

**PRELIMINARY OBSERVATIONS ON THE REPRODUCTIVE CYCLE AND  
UTERINE FECUNDITY OF THE YELLOW STINGRAY, *UROBATIS JAMAICENSIS*  
(ELASMOBRANCHII: MYLIOBATIFORMES: UROLOPHIDAE)  
IN SOUTHEAST FLORIDA, U.S.A.**

**Daniel P. Fahy\* and Richard E. Spieler**

*Oceanographic Center, Nova Southeastern University and Guy Harvey Research Institute 8000 North Ocean Drive,  
Dania Beach, Florida, 33004, U.S.A.  
Email: fahyd@nova.edu  
(\*Corresponding Author)*

**William C. Hamlett**

*Anatomy & Cell Biology Department, Indiana University School of Medicine,  
Notre Dame, Indiana, 46556, U.S.A.*

**ABSTRACT.** – The yellow stingray, *Urobatis jamaicensis* is the most common elasmobranch observed among the coral reefs and associated habitats of Southeast Florida, U.S.A. In coastal waters off Broward County, Florida, gravid females were observed throughout the year. *Urobatis jamaicensis* is an aplacental viviparous species with evidence of a short gestation period (five to six months). Vitellogenesis occurs concurrently with gestation, with the females having both term fetuses and mature ova simultaneously. It is likely that the females have a bi-annual reproductive cycle where each female is capable of producing two broods annually. The ovulation period in the spring/summer reproductive cycle ranged from January to April (peaks in late February/early March) and parturition occurred between June to September (peaks in late July/early August). The autumn/winter reproductive cycle overlaps with the spring/summer cycle, with ovulation ranging between August to September and parturition from November to January. Two functional uteri were observed with a maximum uterine fecundity of seven young. Brood size increased with maternal size and was significantly higher during the spring/summer reproductive cycle ( $\bar{X} = 3.1 \pm 0.179$  SEM, range 1 - 7) in comparison to the autumn/winter cycle ( $\bar{X} = 1.4 \pm 0.110$  SEM, range 1 - 3). Preliminary wet weight determinations indicated that *U. jamaicensis* is highly matrotrophic with an approximate 4,600% increase in weight from mature ova to term fetuses.

**KEY WORDS.** – Elasmobranch, yellow stingray, uterine fecundity, reproductive cycle.

---

## INTRODUCTION

The family Urolophidae (round stingrays and stingarees), consists of 41 recognized species and four distinct genera (*Urobatis*, *Urolophus*, *Urotrygon* and *Trygonoptera*) that occur worldwide (Compagno, 1998; López & Bussing, 1998; Séret & Last, 2003). Some researchers have suggested a division of the family with the amphi-American species (*Urobatis* and *Urotrygon*) being moved to a new family, Urotrygonidae. This may be premature as the phylogeny within the order of Myliobatiformes has not been fully resolved (McEachran et al., 1996; McEachran & de Carvahlo, 2002; Dunn et al., 2003; de Carvahlo et al., 2004; McEachran & Aschliman, 2004). Thus, for the purpose of this study, we will hold to the previous classification. Detailed information of the reproductive cycle of urolophids has been limited to the species *Urobatis halleri* (Babel, 1967), *Urolophus lobatus*

(White et al., 2001), *Urolophus paucimaculatus* (Trinnie, 2003; Trinnie et al., 2005; White & Potter, 2005), *Trygonoptera mucosa* and *T. personata* (White et al., 2002). Nonetheless, a variety of reproductive strategies have been noted within the family: annual vs. bi-annual cycles, gestation periods ranging from 3 to 12 months, separate breeding populations with an asynchronous ovulatory cycle and embryonic diapause (Babel, 1967; Edwards 1980; White et al., 2001, 2002; Trinnie et al., 2005; White & Potter, 2005). Verification of diverse reproductive strategies among genera could provide additional support for a taxonomic division of the family.

*Urobatis jamaicensis* has an extensive range, occurring in the Western Central Atlantic Ocean from Florida to Brazil and is widespread throughout the Gulf of Mexico and the Caribbean Sea (Bigelow & Schroeder, 1953; Robins et al.,

1986; Böhlke & Chaplin, 1993). It is the only urolophid to inhabit the coastal waters of Southeast Florida (U.S.A.) where they are the most common elasmobranch observed among the region's coral reefs and associated habitats (Fahy, 2004). Despite a wide distribution and frequent occurrence, the life history of *U. jamaicensis* remains poorly understood. Research efforts addressing reproduction in *U. jamaicensis* have been restricted to several anatomical studies and limited field observations.

LaMarca (1961, 1964) described the reproductive anatomy of *U. jamaicensis* with additional comments on the functionality of the embryonic spiracular flap (LaMarca, 1963). More recently, several histological and ultrastructural studies on specific reproductive structures have been conducted (Jezoir & Hamlett, 1994; Hamlett & Hysell, 1998; Hamlett et al., 1996, 1999). Young (1993) observed two mating events in Belize during the months of February and March and suggested that the peak reproductive activity occurs during this period. Yañez-Arancibia & Amezcua-Linares (1979) observed gravid females and neonates during the rainy season (May to September) and suggested that the Terminos Lagoon in Mexico serves as a nursery ground. However, Fahy (2004) noted gravid females during all months of the year from field observations in Southeast Florida. Thus, there is no conclusive evidence of its reproductive cycle to date. This paper serves to document the preliminary findings

of a larger on-going study on the reproductive cycle of *U. jamaicensis*.

**MATERIALS AND METHODS**

**Collection and study location.** – Female stingrays were collected with handnets using SCUBA apparatus in coastal waters of Broward County, Florida from February 2003 to April 2005 with at least one gravid female collected in every month of the year. The stingrays were maintained in tanks or holding pens for periods ranging from 2 to 48 hours until laboratory processing. Stingrays were euthanized in a saltwater solution of MS-222 (Finquel, Redmond, Washington). They were then weighed and measured and the entire reproductive tract of each individual was removed. A pair of hemostats was secured to the distal ends of both functional uteri (proximal to the common vagina) to avoid premature abortion of the offspring. Uterine contents were carefully removed and the reproductive tract was stored in 10% formalin for subsequent histological analyses.

**Reproductive biology.** – The stingrays were assigned to one of the following reproductive categories, based on uterine contents and embryonic stage of development: 1) ovarian (mature, non-gestating individuals that contained only ovarian oocytes); 2) uterine (individuals that had recently ovulated

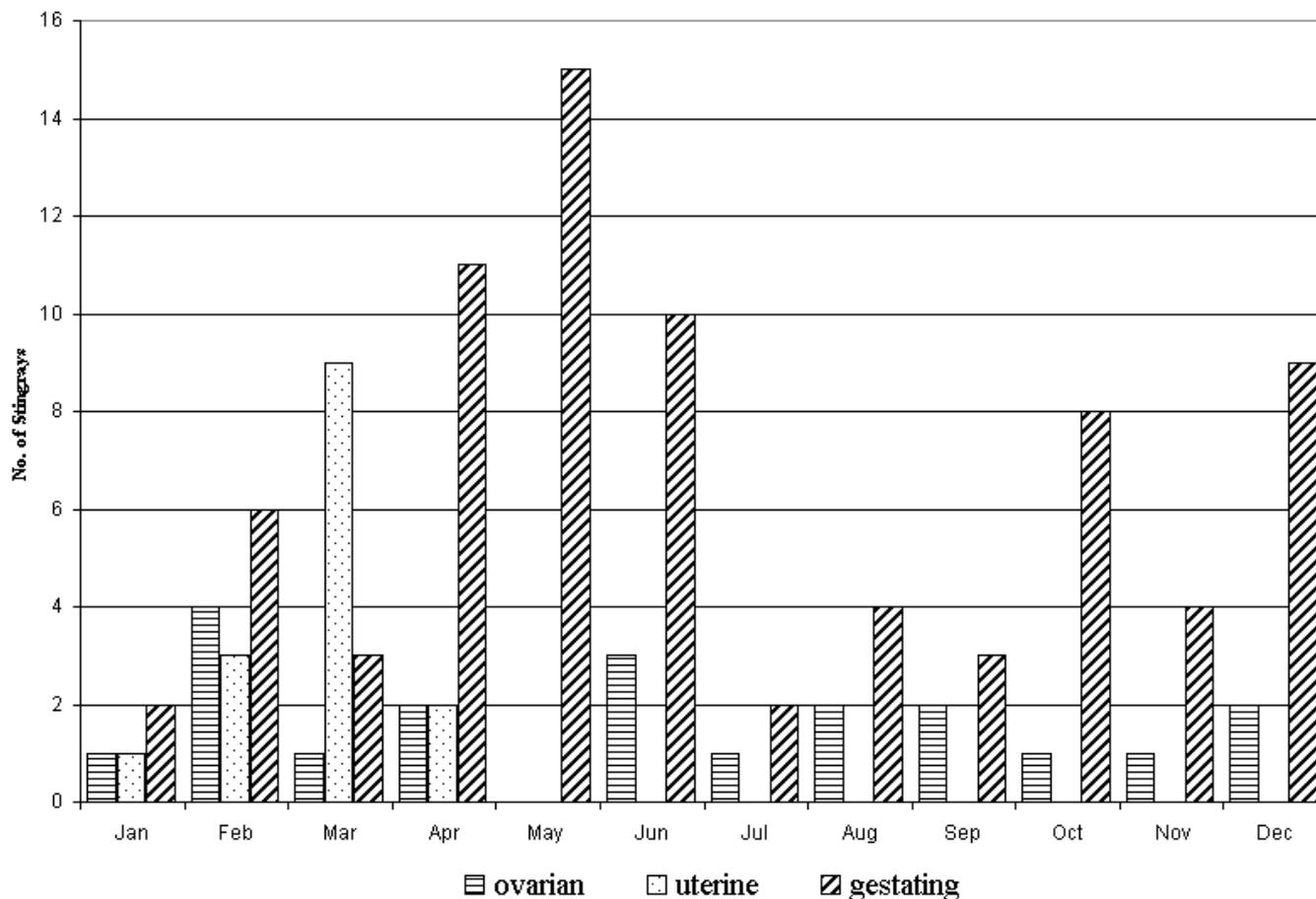


Fig. 1. Monthly observations of female *Urobatis jamaicensis* reproductive cycle indices (for females collected from Feb 2003 to Apr 2005 and pooled by corresponding months). Ovarian = non-gestating individuals with ovarian oocytes; uterine = individuals with uterine ova present with no sign of embryonic development; gestating = pregnant individuals with embryos in various stages of development.

with the uterine ova showing no signs of embryonic development from gross examination) and 3) gestating (individuals that possessed developing embryos in either uterus).

Further classification of embryonic stage of development was determined from average total length (TL, mm) of the brood: 1) early stage (< 50 mm); 2) mid-stage (50 - 99 mm) and 3) late stage ( $\geq$  100 mm) size classes. Specimens collected during corresponding months of different years were pooled together. Linear regression analyses were conducted to compare variation in brood size (combined left and right uterine contents) with increasing maternal size measured in disk width (DW, mm). Seasonal comparison of brood size was conducted in the same manner to identify variations in uterine fecundity. The Mann-Whitney *U*-test (MW) was used to compare total uterine fecundity between seasons and additional comparisons were made between left and right uterine functionality. The seasonal reproductive cycle (spring/summer vs. autumn/winter) was determined from female reproductive condition (ovarian, uterine or gestating) and embryonic stage of development.

**RESULTS**

**Reproductive biology.** – Both uteri are functional (although the left side appears dominant in usage), which is a feature

common to all amphi-American urolophids studied to date (Babel, 1967; Almeida et al., 2000). Ova production was primarily from the left ovary with only two cases of females (both  $\geq$  250 mm DW) with enlarged oocytes (> 10 mm) in the right ovary. There are two ostia that correspond to individual oviducts. However, the structure is fused together ventrally over the oesophagus into a common ostium. The mode of reproduction is aplacental viviparity. Matrotrophic input appears to initiate early in development as copious amounts of uterine fluid (histotroph) was present throughout gestation and external yolk sac contents persist into late stage development. Preliminary wet weight determinations demonstrated a 4,600% increase in weight from uterine ova to term fetuses (~ 150 mm TL), which establishes a high degree of matrotrophy.

**Reproductive cycle.** – Two overlapping periods of embryonic development were observed, suggesting a bi-annual reproductive cycle (Fig. 1). The two peaks observed in the late stage embryos/term fetuses were separated by six months (Fig. 2). Vitellogenesis proceeded concurrently with gestation, as evidenced by continued oocyte growth and observations of females simultaneously carrying mature oocytes and term fetuses. The only period when uterine ova were observed was during the late winter/early spring months (January to April) with a peak during February and March. However, the four-month range in uterine ova suggests a protracted period of ovulation occurs, at least during the initial reproductive cycle.

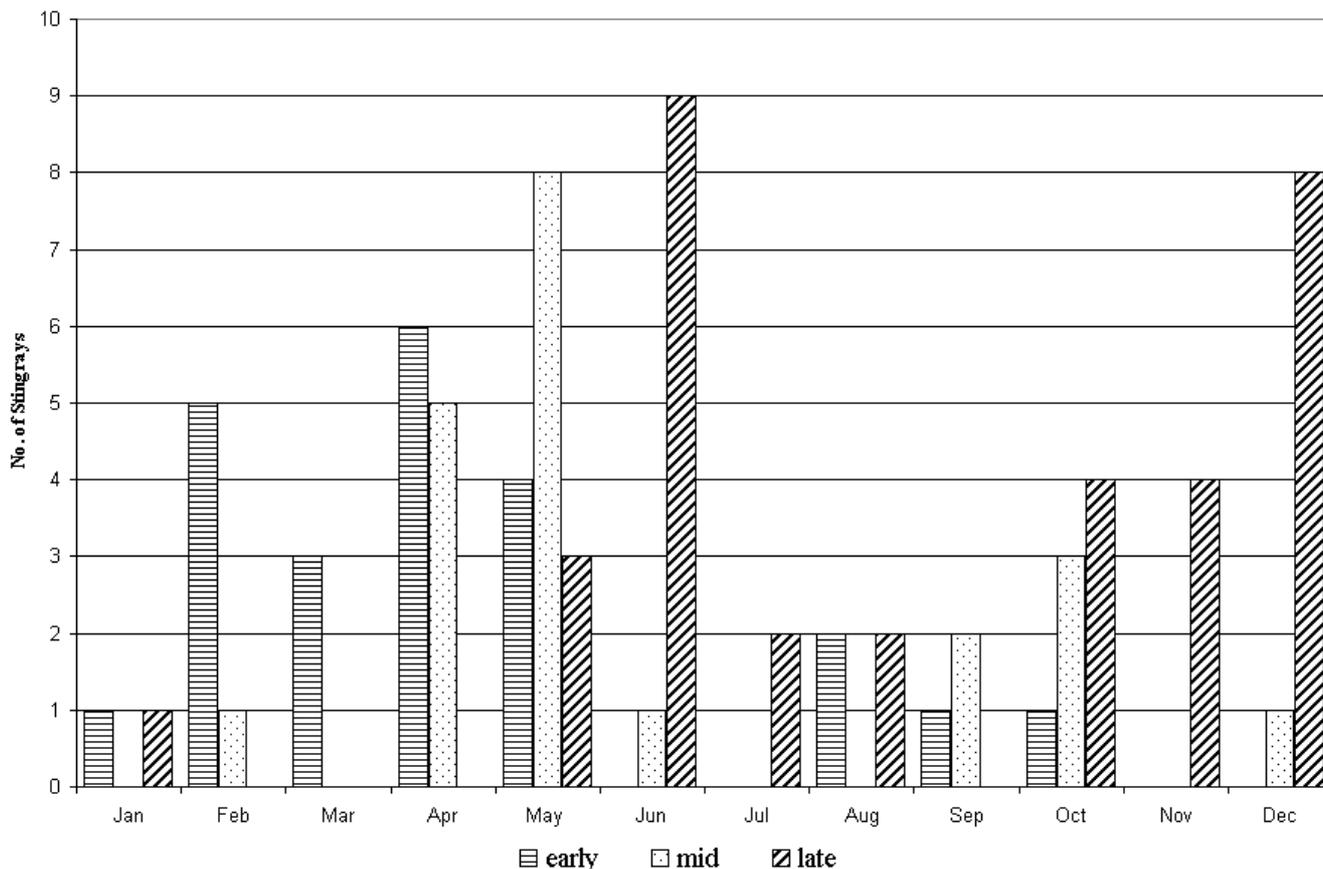


Fig. 2. Stage of gestation for gravid female *Urobatis jamaicensis* (collected from Feb 2003 to Apr 2005 and pooled by corresponding months) expressed in terms of embryonic stage of development indices as reported in total length measurements. Early = 0 - 50 mm; mid = 50 - 99 mm; late =  $\geq$  100 mm.

The onset of the initial reproductive cycle (spring/summer) corresponded with the termination of the second cycle (autumn/winter). Thus, January was a transitional month, with observations of recently post-parturient females or gravid females either containing uterine ova, early stage embryos or late/term stage fetuses. Throughout the month of February, there was a high level of post-parturient/pre-ovulatory females with a number of post-ovulatory and gravid females in early stages of development. In March and April, there were increasing numbers of gravid females observed and the embryos were mostly in early to mid-stage development. By May, all specimens were gestating, ranging from early through late stages of development. The month of June corresponded with the onset of parturition. However, nearly all of the specimens were still in the mid- to late stages of gestation. In July, most of the specimens were either in the late stage of gestation or in near-term condition.

August marked the onset of the second cycle and an apparent second transitional period. The August transition period exhibited both early stage embryos from the second cycle and remaining late stage females from the initial cycle with parturition ranging from June through early September (peaks in late July/early August). September characterized the termination of the initial cycle and all the gravid specimens

observed were in early to mid-stage development. In October, females were observed in all stages of development, similar to the midpoint of the initial cycle (i.e. May). November and December were characterized by increased numbers of females in the latter stages of development. In January, the onset of the initial cycle begins with further overlap between both cycles into February.

**Uterine fecundity.** – Brood size for the first cycle ( $\bar{X} = 3.1 \pm 0.179$  SEM, range 1 - 7) was significantly larger (MW,  $p < 0.005$ ) than the second cycle ( $\bar{X} = 1.4 \pm 0.110$  SEM, range 1 - 3). However, size at parturition appears to be slightly larger during the autumn/winter cycle ( $\bar{X} = 15.0 \pm 0.277$  SEM) than the spring/summer cycle ( $\bar{X} = 14.5 \pm 0.142$  SEM). The observed maternal DW measurements were grouped into 25 mm size classes for further seasonal comparisons of brood size. A significant difference was detected for both the 175 - 200 mm and the 200 - 225 mm size classes (MW,  $p < 0.005$ ), supporting observed elevated fecundity during the first cycle (Fig. 3). However, smaller size classes exhibited lower fecundity regardless of season. No comparisons were possible for the largest size class (225 - 250 mm DW), due to the lack of observations during the second reproductive cycle.

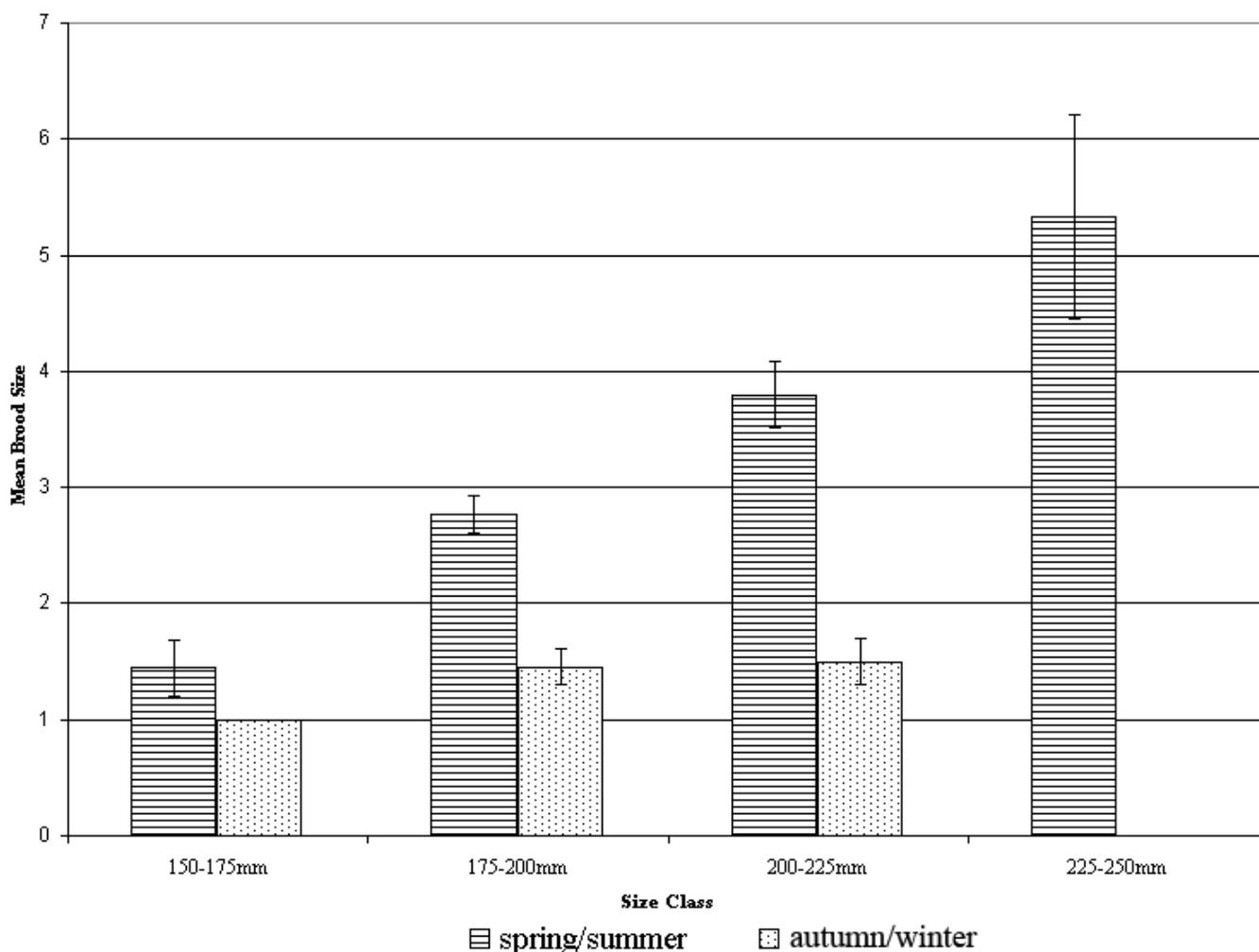


Fig. 3. Seasonal comparison of gravid female *Urobatris jamaicensis* brood size (combined uterine contents) for spring/summer (Mar - Aug) vs. autumn/winter (Sep - Feb) reproductive cycles.

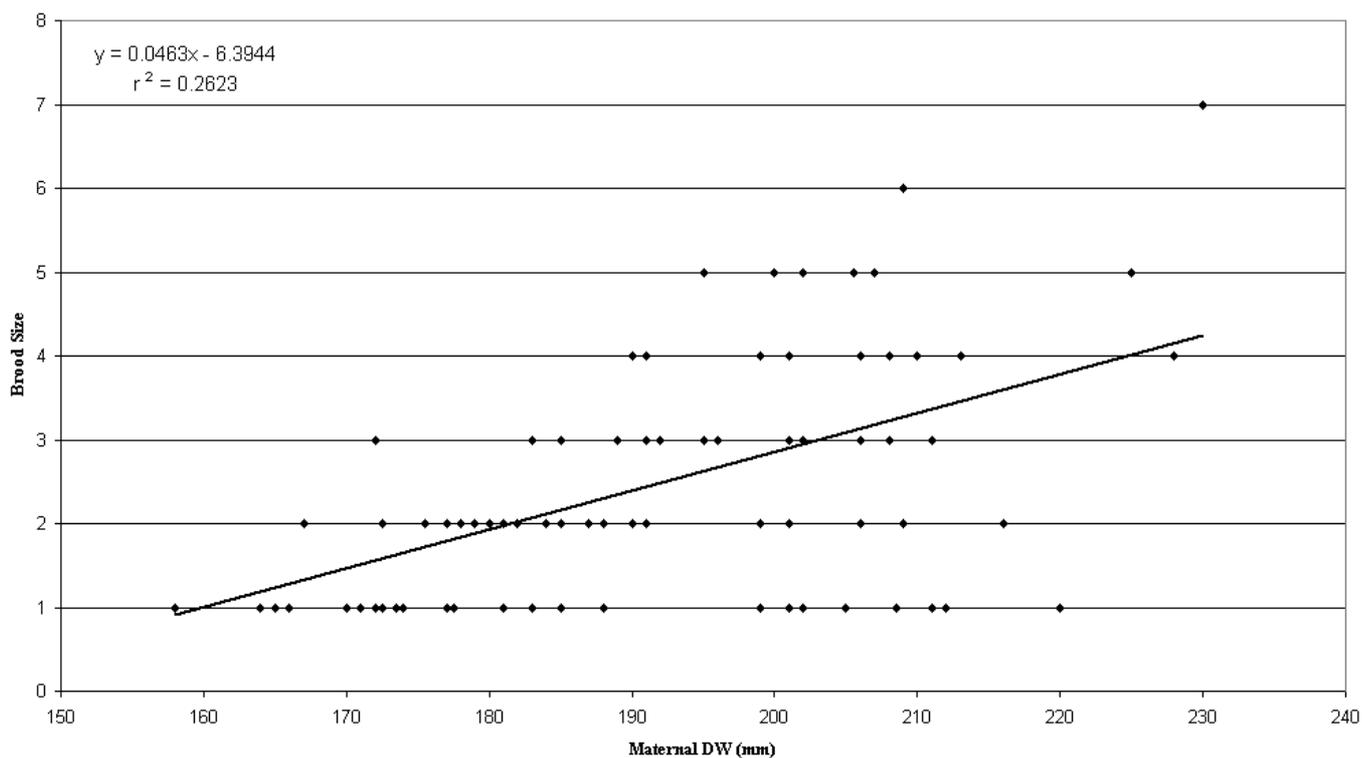


Fig. 4. Linear regression of fecundity (brood size) vs. increasing female size (maternal DW) for total combined observations of gravid *Urobatis jamaicensis* females.

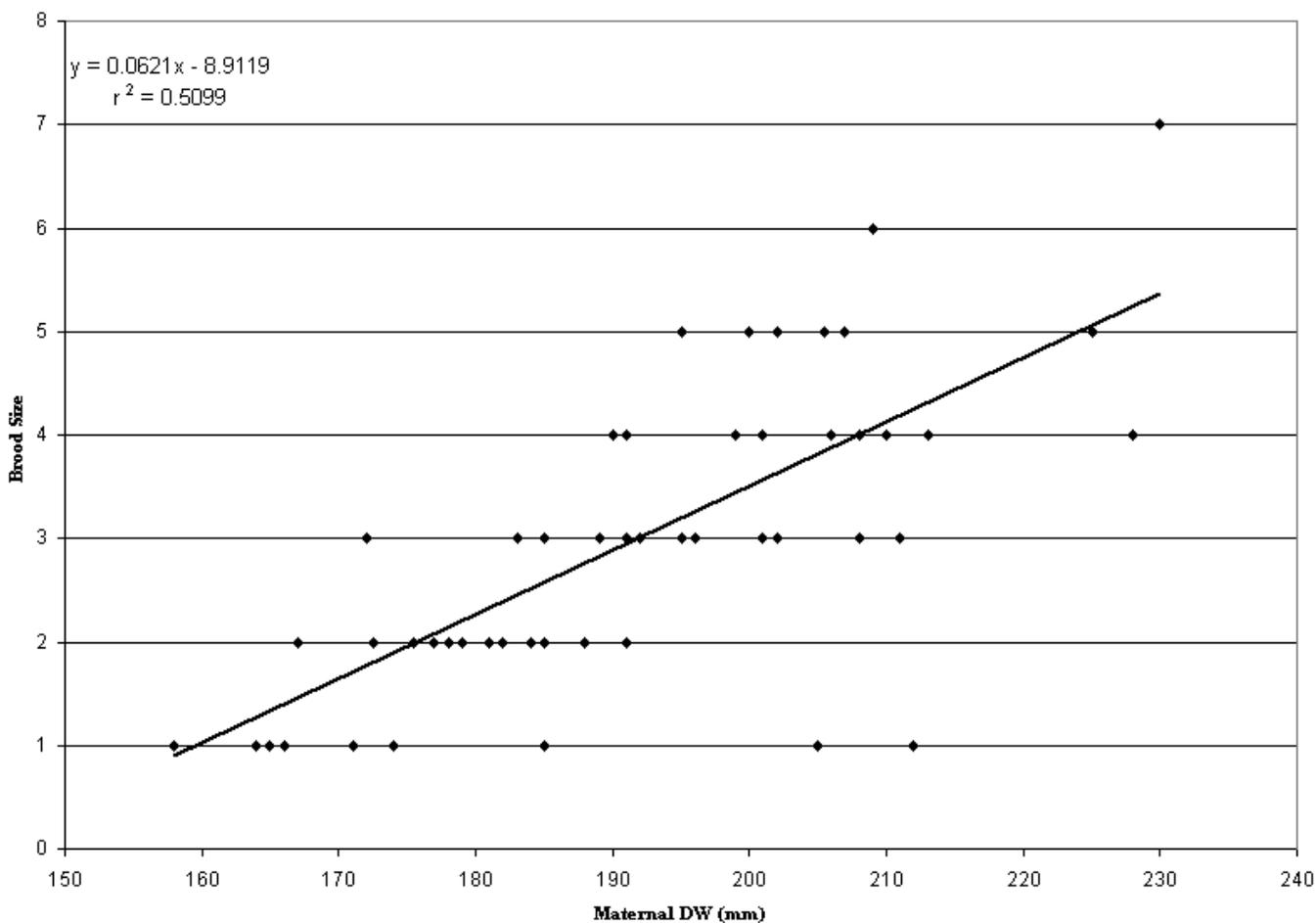


Fig. 5. Linear regression of fecundity (brood size) vs. increasing female size (maternal DW) for gravid *Urobatis jamaicensis* during the spring/summer reproductive cycle (Mar - Aug).

A positive linear relationship was observed between female DW and brood size from total combined observations ( $p < 0.005$ ,  $r^2 = 0.26$ ) (Fig. 4). However, the low  $r^2$ -value indicates a high level of variability in fecundity among total females. Division of total observations into the separate identified reproductive cycles (spring/summer and autumn/winter) demonstrated distinct seasonal differences in fecundity. During the spring/summer reproductive cycle, a significant linear relationship was observed ( $p < 0.005$ ,  $r^2 = 0.51$ ) (Fig. 5). Whereas the autumn/winter cycle had lower fecundity, with no indication of a significant relationship between brood size and maternal size ( $p = 0.132$ ,  $r^2 = 0.10$ ) (Fig. 6). Therefore, peak reproductive activity apparently occurs during the spring/summer cycle and conversely, the autumn/winter cycle is associated with lower fecundity. There was a difference in reproductive tract functionality regardless of season. The left uterus was used significantly more often and contained higher contents (uterine ova or developing embryos) than the right uterus (MW,  $p < 0.005$ ).

### DISCUSSION

Although other cycles may be inferred, simultaneous observations of *U. jamaicensis* with both term fetuses and mature ova indicates the likelihood of a bi-annual

reproductive cycle, with females capable of producing two broods per year. Estimated gestation rates from peak ovulation in late February/early March to a July/August peak in parturition during the initial cycle, suggest embryonic development to term requires five to six months. Previous suggestions of a three-month gestation rate (Jezoir & Hamlett, 1994) were based on reports for the congener, *U. halleri* in California (Babel, 1967). In addition to a three-month gestation, Babel (1967) reported an annual cycle for *U. halleri* with two breeding populations of females displaying an asynchronous ovulatory cycle, spaced six months apart. The majority of the population was reported to ovulate in June with a smaller peak in December. However, the author did not report the ovarian status of post-parturient females or differences in brood size between populations. Therefore, a distinction between the two ovulatory cycles of *U. halleri*, indicating separate breeding populations, requires further examination.

Australian urolophids have an annual cycle with gestation rates of 10 to 12 months (White et al., 2001, 2002; Trinnie et al., 2005; White & Potter, 2005). Although a similar pattern in development cannot be ruled out for *U. jamaicensis*, the two peak periods in parturition (July/August and December/January), concomitant with observations of early stage embryos support a shorter gestation period (five to six months)

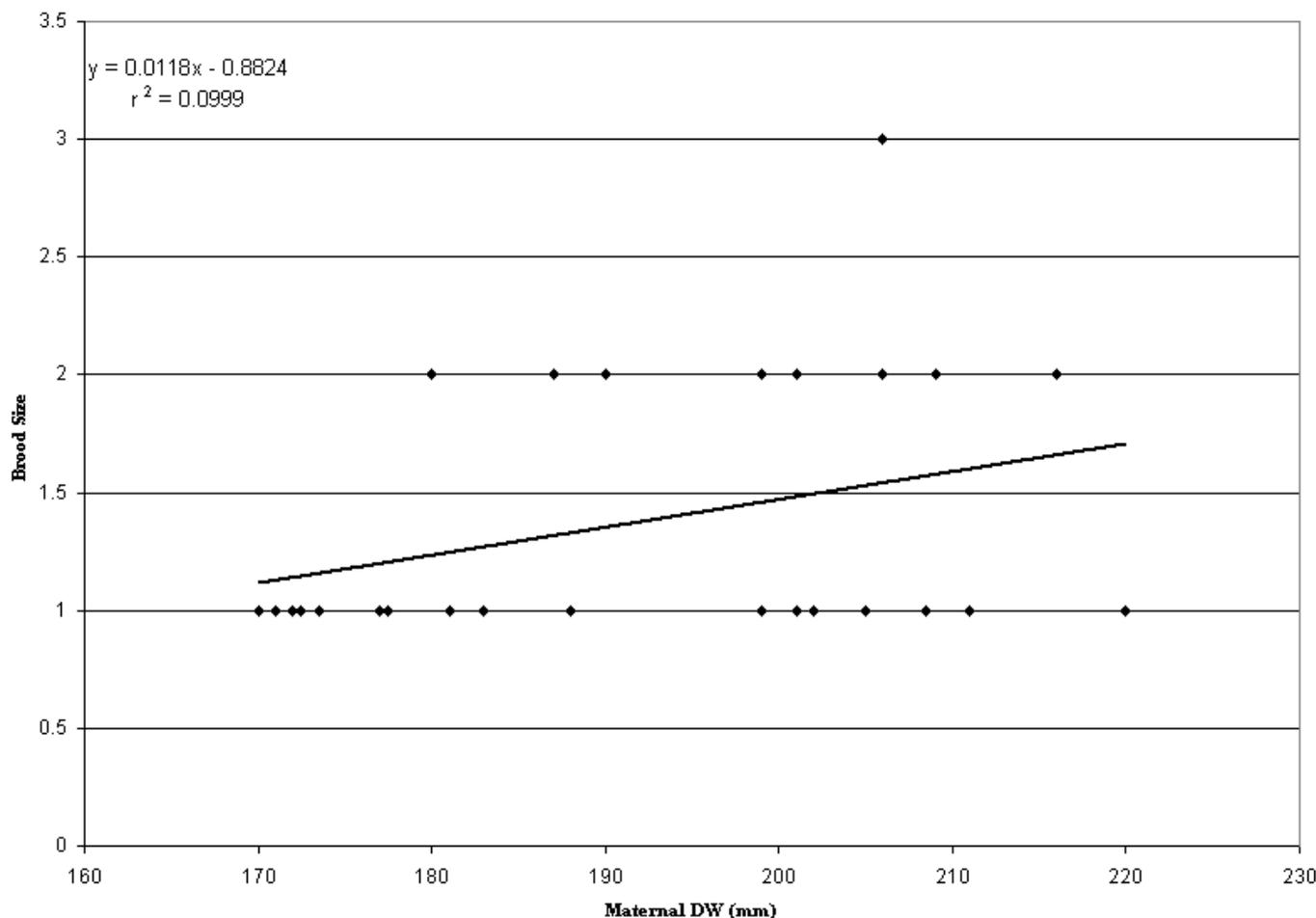


Fig. 6. Linear regression of fecundity (brood size) vs. increasing female size (maternal DW) for gravid *Urobatis jamaicensis* during the autumn/winter reproductive cycle (Sep - Feb).

and a bi-annual cycle. Gestation rates among stingrays are generally considered to be short in duration (two to four months) (Hamlett & Koob, 1998), even though insufficient data is available to fully establish the reproductive cycle for most species. Captive studies on *Potamotrygon circularis* and *P. motoro* have observed up to three cycles in a year, spaced three months apart (Thorson et al., 1983). *Dasyatis americana* exhibited two cycles per year in captivity with gestation rates varying between 4.5 to 7.5 months (Henningsen, 2000). There were several unsubstantiated reports of some stingray species with a potential bi-annual cycle and a five to six months gestation rate, namely, *Gymnura altavela* (Daiber & Booth, 1960), *Dasyatis centroura* (Struhsaker, 1969), *Dasyatis imbricata* (= *Himantura imbricata*) (Devadoss, 1978) and *Rhinoptera bonasus* (Smith & Merriner, 1986).

Seasonal variation in uterine fecundity displayed by *U. jamaicensis* provides further support for a bi-annual cycle. Observations from the spring/summer cycle displayed a positive linear relationship between fecundity and maternal size, whereas the autumn/winter cycle was associated with lower fecundity, regardless of maternal size. Possibly, the increased brood size earlier in the year correlates parturition with more favourable conditions when water temperatures are elevated during the summer months. Simpfendorfer (1992) suggested that elevated water temperatures during summer months in Australia increased neonate growth rates of *Rhizoprionodon taylori* (a species that is relatively small in size at parturition).

The potential for an annual cycle with a longer gestation rate cannot be ruled out for *U. jamaicensis* at this time. Retention of only a portion of the original brood to term could result in reduced fecundity late in gestation as reported for *Urolophus lobatus* in Australia (White et al., 2001). However, observations of *Urobatis jamaicensis* females with embryos in early stages of development (1 - 2 mm TL) from August to October, indicates recent ovulation and the onset of a second cycle, as opposed to premature loss or birth of only a portion of the brood. Likewise, significant differences in fecundity between seasons for *U. jamaicensis* would not be adequately explained by an asynchronous ovulatory cycle. However, ova production and uterine fecundity during the onset of the second reproductive cycle still requires further sampling for verification of the second ovulatory cycle.

Urolophids in Western Australia produce small broods of one to two individuals with a large mean size at parturition: *Urolophus lobatus* (105 mm DW), *Urolophus paucimaculatus* (126 mm DW), *Trygonoptera mucosa* (128 mm DW) and *T. personata* (113 mm DW) (White et al., 2001, 2002; White & Potter, 2005). However, there are reports of higher fecundity in *Urolophus paucimaculatus* from Southeastern Australia (a maximum of six individuals) with smaller offspring (~ 65 - 80 mm DW) within the same 10 to 12 months gestation period (Trinnie et al., 2005). The average size for *Urobatis jamaicensis* offspring was approximately 150 mm TL (~ 80 mm DW), which is considerably smaller than most reports for Australian species. However, the elevated fecundity during the spring/summer cycle, combined

with additional offspring from the autumn/winter cycle establishes a larger reproductive potential. This may offset the risk of predation associated with a smaller size at parturition.

Seasonal variations in brood size observed for *U. jamaicensis* corresponded with slightly larger-sized offspring during the less fecund winter parturition period. The difference in fecundity and size of offspring between seasons (increased fecundity in spring/summer, increased size in autumn/winter) may be explained, in part, by the differential investment of resources by the female into offspring relative to survivorship potential. Possibly, maximizing the production of small young is an appropriate strategy to increase overall brood survivorship in warm temperatures when rapid growth occurs. Conversely, lower fecundity but a larger size at parturition may be the optimum strategy at lower temperatures, when growth rates are decreased. However, the degree of influence that maternal size and brood numbers has on the size of offspring at parturition also requires further investigation. Although the left uterus was dominant, there were several observations when the right uterus was solely in use (holding one to two young) or contained more young than the left side. Babel (1967) reported the right uterus develops slower in *U. halleri* and also suggested that a closer proximity of the left ostia to the ovulating ova was likely to result in greater use of the left reproductive tract. Data for *U. jamaicensis* supports these observations, as fecundity was significantly higher for the left uterine contents (uterine ova or developing embryos) during both reproductive cycles. Therefore, as the animals produce small broods, ova typically enter into the left reproductive tract first and the right tract apparently remains unused until larger broods demand the simultaneous use of both uteri.

#### ACKNOWLEDGMENTS

We express our gratitude to P. Arena, B. Buskirk, D. Bryan, E. G. Fahy, Dr. D. Gilliam and P. Quinn, for their help with the collection of specimens. We would also like to thank the two anonymous reviewers for critical comments on an earlier draft of this manuscript.

#### LITERATURE CITED

- Almeida, Z. S., J. S. Nunes & C. L. Costa, 2000. Presencia de *Urotrygon microphthalmum* (Elasmobranchii: Urolophidae) en aguas Bajas de Maranhão (Brasil) y notas sobre su biología. *Boletín de Investigaciones Marinas y Costeras*, **29**: 67-72. (In Portuguese).
- Babel, J. S., 1967. Reproduction, life history and ecology of the round stingray, *Urolophus halleri* Cooper. *Fisheries Bulletin of the California Department of Fish and Game*, **137**: 1-104.
- Bigelow, H. B. & W. C. Schroeder, 1953. Fishes of the Western North Atlantic. sawfishes, guitarfishes, skates, rays & chimaeroids. *Memoirs of the Sears Foundation for Marine Research*, **1**(2): 416-427.

- Böhlke, J. E. & C. C. G. Chaplin, 1993. *Fishes of the Bahamas & Adjacent Waters*. 2nd Edition. University of Texas Press, Texas. 771 pp.
- Compagno, L. C. V., 1998. Checklist of living elasmobranchs. In: Hamlett, W.C. (ed.), *Sharks, Skates and Rays: The Biology of Elasmobranch Fishes*. John Hopkins Press, Baltimore. Pp. 471-498.
- Daiber, F. C. & R. A. Booth, 1960. Notes on the biology of the butterfly rays, *Gymnura altavela* and *Gymnura micrura*. *Copeia*, **1960**(2): 137-139.
- de Carvahlo, M. R., J. G. Maisey & L. Grande, 2004. Freshwater stingrays of the Green River Formation of Wyoming (early Eocene), with the description of a new genus and species and an analysis of its phylogenetic relationships (Chondrichthyes: Myliobatiformes). *Bulletin of the American Museum of Natural History*, **284**: 1-136.
- Devadoss, P., 1978. Maturation and breeding habit of *Dasyatis (Amphotistius) imbricatus* (Schneider) at Porto Novo. *Indian Journal of Fisheries*, **25**: 29-34.
- Dunn, K. A., J. D. McEachran & R. L. Honeycutt, 2003. Molecular phylogenetics of myliobatiform fishes (Chondrichthyes: Myliobatiformes), with comments on the effects of missing data on parsimony and likelihood. *Molecular Phylogenetics and Evolution*, **27**: 259-270.
- Edwards, R. R. C., 1980. Aspects of the population dynamics and ecology of the white spotted stingaree, *Urolophus paucimaculatus* Dixon, in Port Phillip Bay, Victoria. *Australian Journal of Marine and Freshwater Research*, **31**: 459-467.
- Fahy, D. P., 2004. Diel activity patterns, space utilization, seasonal distribution and population structure of the yellow stingray, *Urobatis jamaicensis* (Cuvier, 1817) in South Florida with comments on reproduction. MSc Thesis, Nova Southeastern University Oceanographic Center, Florida, 120 pp.
- Hamlett, W. C. & M. K. Hysell, 1998. Uterine specializations in elasmobranchs. *Journal of Experimental Zoology*, **282**: 438-459.
- Hamlett, W. C. & T. C. Koob, 1998. The female reproductive system. In: Hamlett, W.C. (ed.), *Sharks, Skates and Rays: The Biology of Elasmobranch Fishes*. John Hopkins Press, Baltimore. Pp. 398-443.
- Hamlett, W. C., D. P. Knight, M. Jezoir, K. Kamm & K. Mitchell, 1996. Ultrastructure of the oviducal gland in the yellow spotted ray, *Urolophus jamaicensis*. Summer Meeting of the Anatomical Society of Great Britain and Ireland, Belfast, Northern Ireland. *Journal of Anatomy*, **188**: 224-225.
- Hamlett, W. C., M. Jezoir & R. Spieler, 1999. Ultrastructural analysis of folliculogenesis in the ovary of the yellow spotted stingray, *Urolophus jamaicensis*. *Annals of Anatomy*, **181**: 159-172.
- Henningsen, A. D., 2000. Notes on reproduction in the southern stingray, *Dasyatis americana* (Chondrichthyes: Dasyatidae), in a captive environment. *Copeia*, **2000**(3): 826-828.
- Jezoir, M. R. & W. C. Hamlett, 1994. Ultrastructure of the uterus and shell gland in the yellow spotted ray: a model for reproductive toxicology. Notre Dame Undergraduate Research Symposium, University of Notre Dame, Notre Dame, Indiana. *Notre Dame Science Quarterly*, **23**(4): 9-11.
- LaMarca, M. J., 1961. The reproductive anatomy of the round stingray, *Urolophus jamaicensis* (Cuvier). PhD Thesis, Cornell University, New York. 147 pp.
- LaMarca, M. J., 1963. The embryonic spiracular fold of the yellow stingray, *Urolophus jamaicensis*. *Copeia*, **1963**(3): 593-595.
- LaMarca, M. J., 1964. The functional anatomy of the clasper and clasper gland of the yellow stingray, *Urolophus jamaicensis* (Cuvier). *Journal of Morphology*, **114**: 303-324.
- López, M. I. & W. A. Bussing, 1998. *Urotrygon cimar*, a new eastern Pacific stingray (Pisces: Urolophidae). *Revista Biologica Tropica*, **46**(6): 271-277.
- McEachran, J. D., K. A. Dunn & T. Miyake, 1996. Interrelationships of the batoid fishes (Chondrichthyes: Batoidea). In: Stiagny, M. L. J., L. R. Parenti & G. D. Johnson (eds.) *Interrelationships of Fishes*. Academic Press, California. Pp. 63-84.
- McEachran, J. D. & M. R. de Carvahlo, 2002. Batoid Fishes. In: Carpenter, K. E. (ed.), *The Living Marine Resources of the Western Central Atlantic. Vol. 1: Introduction, molluscs, crustaceans, hagfishes, sharks, batoid fishes and chimaeras*. FAO Species Identification Guide for Fishery Purposes. Pp. 507-599.
- McEachran, J. D. & N. Aschliman, 2004. Phylogeny of Batoidea. In: Carrier, J. C., J. A. Musick & M.R. Heithaus (eds.), *Biology of Sharks and Their Relatives*. CRC Press, Florida. Pp. 79-113.
- Robins, C. R., G. C. Ray & J. Douglass, 1986. *Peterson Field Guide: Atlantic Coast Fishes of North America*. Houghton Mifflin Company, Boston. 42 pp.
- Séret, B. & P. Last, 2003. Description of four new stingarees of the genus *Urolophus* (Batoidea: Urolophidae) from the Coral Sea, South-West Pacific. *Cybium*, **27**(4): 307-320.
- Simpfendorfer, C. A., 1992. Reproductive strategy of the Australian sharpnose shark, *Rhizoprionodon taylori* (Elasmobranchii: Carcharhinidae), from Cleveland Bay, Northern Queensland. *Australian Journal of Marine and Freshwater Research*, **43**: 67-75.
- Smith, J. W. & J. V. Merriner, 1986. Observations on the reproductive biology of the cownose ray, *Rhinoptera bonasus*, in Chesapeake Bay. *Fishery Bulletin*, **84**(4): 871-877.
- Struhsaker, P., 1969. Observations on the biology and distribution of the thorny stingray, *Dasyatis centroura* (Pisces: Dasyatidae). *Bulletin of Marine Science*, **19**(2): 456-481.
- Thorson, T. B., J. K. Langhamer & M. I. Oetinger, 1983. Reproduction and development of the South American freshwater stingrays, *Potamotrygon circularis* and *P. motoro*. *Environmental Biology of Fishes*, **9**(1): 3-24.
- Trinnie, F. I., 2003. Demographic biology of *Urolophus paucimaculatus*, *Trygonoptera sp B*, *U. cruciatus*, *U. expansus* and *U. bucculentus* (Batoidea: Urolophidae) in South-Eastern Australia. Honours Thesis, Deakin University, Victoria. 121 pp.
- Trinnie, F. I., T. I. Walker, L. Laursen & P. Jones, 2005. Demographic biology of the sparsely-spotted stingaree *Urolophus paucimaculatus* from south eastern Australia. (Abstract) ASIH/AES Joint Meeting, Florida. Pp. 57.
- White, W. T., M. E. Platell & I. C. Potter, 2001. Relationship between reproductive biology and age composition and growth in *Urolophus lobatus* (Batoidea: Urolophidae). *Marine Biology*, **138**: 135-147.
- White, W. T., N. G. Hall & I. C. Potter, 2002. Reproductive biology and growth during pre- and postnatal life of *Trygonoptera personata* and *T. mucosa* (Batoidea: Urolophidae). *Marine Biology*, **140**: 699-712.
- White, W. T. & I. C. Potter, 2005. Reproductive biology, size and age compositions and growth of the batoid *Urolophus paucimaculatus*, including comparisons with other species of the Urolophidae. *Marine and Freshwater Research*, **56**: 101-110.

Yañez-Arancibia, A. & F. Amezcua-Linares, 1979. Ecología de *Urolophus jamaicensis* (Cuvier) en laguna de terminos un sistema estuarino del sur del golfo de mexico. (Pisces: Urolophidae). *Anales del Centro de Ciencias del Mar y Limnología Mexico*, **6**(2): 123-136. (In Spanish).

Young, R. F., 1993. Observation of the mating behavior of the yellow stingray, *Urolophus jamaicensis*. *Copeia*, **1993**(3): 879-880.