottom habitat. Together, these observations appear to indicate some aspect of shallow nearshore habitat in general, rather than a specific habitat type (e.g., seagrass, mangrove, hardbottom) is required for pupping. However, more data are required to conclusively determine the existence of a nursery area for this animal.

Anthropogenic Interactions

There is little literature dealing directly with human/*U. jamaicensis* interaction.

Because of the stingray's abundance in some inshore areas there are multiple reports of *U. jamaicensis* injuring bathers and fishers (Bigelow and Schroeder 1953). Possibly in some areas (e.g., Broward County, Florida; Jamaica) the high abundance of *U. jamaicensis* is related to a paucity of large benthic piscivores due to overfishing (Ferro et al. 2005), this contention receives a measure of support from the fact that the dramatic decrease in *U. jamaicensis* in the Florida Keys over a 14 year span can be correlated to an increase in population of Goliath grouper, *Epinephelus itajara*, (Ward-Paige et al. 2010). However, other possible anthropogenic factors cannot be discounted for changes in *U. jamaicensis* abundances e.g., habitat destruction, harvest (Ward-Paige et al. 2010).

There is one study that used *U. jamaicensis* as the experimental animal for bioassay of Tributyltin oxide (TBTO). TBTO is the main constituent of tin-based antifouling marine paint used on the hulls of ships to prevent the growth of fouling organisms. This study investigated the toxicity and accumulation of tin in the gill tissue of *U. jamaicensis* after acute exposure to TBTO. Results indicated *U. jamaicensis* are hypersensitive to TBTO exposure. The gills showed a distorted, swollen epithelium with exfoliation following acute exposure to as little as 0.05 mg/L TBTO and tissues of treated animals contained a significantly increased tin concentration as compared to controls. There was also evidence of induction of the stress proteins Hsp 70 and HO1. 4-Hydroxynonenol (4HNE) and adduct formation evidence that membrane degradation was a result of lipid peroxidation (Dwivedi and Trombetta 2006). Because *U. jamaicensis* appears to be relatively sedentary, not migratory, and found abundantly in some near-shore environments, it may prove to be a likely candidate to examine biological uptake of onshore generated pollutants.

Captive breeding of *U. jamaicensis* has occurred, but with limited survival of offspring due to unsuccessful parturition and high rates of neonate mortality. Several procedures have been incorporated to manually and pharmacologically induce parturition (Stamper et al. 1998; Hanna 2004; Harms et al. 2004). The novel use of radioopaque concretions (calcium apatite) stored within the fetal spiral valve intestine has assisted in staging developing embryos (Harms et al. 2004). These radiographic features are prominent during early stages and diminished in term stage fetuses.

Tonic immobility (TI) can be induced in many animals, including elasmobranchs, and can be used as an aid in some sampling procedures (e.g., body measurements, taking blood or tissue samples). There is one report on tonic immobility in elasmobranchs that included a preliminary examination of urotrygonids. The author was able to induce tonic immobility in a single male specimen of *U. halleri* by placing the animal in a horizontal inverted position, but was not successful in inducing TI in a female *U. jamaicensis* (Henningsen 1994). However, as the author pointed out, this is too small of a sample size to draw firm conclusions and more research is required.

Conclusion

Urobatis jamaicensis is a small batoid with a widespread range within the greater Caribbean area; it is relatively abundant in patchy distribution and is relatively easy to maintain in captivity. These characteristics, among others, make it a good research subject. When the problems of captive breeding are resolved, this animal, with its rapid breeding cycle, should provide an excellent model in efforts to understand elasmobranch functional morphology and behavior.

The studies cited here offer some insight into the natural history, ecology, nervous/sensory system, respiration, reproduction, vasculature, osmoregulation, and digestion of *U. jamaicensis*. We were able to find little, if any, literature on a number of organ systems in *U. jamaicensis* (i.e., skeletal, muscular, endocrine, and immune systems) and for these we refer the reader to the general, or system-specific, literature on batoids and elasmobranchs.

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