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Fecundity and Reproductive Season of the Round Goby *Neogobius melanostomus* in the Upper Detroit River

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Abstract.—The round goby *Neogobius melanostomus* successfully invaded the Great Lakes perhaps, in part, because of its reproductive strategy, whereby females spawn many times over an extended reproductive season. Female round gobies were collected from the upper Detroit River (by trawling and angling) during spring, summer, and fall of 1996 in order to determine fecundity patterns and length of the reproductive season. Female round gobies were mature at 1 year of age, which is 1 year earlier than has been noted for gobies in Europe. Gravid females were present in May and declined at the end of July, which indicates that spawning occurs from spring until midsummer. Mean fecundity was 198 eggs, and variation in fecundity was correlated with standard length ($r^2 = 0.76$, $P < 0.0001$) of females. Fecundity was lower than that observed for the same species in Europe, but it was generally higher than that of most native species with which gobies would compete. A field experiment showed that artificial nests contained fewer eggs but were used more often by more spawning females than were such nests in Europe. The relatively high fecundity (compared with that of native species), rapid maturation, aggressive behavior, and extended spawning season may favor the continued expansion of round gobies throughout the Great Lakes.

The round goby *Neogobius melanostomus* is one of two species of the family Gobiidae to invade the Great Lakes. Both the round goby and the tubenose goby *Proterorhinus marmoratus* were discovered in low numbers in the St. Clair River in April 1990 (Jude et al. 1992). The round goby is now the more abundant species and is found in all of the Great Lakes (Jude 1997). It is presently one of the most abundant benthic fishes in the Lake Huron–Lake Erie corridor, southern Lake Michigan, and the central and western basins of Lake Erie. Although the long-term effect of the round goby on native fish communities is unknown, the species has been implicated in the severe decline of the mottled sculpin in the St. Clair River (Jude et al. 1995). A number of reasons have been proposed to explain the success of the round goby in the Great Lakes, including its aggressive nature and reproductive strategy (Corkum et al. 1998).

Most gobiid fishes use a reproductive strategy in which the male cares for the eggs (Miller 1984). Reese (1964) divided the gobiid reproduction into five stages: establishment of a territory, nest preparation, courtship behavior, spawning, and parental care of the eggs. This type of reproductive strategy is associated with several life history variables. Fecundity is generally lower, but offspring are larger at hatching, and offspring suffer lower mortality than do other fishes.

The demersal, adhesive eggs are deposited on a fixed overhead surface within a cavity (Miller 1984). Eggs and larvae of the round goby are among the largest of all gobiid species, and a single female will produce relatively few eggs (328 to 5,221) (Kovtun 1978). For example, whereas a 105-mm round goby may contain 1,600 eggs, a similar-sized female of a gobiid from the Pacific, *Sicyopterus japonicus*, may contain 225,000 eggs (Miller 1984). The increased survival of the larger eggs (3.2 mm) of round gobies may be an important reason for the success of the round goby in the Great Lakes. Another goby, *Acanthogobius flavimanus*, that became established in San Francisco Bay (Brittan et al. 1970) and in New South Wales, Australia (Hoese 1973) also produces fewer but larger eggs (Miller 1984).

The round goby is a multiple spawner with an extended reproductive season (Miller 1986). The length of the reproductive season varies considerably depending on locality. In the Black and Caspian seas, spawning may begin as early as April and may continue to the end of June (Romania), July (Sea of Azov), or September (Varna, Bulgaria) (Miller 1986). Spawning occurs at water temperatures that range from 9 to 26°C and at depths that range from 0.2 to 1.5 m (Charlebois et al. 1997). Male gobies will construct nests in a variety of locations, including under logs and stones and inside crayfish burrows or cans (Charlebois et al.

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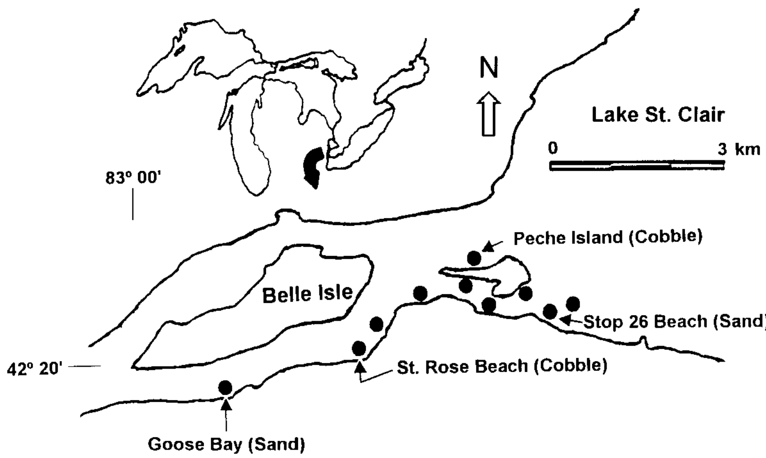

FIGURE 1.—Map of the upper Detroit River showing where round gobies were collected by trawling (closed circles) and sites where artificial nests were placed.

1997). The general nest requirements are a hard, immobile overhead surface and a single opening to the cavity (Miller 1984).

Sexual dimorphism in the round goby is more pronounced than it is in other gobiid fishes. The adult males are characterized by a larger size at maturity, enlarged cheeks, and all-over dark coloration (dark gray to black) (Nikol'skii 1963; Miller 1984). In their native range, male round gobies mature at age 3 to 4 years, whereas females mature at age 2 to 3 years (Bil'ko 1971; Miller 1986). Males also grow faster than females, but they do not feed while guarding the nest (Miller 1984), which may contribute to the early death of males after a single breeding season; females can spawn in more than one season. Male round gobies also have been observed (C. Murphy, University of Alberta, personal communication) using a sneaker spawning strategy (Gross 1991). In this strategy, smaller males with distended abdomens and enlarged genital papilla spawn in the nest of a guarding male when the opportunity arises.

As many as 10,000 eggs from four to six females can be deposited in a round goby nest. Fertilization rates in the round goby can reach 95%, and up to 95% of the eggs in a nest may hatch (Charlebois et al. 1997). However, large nests can suffer higher egg mortality from predation and insufficient aeration (Kovtun 1980). Survival rates of the young are unknown. Although no data exist for the round goby, nest size is positively correlated with the size of the male in other fishes with a similar reproductive strategy (Bisazza and Marconato 1988; Bisazza et al. 1989; Magnhagen and Kvarnemo 1989). Nest densities and subsequent territory sizes are also related to the availability of suitable nest sites (Almada et al. 1994).

The objectives of this study were to determine age- and size-specific fecundity of round gobies in the Detroit River and to examine seasonal variation in reproductive effort. Female round gobies were expected to mature at age 2 (the same age at which maturation occurs in their native range) (Charlebois et al. 1997). We also expected that fecundity would increase with the size and age of females. We examined the fecundity and duration of spawning season of round gobies through field collections and an artificial nesting study in cobble and sandy substrates.

Methods

Field collections.—In order to determine fecundity, female round gobies were collected by a small Otter trawl every 3 weeks during spring, summer, and fall of 1996 from 10 sites in the upper Detroit River (Figure 1). The trawl was equipped with ''rockhopper'' foot gear, and the net opening was 4 m wide by 1 m high. The net was constructed of 40-mm stretch-measure mesh with a 10-mm stretch-measure mesh liner in the cod end. We towed at an average speed of 3.5 km/h during each 10-min haul. Fish were not collected in August because no trawl net was available; however, round gobies were collected by hook and line on July 29.

Fish captured in each trawl tow were sorted into species and counted. All gobies were sexed by examination of the genital papilla (Miller 1984). Female gobies were put into aerated coolers and transported to the laboratory, where fish were sacrificed with CO_2 and individually frozen until lengths and weights could be recorded and otoliths removed. Standard lengths were recorded to the nearest 0.1 mm and total weights to the nearest 0.01 g. Ovaries were removed, weighed to the nearest milligram, and preserved in modified Gilson's fluid (100 mL 60% ethanol; 880 mL water; 15 mL 80% nitric acid; 18 mL glacial acetic acid; and 20 g mercuric chloride) for later egg counts. The modified Gilson's fluid was used because it preserves and hardens the eggs while breaking down the ovarian tissue (Snyder 1983). The preservative only hardened eggs that had begun to accumulate yolk, and only ovaries containing hardened eggs were used in egg counts.

Ages were determined using transverse sections of the lapillar otoliths. Otoliths were mounted on glass slides using cyanoacrylate glue. The mounted otoliths were ground and polished as close to the nucleus as possible on one side using either wet/dry 4,000-grit silicon carbide sandpaper or a lapping film series (3 μm, 1 μm, and 0.3 μm). The otolith was lifted from the slide using a scalpel and was remounted with the polished side down. The second side was ground and polished as close to the nucleus as possible. Ages were determined by viewing otoliths under a compound microscope equipped with dual polarizing filters.

Using the total and ovarian weights, a standard gonadosomatic index (GSI) was calculated to determine the time of spawning and the general reproductive status of females. Eggs were counted by hand with the aid of a stereomicroscope after we first separated the eggs from the remaining ovarian tissue. Only ovaries with mature, yolked, and unovulated eggs were used to avoid underestimating fecundity due to spawned eggs or eggs lost during handling (Heins and Baker 1993). The percentage of gravid females was calculated for each sample date.

Artificial nest experiment.—Artificial nests (15 cm long × 10 cm wide × 5 cm high) were composed of ceramic tile (top, sides, and one end) cemented together with silicone. A half section of polyvinyl chloride (PVC) pipe (15 cm long × 10-cm outside diameter) served as the floor of the nest and was placed on the riverbed. Each ceramic nest (640 g) had sufficient mass to rest on the PVC section without being disturbed under normal flow conditions. Four sites (two cobble and two sand) on the upper Detroit River were selected after SCUBA surveys of the area had been conducted. Thirty-six nests were placed in a 6 m-by-6 m grid at each site, with the opening of each nest randomly oriented north, south, east, or west. SCUBA was used to place and retrieve nests at all sites.

Artificial nests were placed at St. Rose Beach (cobble) and Goose Bay (sand) on June 10 and in Lake St. Clair at Stop 26 (sand) and north of Peche Island (cobble) on June 22 (Figure 1). Water depth was between 1.5 and 2 m at all sites. Beginning June 17, nest sites were visited weekly. On each date, nests were either examined visually (by picking up the ceramic unit and inspecting the undersurface for the presence of round goby eggs) or recorded on video (for later analysis in the laboratory). Video recordings were made using a black-and-white camera in an underwater housing system connected by cable to monitor and VCR on the boat. Video recordings were made at the 24-h setting on the VCR using a professional quality videocassette.

Videotapes were analyzed in the laboratory using computer image analysis (Mocha System, Jantel Inc.) The area of each egg mass or area covered by egg scars was measured using the dimensions of the nest to calibrate the image. In order to determine the number of eggs per unit area, a single nest containing a small number of eggs was selected and the number of eggs counted directly from the video. The area covered by the egg mass was measured using image analysis, and the number of eggs per unit area was calculated.

Results

Field Collection

Mean (±SE) size of mature females was 60.8 (±0.81) mm standard length (SL) and ranged from 42.4 to 92.0 mm SL (n = 136). The mean length of round gobies varied significantly depending on date of capture (one-way analysis of variance [ANOVA], $P < 0.001$, df = 5,115; $F = 5.635$). The mean size of individuals captured on July 29 by hook and line was significantly greater than the greatest mean size of females obtained by trawling (two sample t test, $t = 2.023$, $P < 0.005$). Overall, age-1 females were most abundant (n = 83), followed by age-2 (n = 41) and age-3 (n = 3) females. Size (SL) varied within and overlapped among all age classes (Figure 2). Examination of length-frequency distributions by age showed that age-2 females were more abundant than age-1 females in the May 29 and June 4 collections, but age-1 females predominated in June 17 and July 8 collections. Only age-1 females were collected in the September and October samples. All three age groups were present in only the May 29 and July 29 samples.

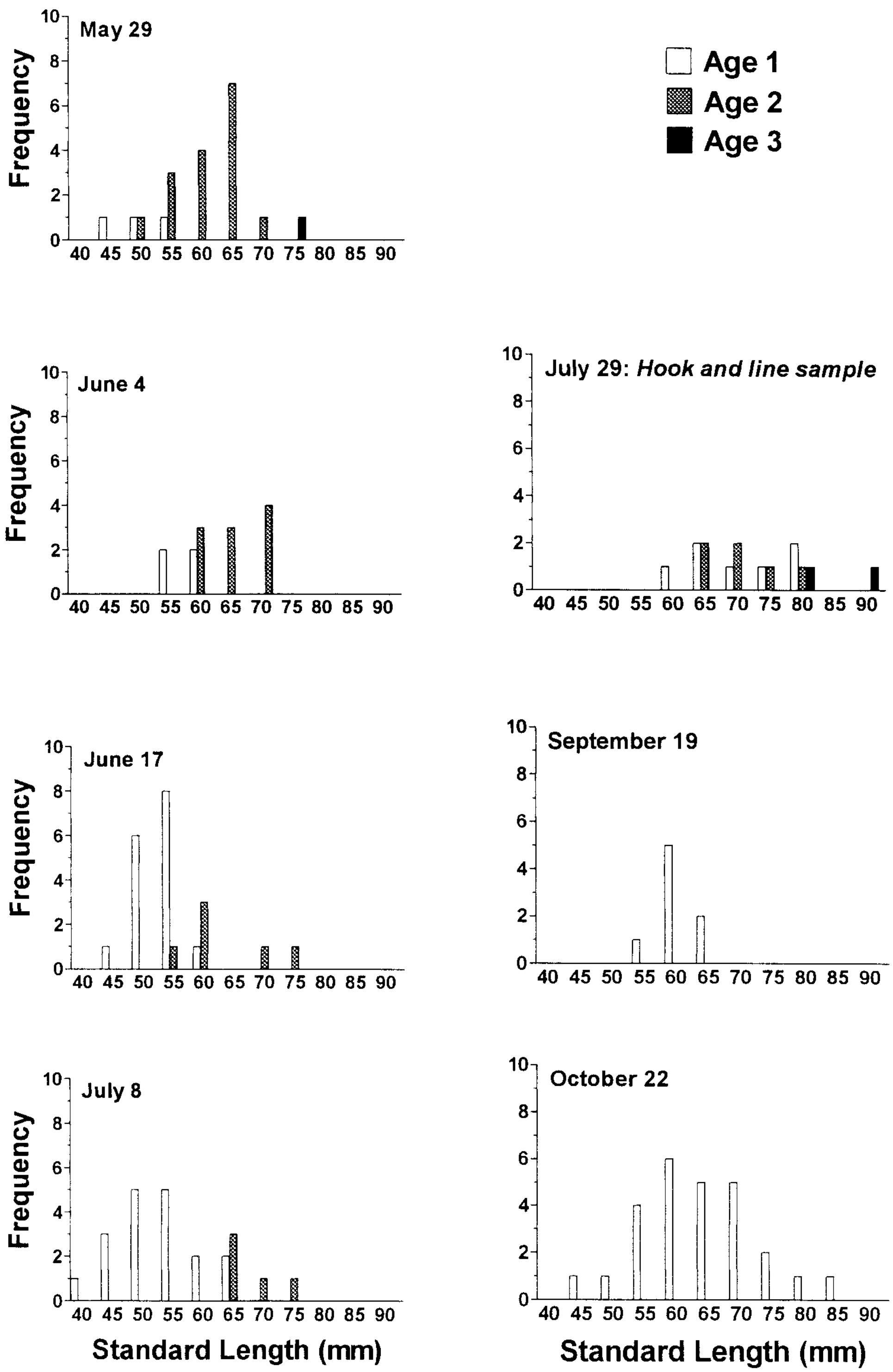

FIGURE 2.—The size-frequency distributions by age for female round gobies collected by hook and line (July 29) and trawling (six dates) during 1996.

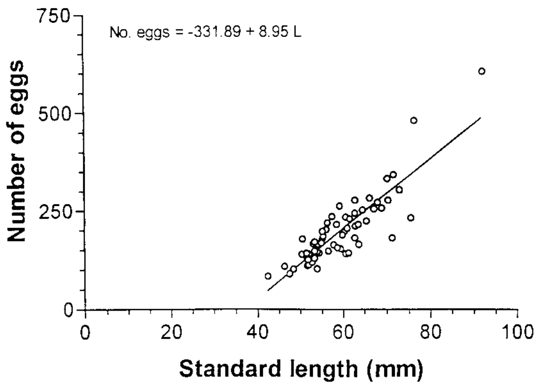

FIGURE 3.—The relation between standard length and number of eggs (r^2 = 0.76, P < 0.0001) for 63 adult female round gobies.

Individual fecundity ranged from 84 to 606 eggs and was significantly correlated with fish size (r^2 = 0.76, P < 0.001; Figure 3). The relation between egg number and SL may be curvilinear, as in many fishes, but to elucidate this relationship would require more large females (only two fish >75 mm SL were collected in our study). The mean (±SE) number of eggs for age-2 (218.3 ± 16.33) fish was significantly higher than that observed for age-1 (163.7 ± 9.24) fish (t = 2.910, P < 0.005).

The percentage of gravid females (pooled among all sample sites) differed significantly among sample dates ($\chi^2_{[0.05, 2]}$ = 7.738). High GSI and percent of gravid females indicated that spawning had already begun by our May 29 sample. The percentage of females declined between July 8 and July 29, and none or few were found later (Figure 4a). There was no significant relation (r^2 = 0.02, P > 0.05) between gonad weight and body weight (which included stomach contents and viscera). The GSI (Figure 4b) showed a similar seasonal trend to the percentage of gravid females. The mean number of eggs per gravid female did not vary significantly with season (one-way ANOVA, P = 0.6, df = 5,60; F = 0.73).

Round gobies spawn at water temperatures from 9 to 26°C (Charlebois et al. 1997). Our study site was located nearby the water intake pipe (depth of 12 m) for the City of Windsor on the Detroit River. Water temperatures were within the spawning range requirements for round gobies from mid-April until the end of the first week in November.

Artificial Nest Experiment

The number of nests that contained eggs varied considerably among sites, with the highest occupation at Goose Bay (n = 13) and the lowest at Stop 26 (n = 4), both of which are sandy sites. An intermediate number of nests were occupied at the two cobble sites, Peche Island (n = 9) and St. Ross Beach (n = 6). Goby eggs were present on August 13 only at the St. Rose site. However, the presence of egg scars in a nest at Stop 26, which did not previously contain eggs, indicates occupancy between July 24 and August 13.

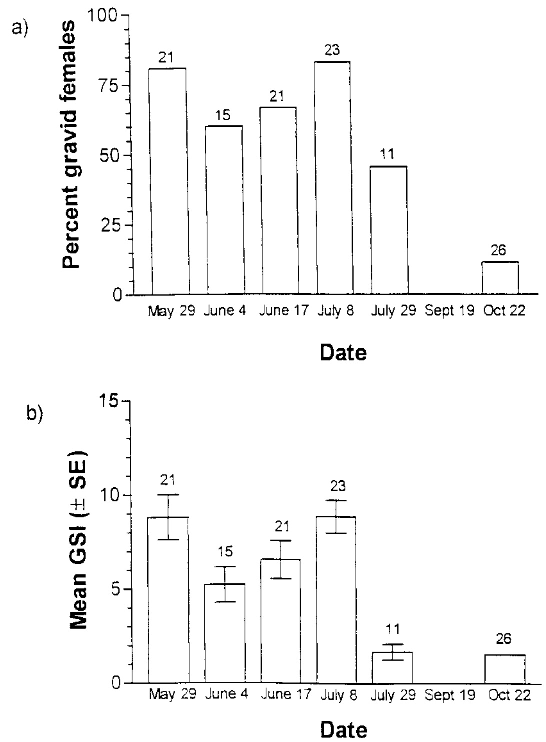

FIGURE 4.—**(a)**The percent of gravid females in the total catch of mature females on each collection date. **(b)** The mean gonadosomatic index (GSI) on each collection date for all mature females captured. The numbers above the bars represent the sample size on each date.

In the nests that contained round goby eggs, the eggs were deposited in a single layer on the overhead surface of the nest as well as on the sides and bottom of nests. On only one occasion did we find a second egg layer, and this layer covered only 3.8 cm^2. In all nests, the egg layer was essentially continuous; irregularities occurred only at the edges of the egg mass. The density of eggs within a nest was 40 eggs/cm^2, and the estimated number of eggs within a nest ranged from 644 to 9,462. Given the maximum fecundity we recorded (606 eggs per female), this would mean that at least 15 females spawned in this nest. We observed no clear

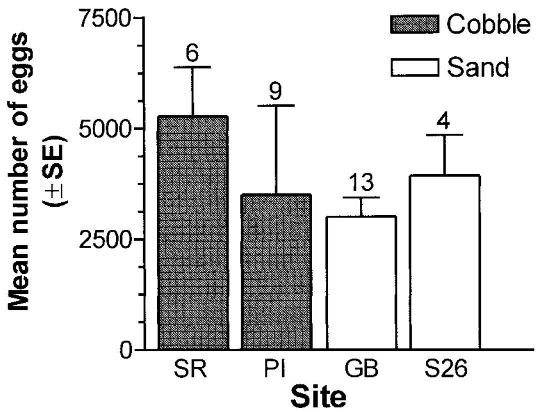

FIGURE 5.—The mean number of eggs per artificial nest at each of the four sites (SR, St. Rose Beach; PI, Peche Island; GB, Goose Bay; S26, Stop 26 Beach). The numbers associated with the error bars represent the number of nests occupied out of the 36 nests positioned at each site.

trend between egg abundance and the substrate type on which nests were placed (Figure 5). The mean (±SE) number of eggs per nest was highest at the cobble site at St. Rose Beach (5,210 ± 1,150) and lowest at the sand site at Goose Bay (3,030 ± 310). The second cobble site at Peche Island contained fewer eggs per nest (3,495 ± 2,070) than did the second sand site at Stop 26 (3,860 ± 830). Nests from which egg numbers were estimated from egg scars were excluded from this analysis. Round gobies often used adjacent nests that were spaced 1 m apart, even at sites where few nests were occupied.

Discussion

The Detroit River round goby population appears to mature earlier and at a smaller size than do gobies in Europe. In Europe, most female round gobies mature at age 2 or 3 (Miller 1986). In the Detroit River, most female round gobies are first maturing at age 1 or, to a lesser extent, at age 2. Additionally, a mature female of only 43 mm SL was collected from the Detroit River; this female was considerably smaller than those found in Europe (Kovtun 1978). In an examination of the fecundity of round gobies from the Sea of Azov, Kovtun (1978) included all round gobies of less than 7 cm in body length as a single size class, thereby suggesting that smaller mature females were relatively uncommon. He did, however, report that some round gobies in the Sea of Azov matured at age 1.

Evidence from the percentage of gravid females captured and from the GSI indicate that round gobies had begun to spawn before our first trawling sample in late May. The presence of eggs on an artificial nest was also observed in mid-August. Although round gobies can spawn at temperatures as low as 9°C, spawning is more prevalent at higher temperatures (Charlebois et al. 1997). On the basis of water temperature alone, spawning may occur in the Detroit River from mid-April until early November. In 1998, gravid females and round goby males with characteristic black breeding coloration were caught with hook and line in the Detroit River in mid-November (L. D. Corkum, University of Windsor, personal observation). Given about 3 to 4 weeks for eggs to hatch at 20°C (Charlebois et al. 1997), we estimate that there were at least three spawning events by round gobies in the Detroit River in 1996.

The GSI has been used successfully to determine reproductive season (Kanabashira et al. 1980; Arruda et al. 1993) for other gobiid fishes. Kanabashira et al. (1980) found that the seasonal change in the GSI corresponded to the abundance of egg-containing nests in the field. Although the nest data in our study are limited, the decline in GSI corresponds with the decline in gravid females observed at the end of July (Figure 4). Hatching dates determined from the age (in days) of 20 young-of-the-year round gobies collected in trawls from the same study area ranged from May 23 to August 5 (MacInnis 1997), which confirms the reproductive season.

In the artificial nest experiment, the amount of spawning activity varied among sites. Although more nests were occupied at the sandy site at Goose Bay (13 of 36) than at the two cobble sites, the sandy substrate at Stop 26 contained the fewest occupied nests (4 of 36). Nest densities may be influenced by factors other than the availability of nest sites, factors such as predation on eggs and available shallow-water habitat. All of our nest sites were up to 0.5 m deeper than the reported preferred spawning habitat depth (0.2–1.5 m) of round gobies (Charlebois et al. 1997). Recently, Wickett and Corkum (1998) observed breeding males and gravid females on shipwrecks in Lake Erie at depths of up to 11 m. At these depths, an aggressive parental male defended eggs in an exposed nest from rock bass and smallmouth bass. However, juvenile round gobies preyed on round goby eggs when the parental male was distracted by other intruders (Wickett and Corkum 1998). We think that egg mortality as a result of predation is low because of the effectiveness of round goby males in guarding nests.

The mean number of eggs per nest was greater at the St. Rose site than at the other three sites. However, the number of eggs at Goose Bay may have been underestimated, because poor visibility degraded the quality of the video image. Round goby nests in Europe can contain up to 10,000 eggs, representing clutches of four to six females (Charlebois et al. 1997). We observed fewer eggs in our study, but we believe that more females were required to provide the eggs in Great Lakes nests because of lower fecundity of small females. The largest round goby (140 mm) in the Detroit River in 1996 was smaller than those observed in the St. Clair River (up to 250 mm). The lack of older, larger fish in the Detroit River is likely because the round goby population is younger (1993) than the St. Clair River population (1990), the site of the first discovery of round gobies in the Great Lakes.

Egg number was significantly correlated to body size in an apparent linear relation, with number of eggs increasing with body size. However, a female round goby in captivity can produce a new batch every 18–20 d up to six times a season (Rashcheperin 1964, cited by Kovtun 1978). In intensive culture, a female can produce up to 10 batches per season (Charlebois et al. 1997). In the wild, females normally produce from two to four batches of eggs per season (Kovtun 1978; Charlebois et al. 1997). Given our estimated production of three spawning events per season at our sample site in 1996 and a batch fecundity of 84 to 606 eggs per individual, we estimate an absolute fecundity of from 252 to 1,818 eggs per round goby female in the Great Lakes. These values are below or just within the lower end of the range (328 to 5,221 eggs) reported by Kovtun (1978) for round gobies in the Sea of Azov.

Although our study did not focus on egg size, the relatively large (≈3 mm) egg size of round gobies may give rise to juveniles that are superior in some way (e.g., in their ability to survive until food resources are found). In gobiids, there is no clear association between egg size and maximum body length (Miller 1984), but in salmonids, large eggs produce large juveniles (Beacham et al. 1985). Females of many amphidromous gobiids with minimal bestowal (reflected in small egg size) produce offspring that are washed downstream after they hatch and then spend about a month at sea feeding on plankton before returning to streams (Miller 1984). In contrast, round goby females have among the highest levels of reproductive effort among gobiids, and the resulting offspring are demersal (Miller 1984). Studies are needed to determine if it is egg size and associated enhanced survival of juveniles and/or fecundity that leads to the reproductive success in round gobies.

The round goby will likely compete with many Great Lakes fishes, particularly those with similar life history strategies. The round goby is already considered to be the main cause for year-class failures of the mottled sculpin *Cottus bairdi* in the St. Clair River and southern Lake Michigan (Jude et al. 1995; Jude 1997). In the laboratory, a round goby will drive resident mottled sculpins out of shelters (Dubs and Corkum 1996). The round goby also might compete with other cavity-nesting species, such as the slimy sculpin *Cottus cognatus,* the deepwater sculpin *Myoxocephalus thompsonii,* the johnny darter *Etheostoma nigrum,* the northern madtom *Noturus stigmosus,* and the brindled madtom *Noturus miurus.* Individual fecundity for the mottled sculpin (69 to 406 eggs per female; Bailey 1952) is similar to that of the round goby; fecundity for the brindled madtom ($n = 40$; Scott and Crossman 1973) is substantially lower than that of the round goby. The madtoms are perhaps the least vulnerable species, because their spawning season barely overlaps with the round goby spawning season (Taylor 1969; MacInnis 1998) and their pectoral and dorsal spines can be used for defense (Scott and Crossman 1973).

The large reproductive capacity of the round goby and its extensive reproductive season also threaten species that spawn only during a limited period. In Europe, male round gobies appear in spawning habitats early in the spring and set up territories before the females arrive (Kovtun 1980). These round gobies could then reduce the spawning success of sculpins and darters by driving them from nests or by eating their eggs. The high reproductive potential of the round goby may favor the continued expansion of round gobies throughout the Great Lakes.

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