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**Abstract**—The thorny skate (*Amblyraja radiata*) is a large species of skate that is endemic to the waters of the western north Atlantic in the Gulf of Maine. Because the biomass of thorny skates has recently declined below threshold levels mandated by the Sustainable Fisheries Act, commercial harvests from this region are prohibited. We have undertaken a comprehensive study to gain insight into the life history of this skate. The present study describes and characterizes the reproductive cycle of female and male thorny skates, based on monthly samples taken off the coast of New Hampshire, from May 2001 to May 2003. Gonadosomatic index (GSI), shell gland weight, follicle size, and egg case formation, were assessed for 48 female skates. In general, these reproductive parameters remained relatively constant throughout most of the year. However, transient but significant increases in shell gland weight and GSI were observed during certain months. Within the cohort of specimens sampled monthly throughout the year, a subset of females always had large preovulatory follicles present in their ovaries. With the exception of June and September specimens, egg cases undergoing various stages of development were observed in the uteri of specimens captured during all other months of the year. For males ($n$=48), histological stages III through VI (SIII–SVI) of spermatogenesis, GSI, and hepatosomatic index (HSI) were examined. Although there appeared to be monthly fluctuations in spermatogenesis, GSI, and HSI, no significant differences were found. The production and maintenance of mature spermatocysts (SVI) within the testes was observed throughout the year. These findings collectively indicate that the thorny skate is reproductively active year round.

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The thorny skate (*Amblyraja radiata*) is a member of the family Rajidae (Robins and Ray, 1986; Collette and Klein-MacPhee, 2002). It is a cosmopolitan species, endemic to both sides of the Atlantic Ocean, from Greenland and Iceland to the English Channel in the eastern Atlantic (Compagno et al., 1989), and from Greenland and Hudson Bay, Canada, to South Carolina, in the western Atlantic (Robins and Ray, 1986; Collette and Klein-MacPhee, 2002). Despite such a wide distribution, knowledge pertaining to the reproductive biology of this species is limited. Templeman (1982) reported the occurrence of egg capsules in *A. radiata,* and Templeman (1987), Del Río (2002), and Sosebee[1] examined size at sexual maturity.

In the Gulf of Maine, these skates were generally discarded as bycatch because of their low commercial value NEFMC.[2,3] Recently, the rapidly expanding markets for skate wing has made this species commercially more viable, especially because *A. radiata* meets the minimum 1¼ pound-cut pectoral fin size sought by processors (Sosebee[1]; NEFMC[2]). Although no comprehensive published data for reproductive cycles currently exist for thorny skates in the Gulf of Maine, information from the few skate species studied so far indicates that sexual maturity at a late age, low fecundity, and a relatively long life span may also be characteristics of *A. radiata's* life history (Winemiller and Rose, 1992; Zeiner and Wolf, 1993; Francis et al., 2001; Frisk et el., 2001; Sulikowski et al., 2003). When these characteristics are coupled with the practice of selective removal of large individuals, the thorny skate population in the Gulf of Maine may be highly susceptible to over-exploitation by commercial fisheries (Brander 1981; Hoenig and Gruber, 1990; Casey and Myers 1998; Dulvy et al., 2000; Frisk et al., 2001). Because of an in-

[1] Sosebee, K. 2002. Maturity of skates in northeast United States waters. Scientific Council Research Document NAFO. no. 02/134, 17 p. [Available from the Northwest Atlantic Fisheries Organ., Dartmouth, NS.]

[2] New England Fishery Management Council (NEFMC). January 2001. 2000 stock assessment and fishery evaluation (SAFE) report for the northeast skate complex, 179 p. NEFMC, 50 Water Street, Mill 2 Newburyport, MA 01950.

[3] New England Fishery Management Council (NEFMC). 2003. Skate fisheries management plan, 142 p. 50 Water St., Mill 2 Newburyport, MA 01950.

creasing commercial importance, declines in biomass levels, and a paucity of specific biological information, commercial harvests of thorny skates in the U.S. portion of the western North Atlantic are now prohibited. Thus, obtaining life history information for this skate species is not only timely (Simpfendorfer, 1993; Frisk et al., 2001), but it has become imperative. The objective of the present study was to describe the patterns of several morphological reproductive parameters manifested during the reproductive cycle of female and male *A. radiata* collected in the western Gulf of Maine.

## Materials and methods

### Sampling

Thorny skates were captured by otter trawl in an area approximately 900 square miles centered at 42°50′N and 70°15′W in the Gulf of Maine. These locations varied from 30 to 40 km off the coast of New Hampshire. Collection of skates occurred between the $10^{th}$ and $20^{th}$ of each month beginning May 2001 and ending May 2003. A comparison of samples taken from the same month between different years revealed no variability. Furthermore, the skates sampled in the present study were obtained from the same population and geographic location. Thus, the data from the same months for different sampling years were grouped together.

Skates were maintained alive on board the FV *Mystique Lady* until transport to the University of New Hampshire's Coastal Marine Laboratory (CML). There, individual fish were euthanized (0.3 g/L bath of MS222). Total length (TL in mm) was measured as a straight line distance from the tip of the rostrum to the end of the tail, and disc width (DW in mm) as a straight line distance between the tips of the widest portion of pectoral fins. Total wet weight (kg) was also recorded. For males, clasper length was measured as the straight line distance from the posterior point of the cloaca to the end of the clasper. The gonadosomatic index (GSI) and hepatosomatic index (HSI) were calculated as gonad weight divided by total body weight multiplied by 100, and liver weight divided by total body weight multiplied by 100, respectively. The epigonal organ was included in both male and female GSI measurements because of its close association with the gonads (Maruska et al., 1996).

### Criteria used to determine reproductively active skates

Females whose reproductive tracts contained ovarian follicles with a minimum diameter of 25 mm and had a shell gland weighing at least 30 g were considered mature (capable of egg encapsulation and oviposition). These numbers were determined from our observations of reproductive tracts containing egg cases that were either fully formed or undergoing various stages of formation. Males with calcified claspers 200 mm long or greater, and with a proportion of mature spermatocysts in the testes of 25% or greater were considered reproductively capable of fertilizing an ovulated follicle. These criteria are consistent with previous studies that reported similar characteristics for other mature elasmobranch species (Koob et al., 1986; Heupel et al., 1999; Conrath et al., 2002; Sulikowski et al., 2004). Male and female thorny skates that did not meet all the criteria were considered to be immature. We also looked for some other indicators of reproductive activity, such as mating bites on female pectoral fins, and evidence of mating activity on male claspers, but they were either absent or not apparent in specimens examined during the study. Sperm storage was not assessed in the present investigation.

### Gross morphology of the female reproductive tract

After removal of reproductive tracts, the ovaries, shell glands, and uteri were dissected out, blotted dry, and weighed to the nearest gram. Ovarian follicle dynamics were evaluated by measuring the diameter (with a caliper) and counting all follicles ≥1 mm in diameter (Tsang and Callard, 1987; Snelson et al., 1988; Sulikowski et al., 2004). For this data set, we averaged the size of the largest single follicle found on the right and left ovaries of each skate. Average follicle diameters, average ovary weights, and average shell gland weights were analyzed to assess temporal patterns during the reproductive cycle.

### Histology of the testis

From male specimens, testes were removed, blotted dry, and weighed to the nearest gram. A single 2–3 mm thick segment was removed from the central portion of a single lobe in the medial area of an individual testis (Maruska et al., 1996; Sulikowski et al., 2004), placed in a tissue cassette, and fixed in 10% buffered formalin until processed by the University of New Hampshire Veterinary Diagnostic Laboratory. There, the sample was dehydrated, embedded in paraffin, sectioned, and stained with hematoxylin and eosin. Prepared slides of testicular tissue were examined and classified into stages of spermatogenic development following the criteria described by Maruska et al. (1996), Hamlett and Koob (1999), and Tricas et al. (2000). For the developmental stages of spermatogenesis described in other elasmobranchs, hormone analyses have confirmed that stages III through VI are associated with reproductive readiness (Heupel et al., 1999; Tricas et al. 2000; Sulikowski et al. 2004). For this reason, we focused our efforts on these specific stages in the thorny skate. Briefly, these stages have the following characteristics: stage III, spermatocysts; stage IV, spermatids; stage V, immature spermatozoa; and stage VI, mature spermatocysts (Maruska et al., 1996). In the present study, the mean proportion of testis occupied by each of these stages was measured along a straight line distance across one representative full lobe cross section of the testis (Maruska et al., 1996; Conrath et al., 2002).

### Statistical analyses

The results are presented as means ±SEM and evaluated by Kruskal Wallis analysis of variance followed by a Tukey's *post hoc* test. Statistical significance was accepted at $P<0.05$. To determine whether a relationship exists in measured morphological and histological reproductive parameters, a Pearson correlation analysis (denoted as $r$) was performed.

## Results

The lack of a robust sample size presents a potential limitation for our study. However, over the last decade, there has been an increasingly precipitous decline in thorny skate populations in the Gulf of Maine, especially larger size specimens (NEFMC[2,3]). These declines were evident in our sampling trips, because large, mature individuals were rarely caught in most trawls. The data presented in this article are the result of 84 sampling trips that took place over the course of two years (approximately three to four trips per month). Moreover, the recent prohibition on thorny skate landings has put an end to any prospects regarding collection of additional specimens in the foreseeable future. Thus, the data set we have presented represents the best available information on the reproductive cycle for this species.

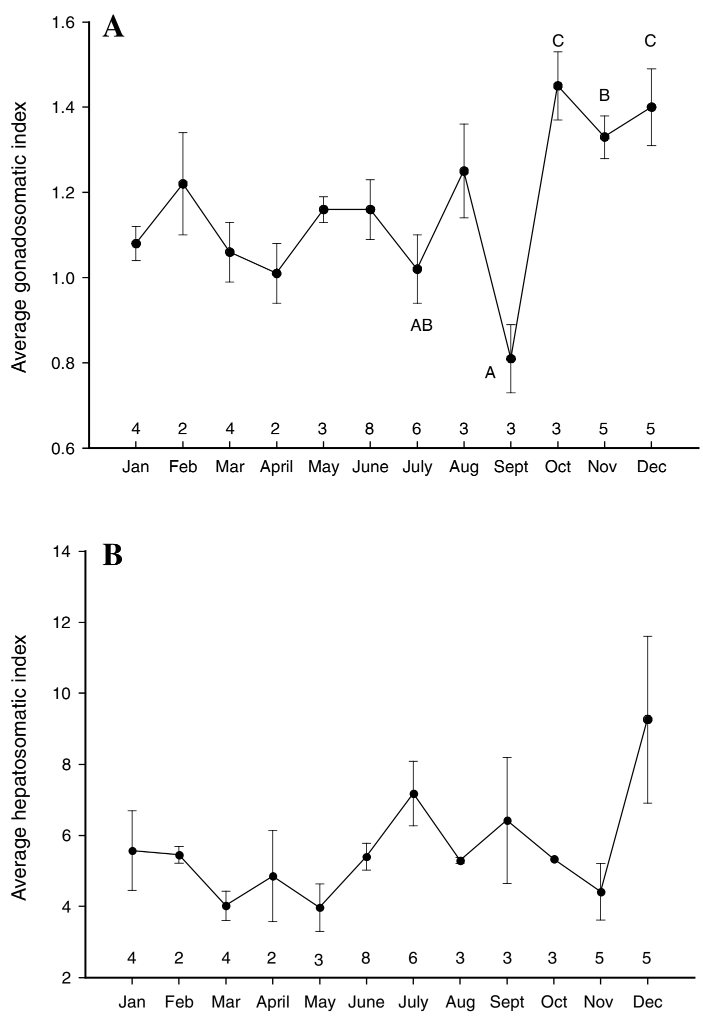


**Figure 1**

Monthly changes in female thorny skates (*Amblyraja radiata*): (**A**) Gonadosomatic index (GSI); (**B**) hepatosomatic index (HSI); (**C**) shell gland weight; and (**D**) diameter of the two largest follicles. Values are expressed as means ±SEM. Sample sizes are indicated above each month. Values designated with different letters are significantly different from each other ($P<0.05$).

### Size ranges

Mature female skates ($n=48$) ranged from 820 to 1050 mm TL (mean=917 ±7 SEM) and from 4.4 to 10.2 kg (mean=7.7 ±0.2 SEM) in total body mass. Mature male skates ($n=48$) ranged from 800 to 1040 mm TL (mean=952 ±11 SEM), and from 5.4 to 10.8 kg (mean=8.4 ±0.3 SEM) in total body mass.

### Assessment of morphological parameters in the female reproductive tract

In females, the average GSI of skates captured in July was lower ($P<0.05$) than those captured in October and December, and those from September were lower than the specimens captured in October, November, and December (Fig. 1A). Because the number of samples from April consisted of only two skates, we were unable to test for statistical differences between other months. Despite this limitation, the two specimens from April displayed similar values to those in July. Average HSI (Fig. 1B) did not change ($P>0.05$) over the sampling period. However, the average shell gland weight (Fig. 1C) from skates captured in October was greater ($P<0.05$) than those captured in September. Because all shell glands from skates captured in February were in the process of encapsulating ovulated eggs, we were unable to obtain accurate individual shell gland weights.

There were no differences ($P>0.05$) observed in the average diameter of the two largest follicles (Fig. 1D), and no pattern of follicle dynamics was discerned. Also, fully formed egg cases, or those in the process of formation, were found in the uteri of skates captured during all months of the year, except June and September.

Additional analysis revealed that GSI was correlated to shell gland weight ($r=0.53$) and average follicle diameter ($r=0.4$). Furthermore, HSI was also correlated to shell gland weight ($r=0.53$) and average follicle diameter ($r=0.7$).

### Assessment of morphological parameters in the male reproductive tract

Histological stages III through VI (SIII–SVI) of spermatogenesis were examined, and GSI and HSI were determined for the 48 males collected during 24 months of sampling. Although the relative proportion of these four stages did not differ among months, it is notable that the production and maintenance of mature spermatocysts (SVI) within the testes persisted throughout the year (Fig. 2A). Similarly, no significant seasonal differences were found in HSI or GSI (Fig. 2, B and C, respectively). In addition, there were weak to no correlations between spermatogenesis and either HSI or GSI ($r$=−0.07 and 0.13, respectively).

### Synchronicity between male and female reproductive cycles

Results from the male and female morphological reproductive parameters indicated that thorny skates are capable of reproducing throughout the year in the western Gulf of Maine. When GSI, follicle diameter in relation to percent composition of SVI, or shell gland weight in relation to percent composition of SVI were compared between male and female thorny skates, no apparent correlation was detected (Fig. 3, A–C). In contrast, when percent composition of SVI (spermatogenesis) was plotted against percentage of captured female skates with egg cases, a strong synchronicity ($r$=0.51) was observed (Fig. 4).

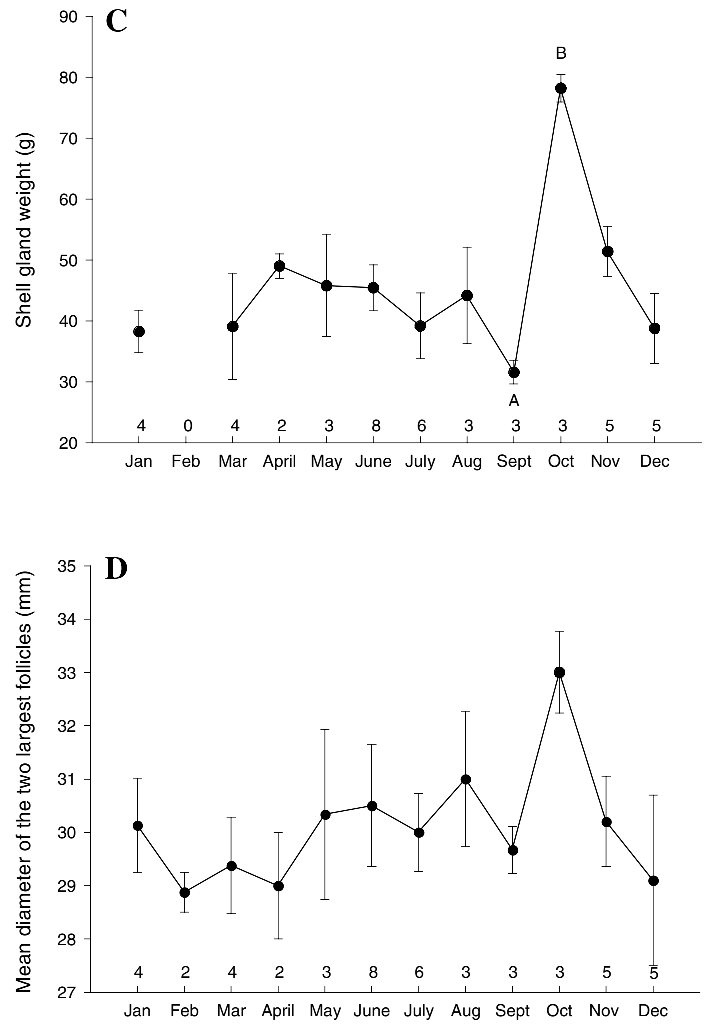


**Figure 1 (continued)**

## Discussion

Elasmobranchs display a wide range of reproductive strategies with morphological and physiological specializations for oviparous or viviparous reproduction (Wourms and Demski, 1993; Hamlett and Koob, 1999). These strategies are associated with one of three basic types of reproductive cycles: 1) reproduction throughout the year, 2) a partially defined annual cycle with one or two peaks, and 3) a well-defined annual or biennial cycle (Wourms, 1977; Hamlett and Koob, 1999). Among oviparous elasmobranchs, some species exhibit cycles with clearly delineated period(s) of reproductive activity interspersed between periods of little or no activity. For example, in the clearnose skate (*Raja eglanteria*), the patterns of estradiol concentrations and follicle dynamics indicate the presence of a well-defined annual reproductive cycle, in which mating and egg deposition take place from December to mid May (Rasmussen et al., 1999). Likewise, hormone and morphological data also indicate a defined annual cycle in the epaulette shark (*Hemiscyllium ocellatum*) (Heupel et al., 1999) and that reproductive activities take place from July to December.

In contrast, other oviparous elasmobranchs exhibit reproductive activity year round. For example, the present study revealed that female thorny skates are capable of reproducing throughout the year. This conclusion was based on GSI, shell gland weight, diameter of the largest preovulatory follicles, and the presence of egg cases in specimens collected over the course of the study. We also observed that GSI and shell gland weight were highest in October. Thus, the period (or periods) of enhanced reproductive activity appears to be an integral part of continuous cycles, although the specific measured parameters or when these periods occur may vary between species.

In a study of thorny skates sampled from August to December in NAFO Division 3N, females were found to be reproductively active over the entire sampling interval, and peak egg case production occurred in September (Del Río, 2002). In contrast, although large preovulatory follicles were present and oviposition occurred throughout the reproductive cycle of the lesser spotted dogfish

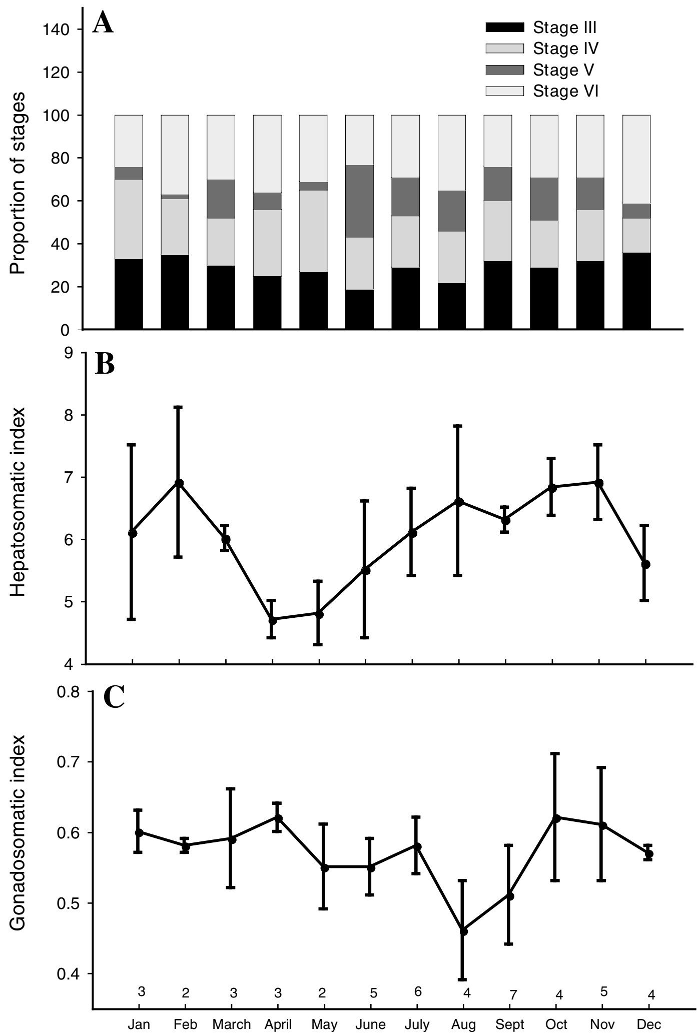


**Figure 2**

Monthly changes in male thorny skates (*A. radiata*): (**A**) The mean percent of each stage of spermatogenesis (stages III through VI) found along a transect line across one representative full lobe cross section of a testis; (**B**) hepatosomatic index (HSI) and; (**C**) gonadosomatic index (GSI). Sample sizes are indicated above each month. Values are expressed as mean ±SEM.

(*Scyliorhinus canicula*) (Henderson and Casey, 2001), ovary weight and egg deposition peaked during spring. Similarly, several morphological parameters and steroid hormones have been shown to peak in female winter skates (*Leucoraja ocellata*) during the summer, and egg-case production is highest in the fall (Sulikowski et al., 2004). Lastly, in *L. erinacea,* examination of follicle dynamics and egg-case production indicated that a higher proportion of females are reproductively active during two periods of time in the reproductive cycle: in the winter and in the summer (Richards et al., 1963).

The fairly consistent pattern of HSI in female thorny skates over the reproductive cycle indicated that liver reserves (such as lipids and proteins used for oocyte growth) were stored and metabolized continuously throughout the year without a significant change in whole organ biomass. This is in contrast to other oviparous species, such as *S. canicula,* which displayed seasonal variations in liver mass as a result of lipid deposition occurring during different times of the reproductive cycle (Craik, 1978).

The continual presence of mature spermatocysts within the testes over the entire sampling period indicateded that male thorny skates are also capable of reproducing throughout the year. Information describing the annual reproductive cycles of oviparous male elasmobranchs is

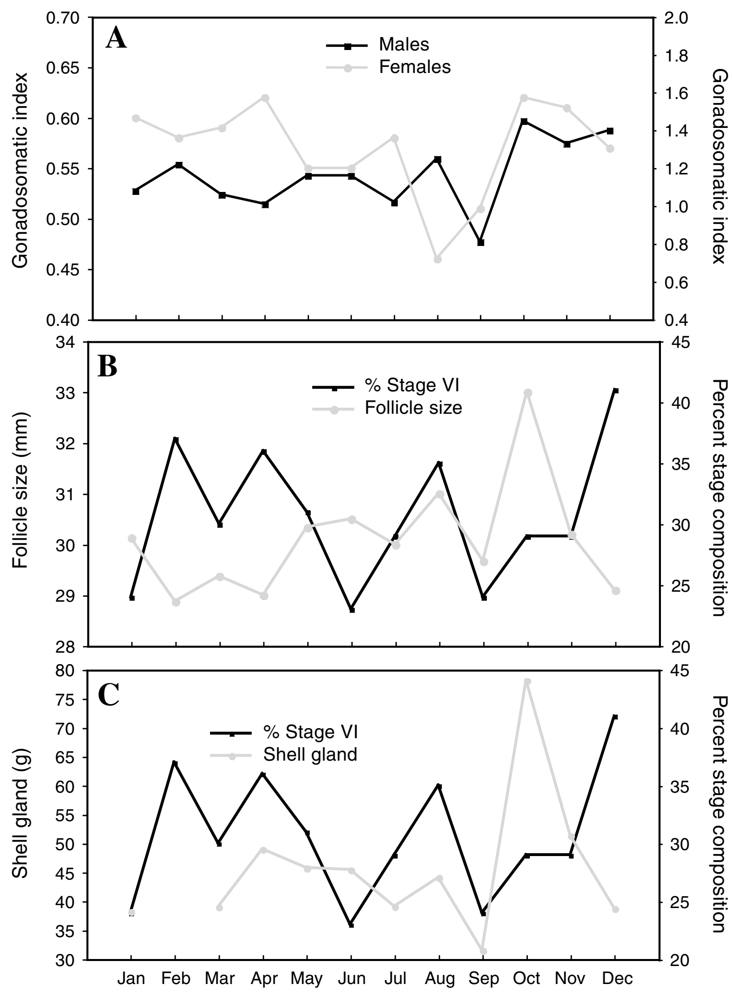


**Figure 3**

Comparisons between male and female thorny skate (*A. radiata*) reproductive parameters over the course of the sampling period: (**A**) GSI; (**B**) diameter of the two largest follicles and percentage of spermatocysts (SVI) and; (**C**) shell gland weight and percentage of spermatocysts (SVI).

very limited because studies have focused on changes in morphological parameters (i.e., Richards et al., 1963; Craik, 1978) or steroid hormone analyses (i.e., Sumpter and Dodd, 1979; Rasmussen et al., 1999) in females. To our knowledge, the only two species in which quantitative methods were used to describe annual reproductive patterns in males were *H. ocellatum* (Heupel et al., 1999) and *L. ocellata* (Sulikowski et al., 2004). These two species exhibit contrasting strategies in their respective reproductive cycles. For example, similar to male thorny skates from the present study, male winter skates appear capable of continuous production of mature spermatocysts throughout the year (Sulikowski et al., 2004). In contrast, examination of the testes and circulating hormone concentrations in *H. ocellatum* indicated that sperm production and androgen concentration display a concurrent seasonal cycle that peaks from June to October (Heupel et al., 1999).

The lack of correlation between GSI or HSI and stage of spermatogenesis in the thorny skate was not surprising because studies do not support the assumption that relative gonad size (or storage products in the liver) and reproductive readiness are positively correlated (Teshima, 1981; Parsons and Grier, 1992; Maruska et al., 1996). For instance, neither peak sperm production (Maruska et al., 1996) nor the pattern of testosterone concentration was correlated with GSI in *Dasyatis sabina* (Snelson et al. 1997) or *L. ocellata* (Sulikowski et al., 2004).

Relatively few studies have assessed whether cyclical patterns of reproductive morphological parameters or hormone concentrations are coordinated between males and females over the course of their reproductive cycles. Among them, coordinated peaks in gonad weight and steroid hormone concentrations in winter skates (Sulikowski et al., 2004) and epaulette sharks (Heupel et al., 1999) were observed in males and females over an annual cycle. In the present study, mature spermatocysts (SVI) and percentage of female thorny skates with egg cases were also synchronized over the course of the study. In contrast, Henderson and Casey (2001) found that the gonadal cycles of male and female lesser spotted dogfish were asynchronous, which they hypothesized to be due to the storage of sperm by females. Sperm storage has been documented in other female elasmobranch species as well (e.g., Pratt, 1993; Maruska et al., 1996) and is thought to be a feature primarily of species that are nomadic or segregated by sex (Pratt, 1993). In the current study, *A. radiata* was neither segregated by sex (both genders were captured in the same area and in the same trawls) nor found to be nomadic in their movement patterns (Templeman, 1987; Sulikowski, unpubl. observ.). Moreover, because males are capable of producing viable sperm and females appear to be reproductively active throughout the year, there is probably no need for the population of thorny skates that we sampled to store sperm. On the basis of the above information, we believe that the reproductive cycle in the sampled population of thorny skates is coordinated over an annual cycle.

In summary, according to the reproductive strategies outlined by Wourms (1977) and later by Hamlett and Koob (1999), the results of the present study indicate that thorny skates have a reproductive cycle that is continuous throughout the year. For females, this conclusion was based on ovary weight, shell gland weight, and diameter of the largest follicles (the preovulatory follicles). For males, this conclusion was based on the presence of mature spermatocysts within the testes over the course of the sampling period. Moreover, comparisons between the proportion of mature spermatocysts within the testes and the percentage of egg-case–bearing females indicate that the reproductive cycles of male and female thorny skates are synchronized. Currently, analyses of circulating steroid hormone concentrations are in progress for the thorny skates used in the present study, which may provide additional insight into the regulation and timing of reproductive events in this species.

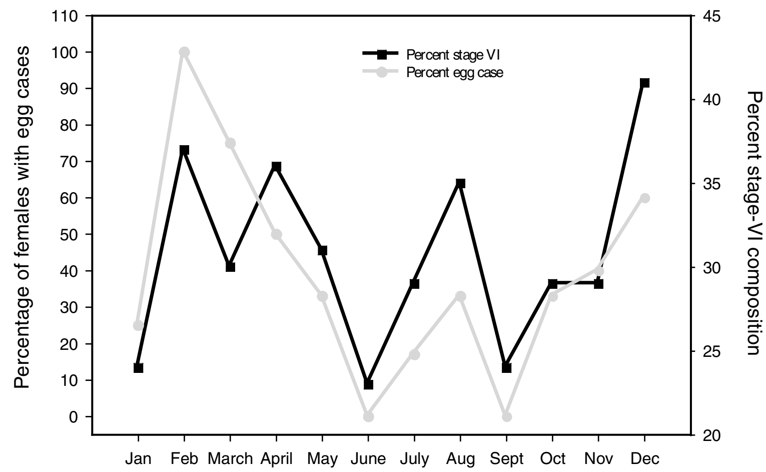


**Figure 4**

Comparisons between the percentage of spermatocysts (SVI) and the percentage of female thorny skates (*A. radiata*) with egg cases.

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