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Reproductive Habits of Round Gobies

Lynda D. Corkum, Andrew J. MacInnis and Robert G. Wickett
Department of Biological Sciences
University of Windsor
Windsor, ON N9B 3P4
(519) 253-4232 ext. 2717 Fax: (519) 971-3609
email: corkum@server.uwindsor.ca

ABSTRACT

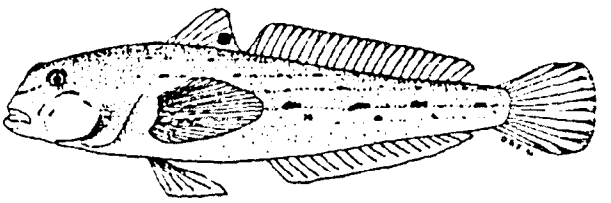
We summarize reproductive habits of an exotic fish, the round goby, in the Detroit River and western Lake Erie. Round gobies in the Detroit River grow faster, mature earlier and are shorter lived than European populations. As with other gobies, there is a significant positive relationship between fecundity and female size and, as expected, females are smaller and lower in fecundity than in their native range. Nesting behaviour in these multiple spawners was observed in the Detroit River from May until August. Recent observations of nesting behaviour on shipwrecks in western Lake Erie indicate that round gobies spawn at much greater depths (10 m or more) than previously reported (~2 m) in North America. Also, round gobies are flexible in the positioning of eggs in nests. Eggs are deposited on either the ceiling or floor of nests. Future research will examine implications of round gobies spawning in deeper waters.

INTRODUCTION

A recent acceleration of human initiated species introductions is leading to the globalization of species (Lodge 1993). The risk is that introduced species may lead to the extinction (or reduction in growth and survival) of native species, resulting in an overall decline in biodiversity (Elton 1958). In addition, invaders may modify ecosystem structure by altering energy flow, habitat and community structure.

In the Great Lakes, there are 25 species of non-indigenous fishes representing 13 families (Mills et al. 1993). Two species, the round goby (*Neogobius melanostomus*) and tubenose goby (*Proterorhinus marmoratus*), belonging to the family Gobiidae were first discovered on the U.S. side of the St. Clair River in April 1990 (Jude et al. 1992). Shortly thereafter, in June 1990, Crossman et al. (1992) recorded round gobies in Canadian waters. Round gobies have rapidly dispersed to all five Great Lakes likely as a result of multiple invasions through ballast water transfer from Europe and from place to place within the Great Lakes. The round goby is native to the Black Sea (excluding the south shore), Sea of Azov, Sea of Marmara, Caspian Sea and associated drainages (Charlebois et al. 1997).

The round goby has several characteristics of successful colonizers. Tolerance of a wide range of environmental conditions, a broad diet, aggressive behaviour, high fecundity, nest guarding by males and a large body size compared with species of a similar benthic lifestyle has allowed the round goby to quickly establish populations in all of the Great Lakes. An overview of round gobies in the Great Lakes is provided by Jude (1997).



Introduced species often coexist with native species because spawning times differ between fishes (Moyle et al. 1986). However, in contrast to native species in the Great Lakes, round gobies are multiple spawners with an extended reproductive season. Therefore, spawning periods of round gobies and other native species overlap. Round gobies also have the advantage of being able to defend nest sites aggressively. Thus, the potential exists for round gobies to dominate nesting sites and to produce large numbers of offspring each year. This reproductive strategy has had negative effects on another cavity spawner, the mottled sculpin (*Cottus bairdi*) (Jude et al. 1995). Other cavity spawners, which may be negatively affected, include the johnny darter (*Etheostoma nigrum*), brindled madtom (*Noturus miurus*), and northern madtom (*Noturus stigmosus*). In this paper, we will outline results of our studies and review the literature on other gobiids that may be relevant to reproductive habits in round gobies. Specific aspects of reproductive habits that we address are age at maturity, patterns in fecundity and egg size, sexual selection, spawning, nesting, and parental care.

AGE AT MATURITY

Sexual dimorphism is more pronounced in the round goby than for other gobioid fishes. Adult round goby males are characterized by their large size at maturity, enlarged cheeks and overall charcoal-black colouration when breeding (Nikol'skii 1963; Miller 1984). In sand gobies (*Pomatoschistus minutus*), spawning females have a distended belly and characteristic black markings around the eye. Secondary sexual coloration has yet to be reported in female round gobies.

The life span of round gobies in their native range is about 4 years, but some specimens may live up to 7 or 8 years (S. Rudnicka, Inst. of Fisheries, Bulgaria, personal communication). In Europe, male round gobies mature at 3-4 y and generally survive a single reproductive season, whereas females mature at 2-3 y. Within a cohort, individual gobies may exhibit differing growth strategies with some individuals growing faster and maturing earlier and others growing slower and maturing later (Bil'ko 1971). Round gobies grow faster, mature earlier and are shorter lived in the Detroit River than in European populations (MacInnis 1997). Age (determined using otoliths) at maturity for females in the Detroit River is 1-2 y, whereas males mature at 2-3 y (MacInnis 1997).

PATTERNS IN FECUNDITY AND EGG SIZE

Smith and Fretwell (1974) suggested that maternal size may influence offspring growth since females of different sizes have different amounts of resources to allocate to offspring. Larger females could have more eggs, larger eggs, or both more and larger eggs than small females (Berrigan 1991). While an increase in egg size is associated with decreased fecundity (the number of eggs in the ovaries of a female fish), the size of young at hatching and their subsequent survival increases with egg size. These factors may be an important reason for the success of the round goby in the Great Lakes.

There is a great range in absolute fecundity in round gobies in their native range. In the Sea of Azov, round goby fecundity increases from year 1 (328 to 3735 eggs) to year 3 (1665 to 5221 eggs) per gravid female (Kovtun 1978). The number of eggs produced by a single round goby female in the Sea of Azov may vary from 200 to 9,771 (Kovtun 1978). In the Detroit River, there is a linear relationship between standard length (r^2=0.76, P<0.001) or weight (r^2=0.76, P<0.001) of females and number of eggs (MacInnis 1997). Depending on body size, mature females of round gobies in the Detroit River contain 84 to 606 ripe eggs (MacInnis 1997). SCUBA divers (W. Ray, University of Windsor, personal communication) reported the maximum length of round gobies (ca. 250 mm) in the St. Clair River near Sarnia, Ontario, to be much larger than the largest round goby (140 mm) in the Detroit River. The lack of older, larger fish in the Detroit River is probably because the Detroit River population is younger (1993) than the St. Clair River population, the site of the first discovery of gobies in the Great Lakes (1990).

Although egg size is often correlated with body size in fish (Fleming and Gross 1990), and large eggs produce large juveniles (Fowler 1972; Beacham et al. 1985), there is no clear association between egg size and maximum body length (Miller 1984). In-

traspecific variation in egg size has been observed in different populations of gobiids (Brothers 1975) and egg size reduction occurs over the breeding season (Kulikova 1977 cited in Miller 1984). Females of many amphidromous gobiids with minimal bestowal (reflected in small egg size) produce offspring that are washed downstream as soon as they hatch and spend about a month at sea as pelagic larvae feeding on plankton before returning to streams (Miller 1984; Moyle and Cech 1996). In contrast, females of the round goby have among the highest levels of reproductive effort among all gobiid fishes and the resulting offspring are demersal (Miller 1984).

SEXUAL SELECTION

Research on sexual selection in gobies has been ignored, yet it is a potential mechanism for population control. Recently, Forsgren (1997) has summarized tactics in mate selection by animals (threshold criteria, sequential comparison, one-step decision, pool comparison and random mating) from the theoretical literature (Janetos 1980; Wittenberger 1983; Real 1990). To optimize fitness, female sand gobies use the threshold-criterion tactic where females inspect males in sequence and choose the first male to meet some minimum criterion (Forsgren 1997). Although sand gobies are bottom dwelling fish, females swam up into the water column (up to 50 cm above the bottom) when searching for mates (Forsgren 1997). In fact, many benthic fishes temporarily rise off the bottom to spawn (Moyle and Cech 1996) or feed (Corkum, personal observation). Costs for mate selection include energy and time expenditures, predation and loss of mating opportunities while evaluating other males.

Nest site abundance is likely an important factor influencing both intrasexual and intersexual selection. In Europe, preferred site distance between round goby nests is 5-10 m (S. Rudnicka, personal communication). Sand gobies (*Pomatoschistus minutus*), colonized artificial nests (flower pots) positioned 2 m apart, but this may reflect colonization of a pool of males without natural nests (Forsgren et al. 1996). In the Detroit River, we set artificial nests made of ceramic tile (15 cm long x 10 cn wide x 5 cm high) in rocky and sandy habitats to examine nest occupancy by round gobies. Thirty-six nests were set one metre apart in a 6 m x 6 m grid at four sites. It was not unusual for adjacent nests to be occupied at any of the sites and eggs were present from early June (when the field study began) until August 13, 1996 (MacInnis 1997). Field observations indicate that spawning by round gobies in the Detroit River begins in May.

Sand goby females seem to use two rules in selecting a mate, male size and courtship display (both intensity and coloration) (Forsgren 1997). When nests are scarce, larger males frequently occupy nests. Smaller males are able to hold nests only when nests sites are abundant (Forsgren et al. 1996). Because male conspecifics prey on eggs in nests, egg survival is higher in nests defended by large males (Bisazza et al. 1989). When nest sites are scarce, females may ignore all rules, become less choosy and mate with the first male encountered. Thus, altering nest site abundance would affect mating success. Round gobies use some structure (rocks, wood, debris) for nests or burrow in the sediment. By eliminating or altering habitat structure, mating success in round gobies should decline. However, the prospect of eliminating habitat structure or modifying potential habitats on a large scale is unlikely.

Female gobies have developed a strategy in which they mate with males that already have eggs in their nests (Forsgren et al. 1996, Kraak and Weissing 1996). Since guarding males of many species of gobies are known to eat eggs or offspring (Kraak & Weissing 1996), this strategy may dilute the risk of the parental male eating newly laid eggs. Thus, the chance of eggs surviving in a nest are greater if several females lay eggs in a nest than if only one female lays eggs in a nest. Round goby males are thought to die after breeding (Charlebois et al. 1997); however, if male round gobies do obtain energy gains from filial cannibalism, then the life expectancy of the parental male may be longer than currently thought.

SPAWNING

Most gobiids are iteroparous (repeat-spawners). The round goby is a multiple spawner with an extended reproductive season and the length of the reproductive season varies depending on geo-

graphic location (Miller 1986). In the Black and Caspian seas, spawning may begin as early as April and continue until the end of June (Romania) or as late as September (Varna, Bulgaria) (Miller 1984). Rashcheperin (1964 cited in Kovtun 1978) reported the extent of the reproductive season in the Sea of Azov from the end of April until the beginning of August where females deposited 5 to 6 batches of eggs at intervals of 18-20 days. Although the sex ratio is equivalent in young round gobies in the Sea of Azov, the ratio becomes female biased (up to 1:1.9) in the spawning population. The female biased sex ratio results in a decline in offspring survivorship because there are fewer males available to guard nests. MacInnis (1997) estimates that individual female round gobies spawn three times per season in the Detroit River. Spawning by round gobies is dependent on water temperature (9 to 26°C) (Charlebois et al. 1997). Moreover, if temperature requirements are satisfied, round gobies may spawn throughout the entire year (Moiseyeva and Rudenko 1976).

Tavolga (1956) found that *Bathygobius soporator*, a species within the same subfamily (Gobionellinae) as the round goby, uses chemical, acoustic and visual communication during spawning. Pheromones are often important for recognition of sex and sexual condition in gobiids (Tavolga 1956; Colombo et al. 1982). For example, aggressive behaviour is displayed among gobies of the same sex; passive behaviour is exhibited between gobies of the opposite sex (MacGintie 1939). Blind gobies likely rely completely on chemical communication (MacGintie 1939). Protasov et al. (1965) was the first to report the use of acoustic signals by round gobies in the Sea of Azov. Cheryl Murphy (University of Alberta, personal communication), studying reproductive behaviour of round gobies from the Detroit River, suggests that round gobies use a variety of signals (pheromones as well as visual and acoustic cues) in courtship behaviour. Once a round goby male has used all available signals to attract females, the male coats the surface of the nest with an exudate from the cement gland and eggs are then glued to the undersurface of the nest presumably by females (Charlebois et al. 1997).

Two morphs of male round gobies have been identified (Type I, parental nest guarding males and Type II, sneakers). Sneaker males (with large testes and genital papilla) do not exhibit the breeding colouration of parental males and are present within round goby populations of the Detroit River and western Lake Erie (C. Murphy, personal communication; R. Wickett, personal observation). Sneaker males also have been reported for common gobies (*Potamoschistus microps*) in the laboratory (Magnhagen 1992) and sand gobies in the field (Forsgren 1997). Forsgren (1997) reported that sneaker males occurred in about 12% of all spawnings. There are substantial energy savings for sneakers that avoid both parental care and nest defense.

NESTING

Fertilization rates in the round goby may be as high as 95% and a male can hatch up to 95% of the eggs in his nest (Charlebois et al. 1997). Survival rates of young are unknown. Although there are no data for the round goby, nest size is positively correlated with male size in other fishes with a similar reproductive strategy (Bisazza and Marconato 1988; Bisazza et al. 1989; Magnhagen and Kvarnemo 1989). Nest densities and subsequent territorial areas also are related to the availability of suitable nest sites (Almada et al. 1994).

Nests are typically constructed under rocks and logs or within any other suitable cavity in shallow water (0.2 to 1.5 m) (Charlebois et al. 1997). In the Detroit River, round gobies readily colonized artificial nests placed at water depths between 1.5 and 2 m (MacInnis 1997). Nests were made of ceramic tile and a single opening with a half section of PVC pipe underneath in both rocky and sandy habitats near Peche Island.

Our recent observations of round gobies on shipwrecks in western Lake Erie revealed that round gobies will reproduce at much greater depths than those previously reported in North America. Robert Wickett observed several black males, gravid (swollen) females and young-of-the-year on the Northern Indiana, a shipwreck in western Lake Erie (41° 54′ N, 82° 31′ W) at depths of 7.6 to 10.7 m. Males defending eggs and young-of-the-year in nests were observed at another shipwreck, the M.I.

Wilcox (41° 59' N, 82° 57' W) offshore of Colchester, Ontario, at depths of 7 m. On the M.I. Wilcox, we observed a guarding round goby male pick up debris from an exposed nest and "spit" material into the water column. A nearby yellow perch captured the discarded debris. Thus, predators that seem to be attracted immediately to exposed nests may obtain energy benefits without interacting directly with prey.

Previously, Izergyn and Dushkina (1994) reported that round gobies spawned on artificial reefs ("polychlorvinyl pipes and polystyrol "little houses" kapron nets, etc.") positioned at depths of 5-7 m in the Sea of Azov. During the period (1984-1990) in which artificial reefs were examined, recruitment of round goby stocks increased ten-fold (Izergyn and Dushkina 1994).

Other observations of round gobies occupying deep water typically relate to their over-wintering habitat. For example, round gobies may be found in 50-60 m of water in the Black Sea during winter (Miller 1986). In the St. Clair River, there is an apparent inverse relationship between the number of round gobies and water depth; however, larger gobies are present throughout the river (Jude et al. 1995). Young-of-the-year round gobies have been observed to migrate offshore at fall turnover in the central basin of Lake Erie (Knight 1997).

Egg density in nests is variable and may be a function of several factors including spawning period, size of parental male, water temperature, or the physical structure of the nest. In the Detroit River, cone-shaped (2 mm x 3-4 mm), adhesive eggs are laid in a single layer and densities of eggs in artificial nests are about 40 per cm^2. The number of eggs in nests calculated from video images of artificial nests range from 644 to 9462, indicating that up to 15 females may lay eggs in a single nest (MacInnis 1997). In Europe, female round gobies tend to have a higher fecundity and therefore fewer females (4-6) lay eggs in a given nest.

In gobiids, eggs are usually attached to the ceiling of nests. The cylindrical/cone-shaped eggs are easily packed together in a single layer, enabling the male to fan a compact patch of eggs efficiently. Moreover, egg position (hanging) and shape aid in cleansing since water will flow around the egg surfaces and sediment particles are easily shed (Miller 1984).

Our recent observations suggest that round gobies are more flexible in the positioning of eggs in nests than previously reported. Typically, eggs are laid on any hard overhead surface in a nest that is guarded by a male. However, examination of nests on shipwrecks in Lake Erie revealed that eggs are deposited primarily on the bottom surface or floor of the nest. The extent to which this occurs and under what conditions is unknown. The deposition of eggs on the floor of the nest may affect egg survival and hatching success if increased effort is required by males for nest maintenance.

Kovtun (1980) reported high (50-70%) mortality due to predation in large nests (8,000 to 10,000 eggs deposited by 4 to 6 females) compared to slight mortality in small nests (2,000 to 3,000 eggs deposited by 1 to 2 females). The increase in mortality due to predation is because a large batch of eggs is more exposed. Also, eggs at the periphery of large nests receive insufficient aeration, causing a further increase in mortality.

PARENTAL CARE

Sargent and Gross (1993) argue that parental care in fishes is typically provided by males rather than females because energy saved in gamete production (reproductive effort) for males can be used for other types of offspring investment (i.e., parental care). Reproductive effort in fish is reflected in the gonadosomatic index (GSI), the percentage of ripe gonadal to somatic weight. In gobiids, male GSI is 0.3 to 3.6 %; for females, the GSI is typically 12 to 25 % (Miller 1984). Thus, most gobiids have a reproductive strategy that is characterized by male parental care of eggs (maintaining oxygen levels by fanning eggs and nest maintenance) and nest defense (aggressive behaviour towards intruders).

Our observations of round goby males guarding nests indicate that males defend nests aggressively (approach, chase, bite, butt) against intruders (round gobies, rock bass, young-of-the-year smallmouth bass, yellow perch, logperch). The most suc-

cessful intruders were immature round gobies. These fish reached the periphery of an exposed nest and fed on eggs.

Males are assumed to stop feeding when they guard nests against predators and fan eggs to ensure sufficient aeration and reduce fungal infections. It is unknown if nest guarding males will survive one or more spawning events throughout a season. We have videotaped males defending nests against other gobies. Two parental males fought for extended periods over exposed eggs. Although neither male was injured, the energy costs of fighting must be high.

FUTURE RESEARCH

Future research will test implications of round gobies spawning in deep waters. Do abiotic factors such as water temperature alter reproductive success between on and off-shore habitats. Larger eggs are characteristic of females developing at lower temperatures in many ectothermal organisms including fish (Oncorhynchus kisutch) (Fleming and Gross 1981). Accordingly, egg size and size of offspring may differ among round gobies that reproduce in deeper, colder waters than in shallow, warmer waters. If so, reproductive success of round gobies in the deeper waters of Lake Erie may be greater than in shallower waters. Alternatively, if spawning on shipwrecks is restricted to western Lake Erie where water is well mixed, water temperature may be less important than other factors affecting reproductive success in round gobies.

Other species of fish, such as rock bass and smallmouth bass, are commonly observed on shipwrecks in Lake Erie. Many fishes are known to be attracted to artificial reefs (Brock 1994). The presence of such piscivores in close proximity to nesting gobies raises several questions regarding predation risk and nesting success of round gobies in similar near and off-shore habitats.

We anticipate that as in the Sea of Azov, recruitment of round gobies will increase substantially in Lake Erie owing to the presence of artificial reefs (shipwrecks) and natural reefs.

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