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Aspects of the life history of the round goby, Neogobius melanostomus (Perciformes: Gobiidae), in the Detroit River (Ontario, Michigan).

Andrew Jason. MacInnis
University of Windsor

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Aspects of the life history of the round goby, *Neogobius melanostomus* (Perciformes: Gobiidae), in the Detroit River

by

Andrew J. MacInnis

A Thesis Submitted to the
Faculty of Graduate Studies and Research
Through the Department of Biological Sciences
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of Master of Science at the
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Abstract

This study was designed to investigate several aspects of the life history of the exotic round goby in the Detroit River including age, growth, survivorship, fecundity, and reproduction.

Immature and female round gobies dominated the trawl collections during 1996 with adult males being rare or absent. Annulus formation in the otolith was determined to occur at the end of May. Age 1 round gobies were consistently the most abundant age class followed by age 2. Only 3 individuals greater than age 2 were collected and age 0 individuals did not appear in the collections until the end of July. The relationship between otolith radius and standard length was non-linear and showed increased scatter with increased fish size. Back-calculation of size at age was most accurate using the non-linear body proportional hypothesis. Overall fits of the von Bertalanffy growth function were relatively poor because of the variability in size at age. It was not possible to determine differences between the growth rates for males and females because of limited data for the males.

The spawning season for the round goby extends from May until early August in the Detroit River. Female round gobies are maturing as small as 43 mm SL and age 1. The mean fecundity for the round goby is 198 eggs (range 84 - 606 eggs, S.E. = 11.03) and was significantly correlated to both length and weight. The fecundity of age 1 (164 ± 9.24 S.E.) females was significantly less the fecundity of age 2 (218 ± 16.33 S.E.) females.

A field experiment using artificial nests was used to examine reproductive success. The number of eggs in a nest was estimated using computer image analysis and the results indicate that up to 15 females were spawning in each nest. Few differences in the number nests occupied were observed between the cobble and sand substrate sites.

A rapid growth rate and early maturity coupled with a high fecundity and extended reproductive season contribute to the success of the round goby in the Detroit River. These factors will ensure the continued expansion of the round goby throughout the Great Lakes.

Acknowledgements

I would like to express my thanks to my supervisor Dr. Lynda Corkum for her advice and support during the time I spent at the University of Windsor. I would also like to thank my committee members Dr. P.F. Sale, Dr. J.H. Leach, and Dr. J. Cohen for their helpful input and advice. Additional thanks go to Dr. P.F. Sale for use of his compound microscope and image analysis system. Thanks also Dr. H.J. MacIsaac for the use of his underwater video system and to Dr. B. Danilowicz for his assistance with otolith reading and data analysis.

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To Sara and my family, thanks for all your support and for listening to me rattle on about gobies and other fish.

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Table of Contents

List of Tables

List of Figures

Introduction

Many biological invasions can be viewed as natural evolutionary processes (Hengeveld 1989, Vermeij 1991), though in recent times these processes have been greatly speeded up due to anthropogenic factors and some may have never occurred naturally without human intervention (Lodge 1993). Of the many introductions of non-indigenous species which have occurred worldwide a large number are never successful and are therefore never reported (Simberloff 1981). Successful invasions are more often reported, though even these may represent a biased sample of intentional introductions and invasions that have had a negative impact. Further confounding a true representation of the number of non-indigenous species established worldwide are cryptogenic species. These are species that cannot be defined as either native or introduced in a given region (Carlton 1996). In general, successful invasive species are those which have a tolerance of a wide range of environmental conditions (Ehrlich 1989). Three different modes of entry for non-indigenous species are known (Ruesink *et al.* 1995). These are intentional introductions, escaped individuals following import, and accidental introductions, usually due to anthropogenic transport or habitat modification.

Impacts of non-indigenous fishes

Introductions of aquatic species into North America have been occurring since at least the 1800s and have been both intentional and accidental. Non-indigenous fishes fall into both of these categories, though a considerable number of fish introductions have been intentional (> 40% in the United States (Courtenay *et al.* 1984)). The primary reason for intentional introductions is that introduced fish are perceived as superior to the native fish community for food or sport fisheries, or for biological control (Li and Moyle 1993). Through intentional introductions, largemouth bass (Centrarchidae: *Micropterus salmoides*), rainbow trout (Salmonidae: *Oncorhynchus mykiss*), brown trout (Salmonidae: *Salmo trutta*), and mosquitofish (Poecilidae: *Gambusia affinis*) have become distributed world wide.

Moyle *et al.* (1986) listed a number of possible impacts that introduced fishes may have on the native fish community. These included elimination of native species, reduced growth and survival of native species, changes in community structure, or no effect at all. The most dramatic example of the elimination of native species occurred in Lake Victoria where an estimated 200 species of endemic cichlids were driven to extinction following introduction of the Nile perch (Goldschimdt *et al.* 1993). Waters (1983) documented the replacement of native brook trout by brown trout over a 15 year period in a Minnesota stream. In the Great Lakes, the sea lamprey was responsible for the near extirpation of native lake trout and coregonids (Lawrie 1970). Few cases of reduction in the growth and survival of native fishes following the introduction of a potential competitor have been documented (Moyle *et al.* 1986). One recent example would be the year class failure of the mottled sculpin in the St. Clair River following the introduction of the round goby. However, the mottled sculpin is persisting in the deepest parts of the river (Jude *et al.* 1995). In general, fish communities are able to adapt quite quickly to the introduction of new species and the structure of the community is quite persistent although the species present may change (Moyle 1986, Moyle and Light 1996). In cases where there is no observed effect, Moyle *et al.* (1986) suggest that caution be used in making any conclusions.

Non-indigenous fishes in the Great Lakes

In the Great Lakes, introductions of non-indigenous organisms have been occurring since at least the early 1800's. Of the more than 139 non-indigenous aquatic organisms known from the Great Lakes, the non-indigenous fishes are represented by 25 species in 13 families (Mills *et al.* 1993). Some of the more important fish species, both ecologically and economically, that have been introduced either intentionally or accidentally are the common carp (Cyprinidae: *Cyprinus carpio*), the sea lamprey (Petromyzontidae: *Petromyzon marinus*), several species of Pacific salmon (Salmonidae: *Oncorhynchus* spp.), and more recently the ruffe (Percidae: *Gymnocephalus cernuus*) (Mills *et al.* 1993, Leach 1995).

The common carp was originally introduced with the intent of creating a food fishery (Crossman 1968). However, it quickly became abundant in near shore areas and impacted native fish species through competition for food and destruction of habitat through its feeding habits (Emery 1985). To date, the sea lamprey has been probably the most detrimental fish introduction in the Great Lakes and caused the near extirpation of lake trout and coregonids in the upper lakes and subsequent collapse of the commercial fishery for these species (Lawrie 1970). The severe decline in the lake trout population and in the populations of other large piscivores, such as burbot, led to dramatic increases in the populations of alewife, another exotic in the Great Lakes (Leach 1995). This prompted fisheries managers to introduce a number of species of Pacific salmon in the hopes of controlling the alewife population and creating a new sport fishery (Leach 1995).

The introduced Pacific salmonids have negatively impacted the native salmonids through competition, predation, habitat modification, genetic effects, and disease (Krueger and May 1991).

The ruffe is a more recent invader of the Great Lakes, having been first discovered in the St. Louis River, Lake Superior in 1986 (Biological Resources Division, U.S. Geological Survey). The ruffe has the potential to severely impact several native species in the Great Lakes, particularly the yellow perch (Busiahn and McClain 1995).

Two more exotic fish species belonging to the family Gobiidae were discovered in the Great Lakes in the St. Clair River in April 1990 on the U.S. side (Jude *et al.* 1992) and on the Canadian side in June 1990 (Crossman *et al.* 1992). The first goby found was the tubenose goby, *Proterorhinus marmoratus*, native to the Black Sea and Caspian Sea in Europe. Since its first discovery the tubenose goby has expanded its range to include Lake St. Clair and the upper Detroit River (Muzzall *et al.* 1995, Thomas and Haas 1996, this study). The round goby, *Neogobius melanostomus*, was discovered at the same time as the tubenose goby although fewer individuals were collected (Jude *et al.* 1992).The round goby also is native to the Black Sea and the Caspian Sea. Interestingly, the tubenose goby is endangered in its native range due to habitat destruction (Jude *et al.* 1992) while the round goby has expanded its range into the Moscow River basin and several reservoirs on rivers connected to the Black Sea and Caspian Sea (Marsden *et al.* 1996). Round gobies had also expanded into the Aral Sea but have since died out due to an extreme increase in salinity (up to 200 ppt). In 1990, the round goby also was reported from the Gulf of Gdansk in the southern Baltic Sea (Skora and Stolarski 1993). Both the round goby and the tubenose goby are believed to have arrived in North America via ballast water transfer.

Range and impacts of the round goby in the Great Lakes

After the initial discovery of the round goby in the St. Clair River (Crossman *et al.* 1992, Jude *et al.* 1992), it has spread rapidly throughout the Great Lakes. The round goby is now found throughout the St. Clair River, Lake St. Clair, and the upper Detroit River. More recent records of *N. melanostomus* from the Grand Calumet River and South Haven (Lake Michigan), The Grand River and Red Creek (Ohio), the Port Colbourne (Lake Erie) and in Duluth Harbour (Lake Superior) and Cape Vincent (Lake Ontario) are likely the result of intra-basin ballast water transfers (Ontario Ministry of Natural Resources Fact Sheet, 1995; Minnesota Sea Grant News Release, 1995). However, the round goby and gobies in general are able to colonize new areas successfully (Hoese 1973, Vaas *et al.* 1975, Middleton 1982, Al-Hassan and Miller 1987, Ryan 1991, Skora and Stolarski 1993). Gobies may be especially adapted to transport in ballast water due to their ability to tolerate degraded water conditions and their cavefish-like lateral line system (Miller 1986, Gee and Gee 1991). Of the 10 species of fish listed by Carlton (1985) as having been likely transported to their new location in ballast water, four were Gobiidae.

One of the largest established populations of *N. melanostomus* is in the St. Clair and upper Detroit rivers including Lake St. Clair (Thomas and Haas 1996). Other large populations of the round goby are also present in southern Lake Michigan and the central basin of Lake Erie (Knight 1996, Marsden *et al.* 1996b). In the St. Clair River, the round goby has quickly become one of the most abundant species of benthic fish with densities as high as 1 goby / m^2. Densities of the round goby of 1.8 - 17 / m^2 have been reported from the central basin of Lake Erie (Ohio) and of 40 / m^2 in Grand Calumet Harbour, Lake Michigan (Marsden *et al.* 1996). In the St. Clair River, the round goby has had a detrimental impact on two benthic fishes, the mottled sculpin (Cottidae, *Cottus bairdi*) and to a lesser extent the logperch (Percidae: *Percina caprodes*) (Jude *et al.* 1995). The round goby also has the potential to impact a number of other benthic fish species throughout the Great Lakes including the darters (Percidae: *Etheostoma* spp., *Percina* spp.), the sculpins (Cottidae: *C. bairdi*, *C. cognatus*, *Myxocephalus thompsoni*), and the madtoms (Ictaluridae: *Noturus* spp.). Some of these species that may potentially be impacted by the round goby are listed by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC). The brindled madtom, *Noturus miurus* is listed as vulnerable while the channel darter, *Percina copelandi*; the margined madtom, *Noturus insignis*; and the deepwater sculpin, *Myxocephalus thompsoni* are listed as threatened by COSEWIC (Campbell 1996). Besides performing a variety of roles in the benthic community these native fishes are also important to the major piscivores; lake trout (Salmonidae: *Salvelinus namaycush*), smallmouth bass (Centrarchidae: *Micropterus dolomieu*), and walleye (Percidae: *Stizostedion vitreum*). If the round goby does displace these species it is unknown what the effect may be on these and other piscivores as well as other benthic fishes.

Predatory fish may switch to feeding preferentially on the round goby because of its abundance or to feeding more heavily on other prey items such as cyprinids. Fish are able to change their behaviour in response to many stressors including food availability

(Dill 1983). Currently, it is unknown to what extent native piscivores prey on gobies but gobies are used extensively by anglers as bait for smallmouth bass. Species that have been reported to prey on *N. melanostomus* in the Great Lakes include smallmouth bass, walleye, rock bass, yellow perch, mottled sculpin, tubenose goby, stonecat and brown trout (Jude *et al.* 1995). Smallmouth bass will probably be one of the major predators of round gobies as all of the smallmouth bass examined by Jude *et al.* (1995) contained round gobies in their stomachs. However, the round goby may be a more difficult prey item to capture as its neuromasts are free on its body as opposed to being partially enclosed in a canal (lateral line) which is the case for all native fish species in the Great Lakes (Miller 1986). This may confer an advantage to the round goby since it is more sensitive to motion in the water and therefore able to detect predators and prey at a greater distance (Jude *et al.* 1995). The round goby may also be cannabalistic on eggs and newly hatched juveniles. Potentially, the round goby could be a predator on the eggs of walleye and bass as well as on the demersal eggs of other species. Round gobies have also been shown to be an effective predator of lake trout eggs and fry which may threaten lake trout rehabilitation efforts in the Great Lakes (Chotkowski and Marsden 1996).

Certainly the food web will be weakened with the predominance of the round goby because the goby is replacing a variety of native fish species with differing ecological roles. *Neogobius melanostomus* has and will continue to establish itself by forcing native benthic fishes out of optimal spawning sites and thereby limiting their reproduction and also through predation on the smaller native species (Jude *et al.* 1992). The round goby also has the potential to alter food web dynamics considerably throughout the Great Lakes as it is an extensive predator on zebra mussels (Ghedotti *et al.* 1995, Jude *et al.* 1995, Ray and Corkum *in press*). Zebra mussels have shifted the food web in Lake Erie from being pelagic-oriented to being benthic-oriented due to their extensive filtering capabilities (MacIsaac *et al.* 1992, Leach 1993). Depending on the extent to which native piscivores prey on the round goby, energy flow may shift back to the pelagic component of the food web (Jude *et al.* 1995).

Introductions of gobiid fishes elsewhere in the world have disrupted native fish communities (Brittan *et al.* 1970, Vaas *et al.*1975, Middleton 1982, Matern and Fleming 1995, Skora 1996 cited in Marsden *et al.* 1996) and this can also be expected of the round goby. In San Francisco Bay, the goby *Tridentiger bifasciatus* is threatening the already endangered tidewater goby (*Eucyclogobius newberryi*) (Matern and Fleming 1995) and the yellowfin goby, *Acanthogobius flavimanus*, has been linked to changes in fish abundance in Suisun Marsh, California (Meng *et al.* 1994). Invasion of the black goby, *Gobius niger*, was blamed for the decline of the sand goby, *Pomatoschitus minutus*, in the Veerse Meer, Netherlands.

Biology of the round goby

The round goby can attain a maximum length of up to 220 mm and commonly reaches lengths greater than 100 mm. This is considerably larger than most native benthic fishes in the Great Lakes such as the mottled sculpin ($\bar{x}$ = 76 mm, max. = 132 mm) and the logperch ($\bar{x}$ = 89 mm, max. = 121 mm) (Scott and Crossman 1973). The round goby also appears to be more aggressive than many native species and has been shown to displace resident mottled sculpins from a shelter in the lab (Dubs and Corkum 1996). The maximum lifespan for round gobies is four years (Miller 1986) but some individuals can live as long as 7 or 8 years (S. Rudnika, Institute of Fisheries, Bulgaria, personal communication). Male round gobies mature primarily at age three and generally only survive a single reproductive season, whereas the females generally mature at age two and at a smaller size than do males (Miller 1984 and 1986). Male round gobies also have a greater growth rate than females after their first year of life (Bil'ko 1971). Within a cohort, individual gobies can also exhibit differing growth strategies with some individuals growing faster and maturing earlier and some growing slower and maturing later (Bil'ko 1971).

The eggs of the round goby are demersal adhesive and are spawned on any hard overhead surface in a nest which is guarded by the male. Males migrate on to the spawning grounds in the early spring and set up territories prior to the arrival of the females (Kovtun 1980). Nests are constructed under rocks and logs or within any other suitable cavity in shallow water (0.5-2 m depth) (Marsden *et al.* 1996; S. Rudnika, personal communication). Males defend the nest against egg predators (primarily other gobies), and fan the eggs to ensure sufficient aeration. A single nest may contain the eggs of several females (Marsden *et al.* 1996). Parental males die after a single reproductive season while females usually spawn for two to three seasons (Miller 1984 and 1986). Males exhibiting an alternative reproductive strategy have been observed in the laboratory (C. Murphy, University of Alberta, personal communication). These males did not exhibit the secondary sex characters of the parental males and were smaller in size than parental males although the gonads were about triple the normal size. These males adopted a satellite spawning strategy (Gross 1991). Female round gobies may spawn up to six times in a single spawning season although 2-4 times per season is more common (Kovtun 1978; S. Rudnika, personal communication).

Objectives

The purpose of this study was to determine some of the life history parameters of the round goby in the Great Lakes, specifically the Detroit River. Chapter 1 presents information on the population structure, age, and growth of the round goby in the Detroit River. An effective protocol for determining the ages of round gobies is presented and validated. Using this protocol it was possible to determine the age and sex structure of the population. The growth rates for male, female, and immature round gobies were described using the von Bertalanffy growth function. The second chapter presents the results of an investigation into the reproductive biology of the round goby. The length of the spawning season in the Detroit River was determined as were the age and size specific fecundities for females. The second part of Chapter 2 presents the results of an experiment using artificial nests to examine reproductive seasonality in the round goby and nest size and density with respect to substrate type.

Chapter 1: Age and Growth

Introduction

Basic life history information is critical to the management of any species (Radtke *et al.* 1988). This information is necessary for determining population structure and dynamics as well as predicting and assessing interactions with other species (Baltz 1990). Currently, little is known of the basic life history parameters of the round goby in North America and its population dynamics are unknown (Marsden *et al.* 1996). Obtaining information on the life history of the round goby in the Great Lakes has been identified as a research priority (Marsden *et al.* 1996). What little information that is known is based primarily on Russian literature from the 1960's and 1970's as the round goby was an important component of the commercial gobiid catch in the Black and Caspian Seas (Miller 1986). However, the round goby population is no longer abundant enough to support a commercial fishery in its native range. This is primarily due to loss of habitat from heavy siltation and low oxygen concentration at the sediment surface (S. Rudnika, Institute of Fisheries, Bulgaria, personal communication).

The round goby can attain a length of up to 220 mm and a lifespan of 4 years (Miller 1986) although individuals with a life span of 7 - 8 years have been reported from the Black Sea (S. Rudnika, personal communication). Males generally mature at an age of 3 years though some mature at an age of 4 years and females mature at a smaller size and an age of 2-3 years (Miller 1986). Adult males are thought to die after a single spawning season (Bil'ko 1976, Miller 1984 and 1986), but to what extent this occurs in the Great Lakes is unknown. Bil'ko (1971) found that male round gobies grow faster than females in their second and third year of growth but that growth rates for both sexes are similar during the first year of growth. It was also noted that mortality rates can vary within a sex because of higher mortality rates for faster growing individuals within the same year class. In the Sea of Azov, year class strength in round gobies is significantly related to the sex ratio of adult males and females (Kovtun 1980). When the number of females exceeds the number of males, survival of juveniles to the underyearling stage is greatly reduced.

Another process which may affect the year class strength of the round goby is the overwinter survival rate of young-of-the-year (YOY) fish. Some freshwater fish species exhibit size-selective winter mortality, where some YOY are unable to attain a size great enough to escape winter mortality (Toneys and Coble 1979, Shuter *et al.* 1980, Post and Evans 1989). In the previous studies, the fish species examined (yellow perch, smallmouth bass, sunfish) are all species with relatively short spawning seasons unlike the round goby which can have a spawning season that extends from May to September (Miller 1986). In this case size-selective winter mortality may be increased, particularly in those fish which hatched latest in the season and had the shortest growing period. This effect was demonstrated by Henderson *et al.* (1988) in the sand smelt, a marine batch spawner with demersal eggs and an extended spawning season. This effect was also seen in largemouth bass and fathead minnows, two Great Lakes fishes with male parental care of the eggs (Toneys and Coble 1979). If size-selective mortality does occur in the round goby the degree to which it occurs will depend greatly upon the length of the spawning season.

An essential component of any study of fish population dynamics is to be able to accurately determine the age of individuals. Daily and annual increments have been shown to occur in the otoliths of many temperate fishes (Brothers *et al.* 1975). Bil'ko (1971) successfully aged round gobies using otoliths mounted on glass slides, but it is not mentioned which otolith pair is used. Presumably, the sagittae were used because of their larger size which facilitates easier handling; also use of the lapilli is a fairly recent trend in the literature (Secor *et al.* 1992). However, the lapilli have the most distinct daily increments and are not subject to shifts in the growth axis as are sagittae (Brothers 1987, Secor *et al.* 1992). The most important component of any age study is proper age validation (Beamish and McFarlane 1983, 1987). It is possible to validate the formation of both daily and annual increments. Back-calculation is a second technique commonly used in age and growth studies which has often been misapplied (Francis 1990). Back-calculation is generally performed without regard to the assumptions or hypothesis of the formula used. Bil'ko (1971) back-calculated round goby sizes using a previously compiled empirical scale. It is not mentioned how the scale was compiled or what the assumptions of the method were.

The primary objective of this study was to describe the age and growth, as well as the age and size structure of the round goby population in the Detroit River. Ageing was accomplished by first validating the occurrence of annual marks in the otoliths and the occurrence of daily increments in the otoliths of YOY. The second goal was to back-calculate size in order to fit the data to a von Bertalanffy growth function so that growth curves for males and females could be compared. This was to determine if sexual dimorphism in size is due to differing growth rates or a result of later maturity in the males. It also was determined if size-selective winter mortality is one of the factors contributing to year class success in the round goby.

Methods

Goby collections:

To determine population structure and growth rates, round gobies were collected every three weeks from the upper Detroit River and western Lake St. Clair (Figure 1.1) during the summer and fall of 1996 using a small otter trawl. The trawl was equipped with 'rockhopper' foot gear and the dimensions of the net opening were 4 m wide by 1 m high. The mesh size of the net was 40 mm stretch measure on the body of the net with 10 mm stretch measure mesh in the cod end. Trawling was conducted from a 23' boat with twin 70 hp outboard engines and the net was operated by hand. The net was towed at an average speed of 2 knots for 10 minutes per haul. Round gobies were collected by trawling on May 6 and 29, June 4 and 17, July 8, September 19, and October 22 of 1996. On July 29, 1996 round gobies were collected by hook and line and no fish were collected during August as no trawl net was available during this period.

All fish captured while trawling were identified and enumerated. Round gobies were kept in aerated coolers for transport back to the lab. There fish were euthanized with CO_2, individually frozen, and stored in sealed Whirlpacks®. Freezing was the preferred method of preservation as it would not damage the otoliths (Geffen 1987)and would cause little change in body shape or weight (Butler 1992). Round gobies were sexed by examination of the genital papilla (Miller 1984) and assigned to one of six categories:

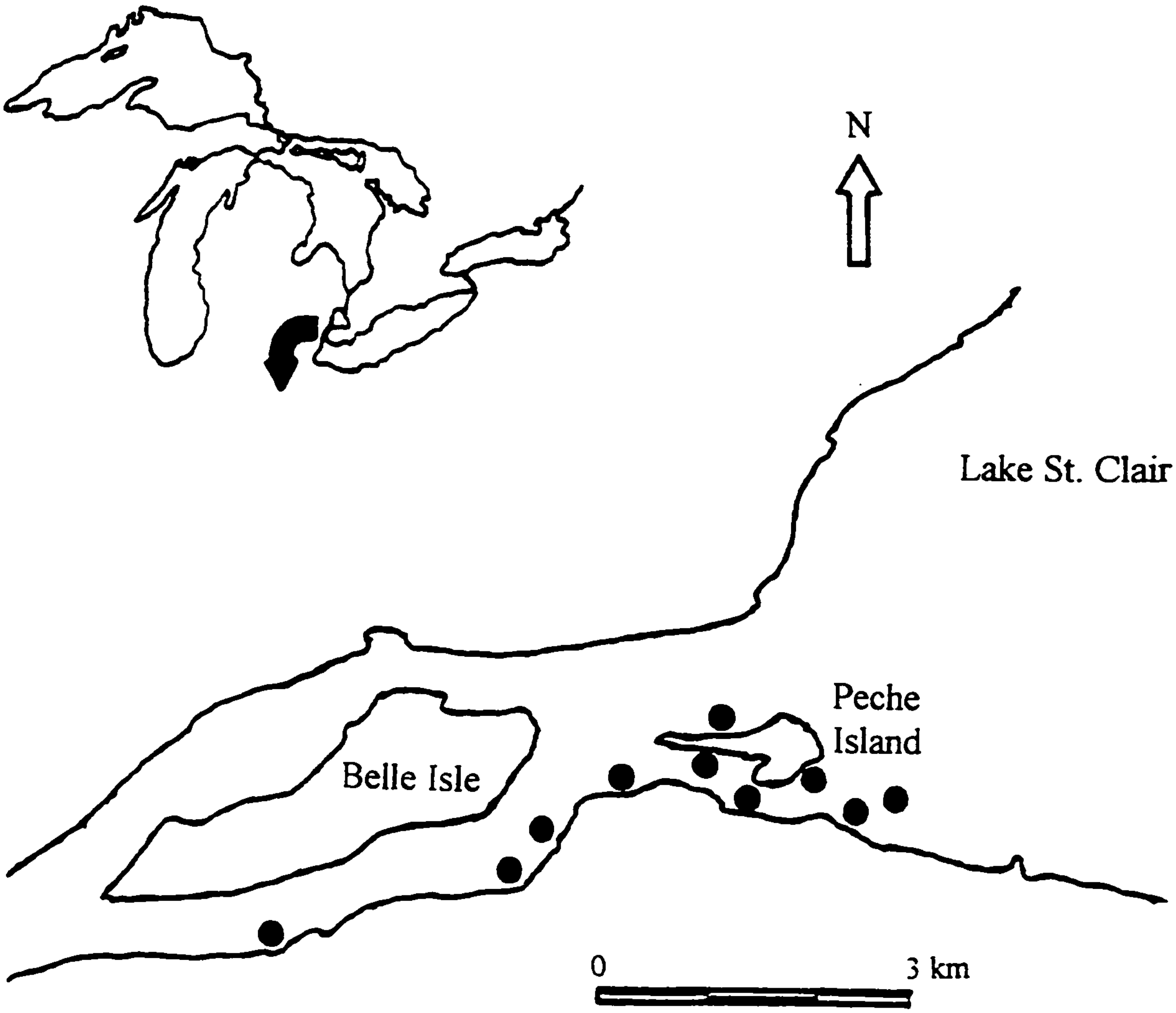


Figure 1.1 The upper Detroit River and southwestern Lake St. Clair showing the locations where round gobies were collected by trawling.

guarding male, sneaker male, immature male, mature female, immature female, and immature (Figure 1.2). Male round gobies have a long, triangular-shaped papilla with a broad base and narrow tip while in females the papilla is shorter and rectangular in shape being broad at both the base and tip. Adult parental males can also be distinguished by their all over dark grey to black colouration and their enlarged cheek muscles (Nikol'skii 1963, Miller 1984). Mature individuals of both sexes can be distinguished by the length and thickness of the papilla with the papilla being larger in the mature individuals. Sneaker males were distinguished from adult males by their small size (approximately $\leq$ 50 mm SL), large genital papilla, and lack of male secondary sex characteristics.

Standard length and weight were plotted to see if the round goby followed the typical weight-length relationship for fishes expressed by the equation:

Equation 1.1 $$W = a L^b$$

where W is weight, L is length, a is a constant, and b is second parameter describing the curve. The parameter b describes the nature of the weight-length relationship for a particular fish species. When b is less than three the fish becomes less rotund as length increases, a value equal to 3 growth may be isometric or the fish may change shape, and a value greater than 3 indicates that the fish becomes more rotund as length increases (Anderson and Gutreuter 1983). The values for a and b were estimated by linear regression after $\log_{10}$ transformation of the data. Relative condition factors were also calculated for individual fish on each sample date using the formula:

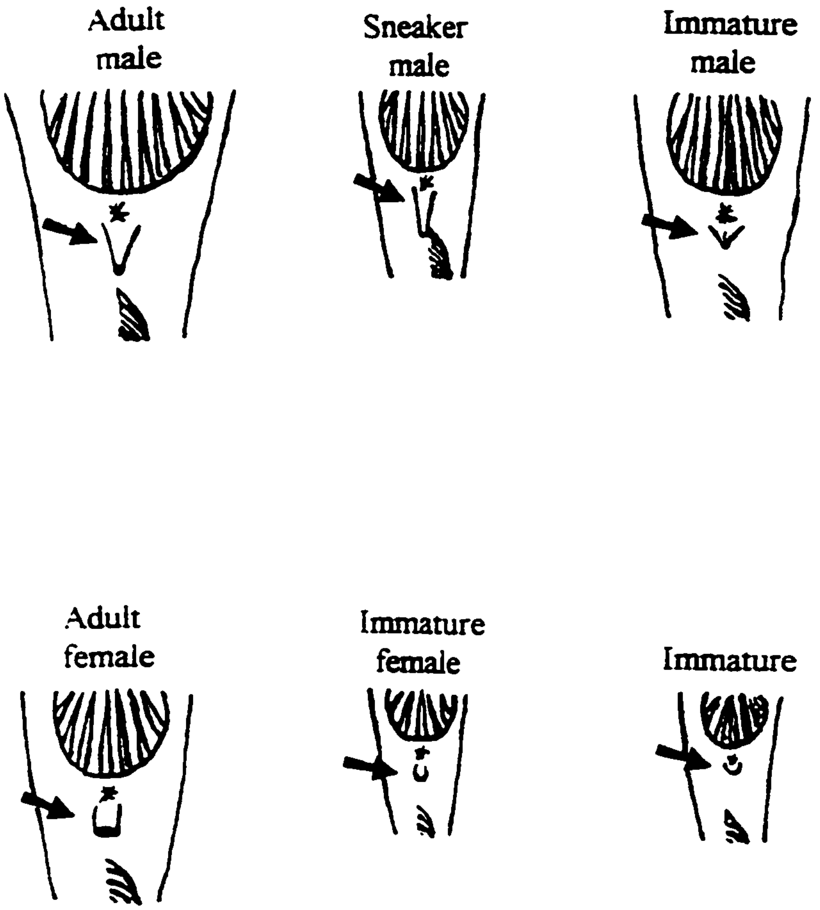


Figure 1.2 The genital papillae of adult male, sneaker male, immature male, adult female, and immature female round gobies. Gobies which were to small for accurate sex determination were classified as immature.

Equation 1.2 $K = W / L^3 \times 100$

where W is weight in grams and L is the length in millimetres. A number of other measures of relative condition have been proposed but indices of this form were determined to be the most appropriate measure of fish condition (Bolger and Connolly 1989).

Ageing:

The otoliths were dissected from the gobies using a stereomicroscope and stored dry in glass vials. The vials were labelled sequentially and each vial contained the otoliths of a single fish. Both the sagittae and lapilli were removed although occasionally it was not possible to locate one of the lapilli or one had been damaged during dissection. The lapilli were the only pair of otoliths used for ageing since they have the most distinct increments (Brothers 1987). Each lapillus was mounted on a glass slide using cyanoacrylate glue. Both otoliths of the pair were mounted on separate glass slides and the slide was labelled with the vial number and lettered A or B to distinguish between each member of the pair. All the 'A' otoliths were then ground and polished down to the nucleus on one side in the transverse plane using wet/dry 4000 grit silicon carbide sandpaper or a lapping film series (3 μm, 1 μm, and 0.3 μm). Care was taken not to grind through the edge of the otolith while still getting as close to the nucleus as possible. After polishing on one side the otoliths were carefully lifted from the slide using a #15 scalpel blade and remounted with cyanoacrylate glue polished side down. Once the glue was dry the otoliths were ground as close to the nucleus as possible without grinding through the edge. If any otoliths had been lost or rendered unreadable during polishing the corresponding otolith of the 'B" set was prepared.

For age determination, otoliths were viewed under a compound microscope equipped with dual polarizing filters and connected to a black and white CCD video camera and video monitor. Once a suitable image was present on the monitor the image was captured and analyzed using computer-aided image analysis (Mocha System, Jandel Inc., California). Ages were assigned by counting the number of annuli visible in the otolith. Fish without any visible annuli were assigned an age of 0. The age in days was also determined by a direct count of the daily rings in the otolith for these fish. The distance in millimetres from the nucleus to each annulus and from the nucleus to the edge of the otolith was measured on the longest axis of the otolith using image analysis. The distance from the last annulus to the edge of the otolith (marginal increment) was also measured on the same axis. The date of annulus formation was then determined using marginal increment analysis. Marginal increment analysis determines the date of annulus formation by following increase in width of the newest increment (from the most recent annulus to the edge of the otolith) over time (Mgaya 1995). Only fish with a single annulus present were used for marginal increment analysis since these would be the fastest growing fish in the population and would therefore have the fastest growing otoliths and show the most visible increases in increment width.

The occurrence of daily rings in young-of-the-year (YOY) round gobies was validated by marking the otoliths and then rearing the gobies in the lab and sacrificing a given number at set time intervals. This method has a high reliability for detecting daily rings (Geffen 1987). In the first attempt at daily ring validation the otoliths were marked by immersing the juvenile gobies in a 300 mg/L solution of alizarin red S (Beckman and Schulz 1996). This chemical was used as a marker since it eliminates the need to use fluorescent microscopy to detect marks as is necessary with tetracycline and other common marking agents. A second attempt at marking was also made this time using oxytetracycline hydrochloride (OTC) as the marking agent. Tetracycline has been used in a variety of fish species and is the best method for age validation in juvenile fishes of unknown age (Geffen 1992). Fish were immersed in a 400 mg/L solution of OTC buffered with tris for 8 hours and then reared in the laboratory on a diet of Tetramin* fish flakes. Alizarin marked fish were reared on combination diet of frozen blue mussels (*Mytilus edulis*) and frozen bloodworms (Chironomidae). For both these marking methods the presence of daily rings was confirmed by linear regression of the major increment count on days after marking. The slope of the regression line should not be significantly different than one indicating that one increment formed each day following marking and the r^2 value should be high.

Back-calculation of size:

Fish size (standard length) was related to otolith size (radius) using linear regression. Two separate regressions were performed on the data. The first regression was of otolith radius on standard length and the second was of standard length on otolith radius. The values for the slope and y-intercept of these two regressions were then used in back calculating fish size at age. Back-calculation was carried out according to the two hypotheses of Whitney and Carlander (1956) which are: "if the scale were 10% larger when the fish was caught than the average scale for that size of fish, the scale would be

10% larger than normal throughout the life", and "if a fish at time of capture were 10% smaller than the average fish with that size of scale, the fish would be 10% smaller throughout life". These are referred to as the scale proportional (SPH) and body proportional (BPH) hypotheses, respectively (Francis 1990). The formulas for when the otolith size - fish size relationship is linear are:

Equation 1.3 $L_i = -(a/b)+(L_c+a/b)(S_i/S_c)$ (LSPH)

Equation 1.4 $L_i = [(c+dS_i)/(c+dS_c)]L_c$ (LBPH)

where L_c is the fish length at time of capture, L_i is the fish length at time i, S_c is the otolith radius at the time of capture, and S_i is the otolith radius at time i. The parameters a and b are the intercept and slope from the regression of otolith radius (S) on fish length (L), and the parameters c and d are the intercept and slope from the regression of L on S. Both of these hypotheses also have formulas which correspond to a non-linear otolith size - fish size relationship. The non-linear back-calculation formula which follows the SPH is a slight modification by Smedstad and Holm (1996) of the non-linear formula which follows the BPH formula attributed to Monarstyrsky (Bagenal and Tesch 1978). These two formulas are expressed as follows:

Equation 1.5 $L_i = (S_i/S_c)^u L_c$ (NLSPH)

Equation 1.6 $L_i = (S_i/S_c)^v L_c$ (NLBPH) where u is the slope of the regression of log (S) on log (L) and v is the slope of the regression of log (L) on log (S).

The degree of error in back calculation in the linear and nonlinear models was expressed as the difference between the SPH and BPH forms of each model (Francis 1990). The size-at-age results of back-calculation using each of these formulas were then compared by inspection to the minimum size, maximum size, range and mean size of fish collected in the field at the time of annulus formation in order to select the best back-calculation formula. Also, frequency distributions of back-calculated size at age for each formula were compared to their respective size-at-age frequency distributions of field-collected fish. All comparisons between back-calculated sizes and actual sizes were made within a cohort to reduce possible sources of variation. Back-calculated sizes were also tested for the occurrence of Lee's phenomenon by a t-test to determine if the mean back-calculated size at age 1 is significantly different for age 1 and age 2 round gobies. Lee's phenomenon occurs when the back-calculated length at age 1 decreases as the length of the fish used increases (Francis 1990).

<u>Growth</u>:

Fish sizes were plotted and fitted to a von Bertalanffy growth function to determine overall growth rates and to see if male and female growth rates differed. The von Bertalanffy growth function has been widely used in length-growth studies of fishes (Ricker 1975, Moreau 1987) and is represented by the equation:

Equation 1.7 $$L = L_{\infty} (1-e^{-k(t-t0)})$$

where L_∞ is the theoretical maximum size a fish approaches, k is the rate at which length approaches L_∞, and t_0 indicates the hypothetical time at which a fish would have a size of zero (Tesch 1968, Ricker 1975). The parameters L_∞ and k of the growth function were estimated by plotting the back-calculated sizes on a Walford plot (Walford 1946). On a Walford plot the size at one interval (L_x) is plotted on the x-axis and the size at the next interval is plotted on the y-axis. The value for L_∞ is the intercept between the regression line for the data and a line with a slope of one and X and Y intercepts of zero. This value is more simply determined using the following formula:

Equation 1.8 $$L_\infty = a / (1-b)$$

where a is the y-intercept of the regression line and b is the slope. The parameter k (Equation 1.7) is equal to b, the slope of the regression line. Values for L_∞ and k were then used as the initial values for non-linear regression to determine the curve of best fit for male, female, and combined size and age data for both the back-calculated sizes and the sizes of field collected fish at the time of annulus formation. The curves of best fit were also plotted with the theoretical growth curves determined from the variables estimated from the Walford plot. The value for t_0 used in the theoretical growth curves was the mean of the values estimated from non-linear regression.

Results

Goby collections:

The number of round gobies collected per trawl was highly variable and ranged from 0 to 82 individuals with from 15 to 30 individuals being a common catch in an uninterrupted trawl (occasionally the net would get snagged and the trawl would be cut short). The two most common species collected other than the round goby were yellow perch (Percidae: *Perca flavescens*) (21% of the catch numerically) and rock bass (Centrarchidae: *Ambloplites rupestris*) (22% of the catch numerically). Several species of Cyprinidae were regularly captured and included the bluntnose minnow (*Pimephales notatus*), spot-tail shiner (*Notropus hudsonius*), and hornyhead chub (*Nocomis biguttatus*). Other species captured were white perch (Percichthyidae: *Morone americana*), white sucker, (Catostomidae: *Catostomus commersoni*), northern madtom (Ictaluridae: *Noturus stigmosus*), brindled madtom (Ictaluridae: *N. miurus*), logperch (Percidae: *Percina caprodes*), channel darter (Percidae: *Percina copelandi*),largemouth bass (Centrarchidae: *Micropterus salmoides*), walleye (Percidae: *Stizostedion vitreum*), and tubenose goby (Gobiidae: *Proterorhinus marmoratus*). Tubenose gobies were collected from all trawl sites but were more common at the sites in Lake St. Clair and the Detroit River sites closest to Lake St. Clair.

There was considerable variation in the number of round gobies collected on each sample date with collections ranging from 25 to 110 individuals, with those collections occurring on September 19 and June 17 respectively. Round gobies were always collected in shallow water (< 4 m depth, usually from 2-3 m) and were rarely caught in deep water

(> 5 m). On the earliest sample date, May 6, no round gobies were collected. The number of gobies collected on September 19 was low due to the presence of large amounts of macrophytes, which reduced the efficiency of the trawl by filling up the net. The mean size of gobies collected also varied significantly depending on the date of collection (one-way ANOVA $p < 0.001$, df = 5, 354, F = 12.79) (Figure 1.3). The collections from July 29 were made by hook and line as the trawl net was unavailable. Since this method of capture has a different selectivity this collection was not included in the ANOVA. Round gobies collected on July 29 had a larger mean size ($\bar{x} = 69.12$ mm, S.E. = 1.492) than the largest collection of round gobies by trawling (June 4, $\bar{x} = 61.56$ mm, S.E. = 2.038) but the difference was not significant (two-sample t-test, t(2-tailed) = 1.983, $p = 0.09$)

Immature round gobies were the most common group of round gobies in the trawl collections followed by adult females (Figure 1.4). The greatest number of immature gobies were collected on June 17 and the majority were under 50 mm SL. This same group of appears to still be present in the July 8 collection although there is an increase in size with gobies from the 25 mm size class being absent on July 8 (Figure 1.4). This group of immature fish appears to be the only clear cohort of round gobies present. On the other samples dates there is no clear distinction between cohorts. It appears a new cohort is present in the October 22 sample based on the presence of round gobies less than 35 mm SL which were absent from the September 19 sample. Adult male round gobies were generally uncommon or absent in trawl collections but were most abundant in the October 22 collection (Figure 1.4). This was also the only date when any large adult male round gobies were collected. On the other sample dates the rest of the immature round gobies

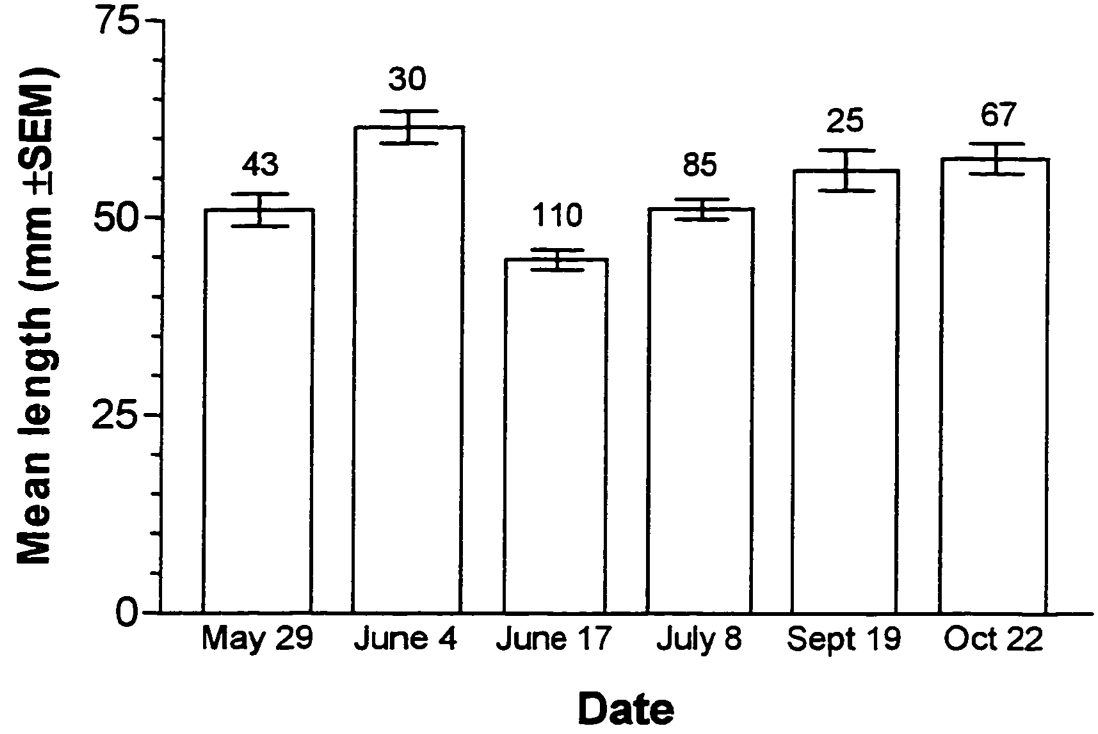


Figure 1.3 The mean size of gobies collected by trawling for sample date during 1996. The numbers above the bars are the sample size for each date.

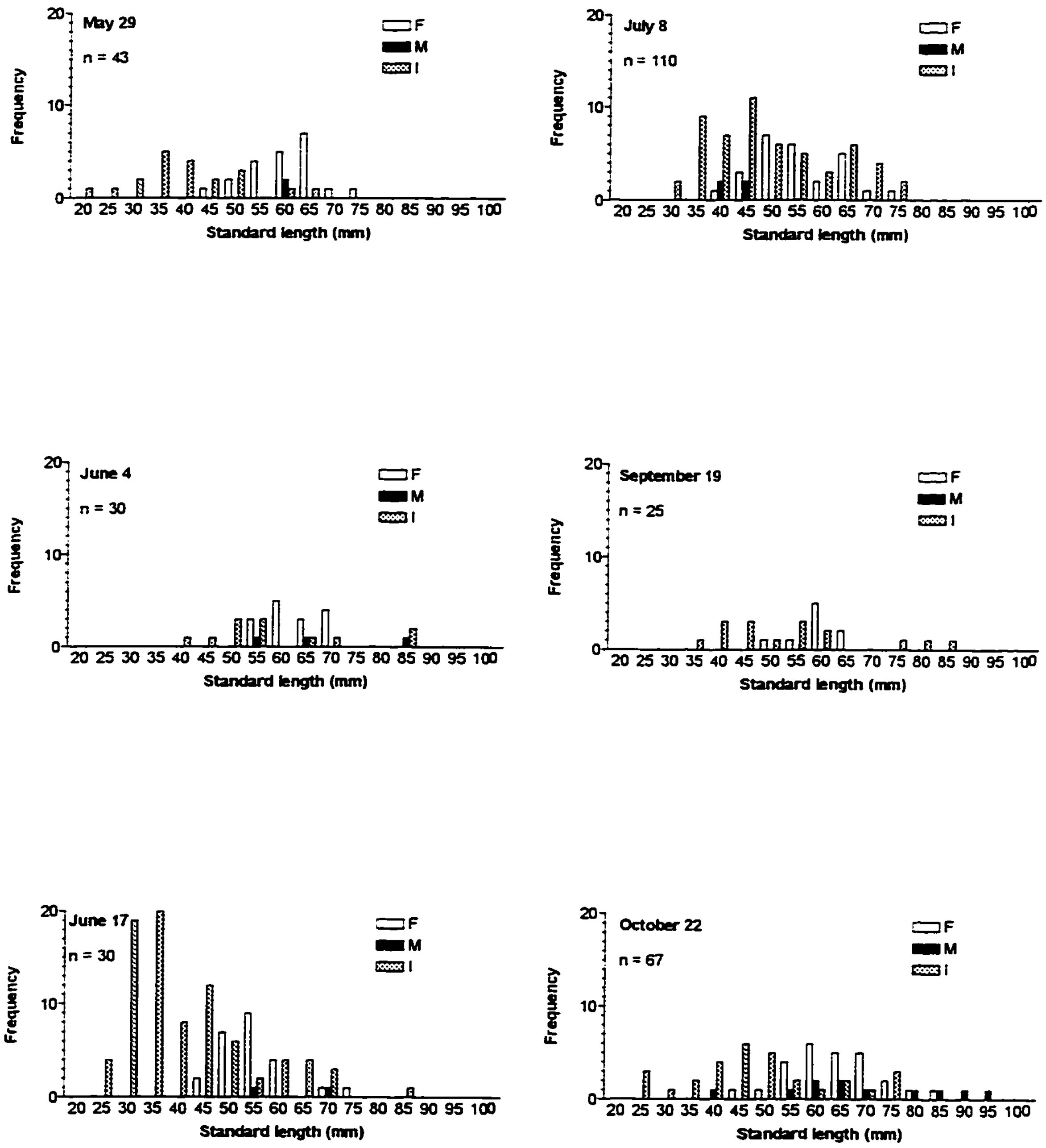


Figure 1.4 The size frequency distribution by sex for all gobies collected by trawling during 1996.

are predominately immature males. The July 29 collection by hook and line showed a similar pattern to the trawl collections but the smallest round gobies were absent from these collections (Figure 1.5). In this collection, immature round gobies were again dominant although more large individuals were caught. Immature round gobies were also much more common than adult females in the same size classes on this date (Figure 1.5).

When standard length was plotted against weight, the data followed the typical curve for fishes with some increasing scatter with fish size (Figure 1.6). Following $\log_{10}$ transformation the data showed a highly significant linear relationship ($r^2 = 0.99$, $p < 0.0001$) (Figure 1.7). From the regression equation, the parameters for the weight-length equation were determined. The parameter *a* was equal to 7.6×10^{-6} and the parameter *b* was equal to 3.26 indicating that weight increases at a faster rate as length increases or that gobies become more rotund as they increase in length. The fit of this weight-length equation to the non-transformed data as determined by non-linear regression was excellent ($R^2 = 0.98$) The relative condition also increased significantly from May to September ($r^2 = 0.84$, $p < 0.005$) (Figure 1.8).

Ageing:

Marginal increment analysis showed annulus formation to occur during late May (Figure 1.9). Examination of the otoliths from May 29 and June 4 showed the annulus to be just forming at the margin but often the increment was too narrow to be effectively measured on the computer. For validating the occurrence of daily rings in YOY gobies, alizarin appears to be unsuccessful as a marking agent. The mortality rate of gobies while in the solution and after marking was quite high and of the fish that did survive no marks

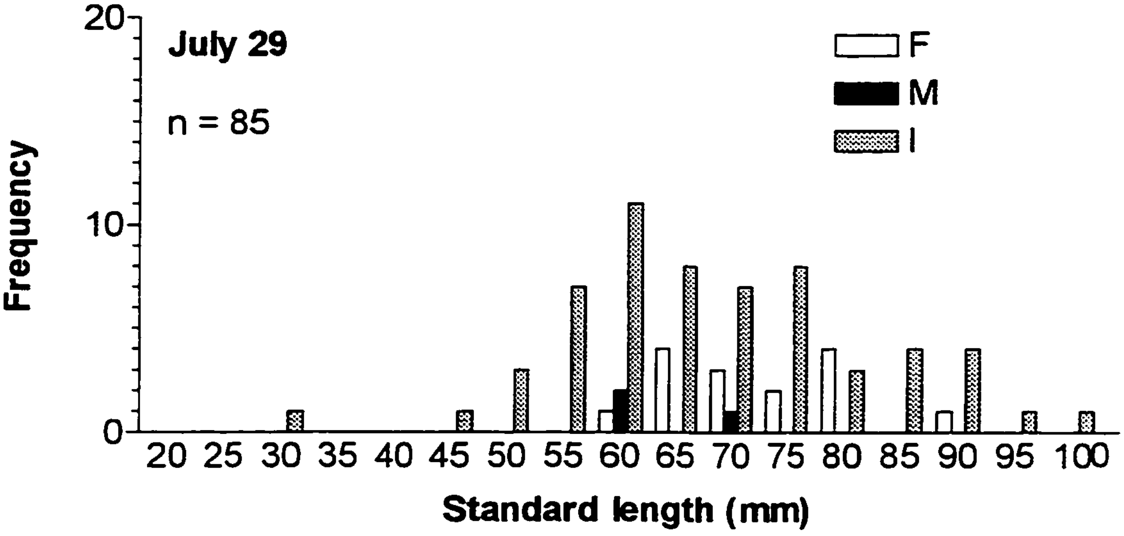


Figure 1.5 The size frequency distribution by sex for gobies collected by hook and line on July 29, 1996.

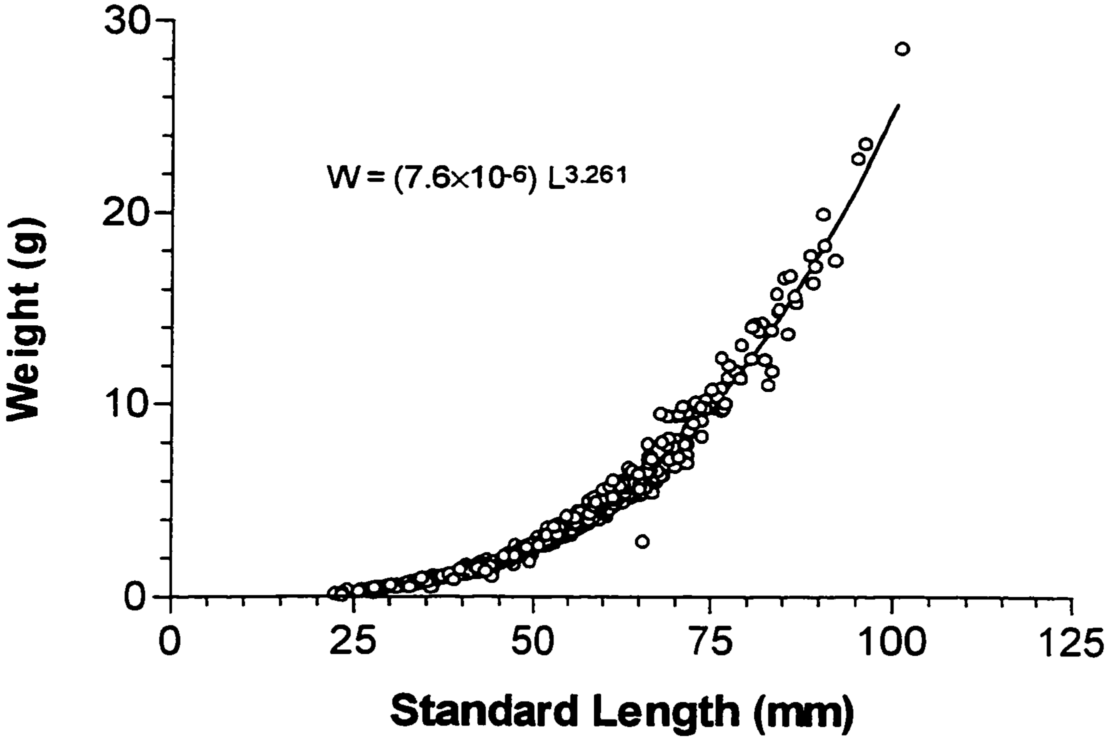


Figure 1.6 The weight-length relationship for the 435 gobies collected during 1996.

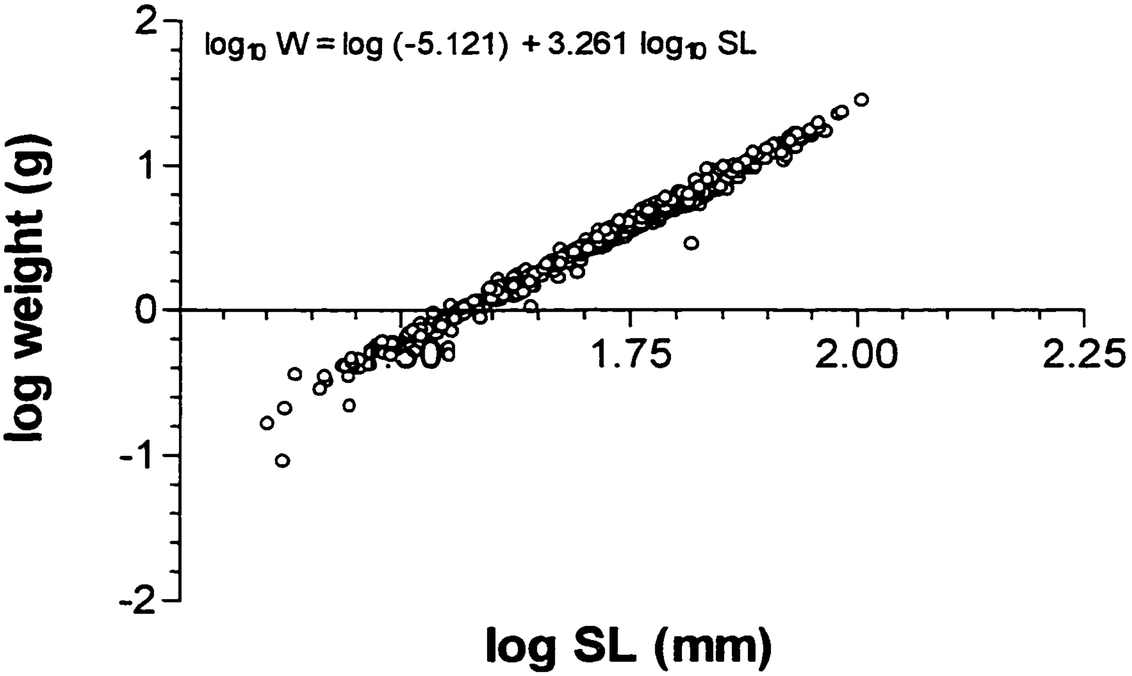


Figure 1.7 The relationship between $\log_{10}$ weight and $\log_{10}$ standard length for the 435 gobies collected during 1996.

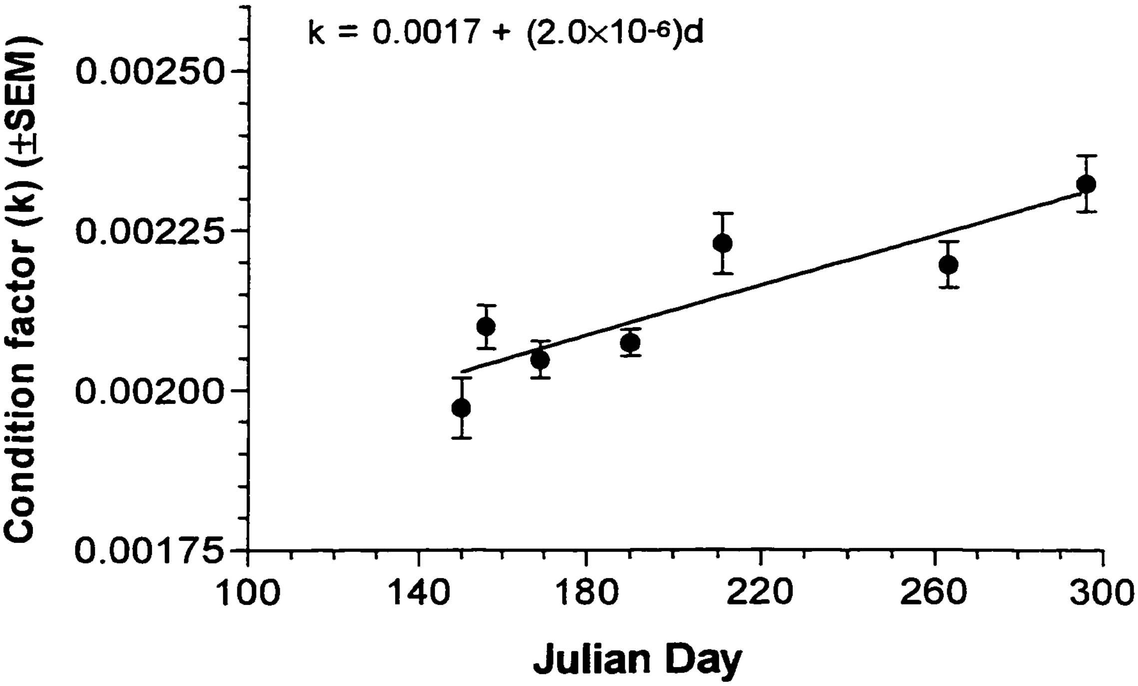


Figure 1.8 The mean condition factor by date for all goby collections in 1996. Data points correspond to collections from May 29, June 4, June 17, July 8, July 29, September 19, and October 22.

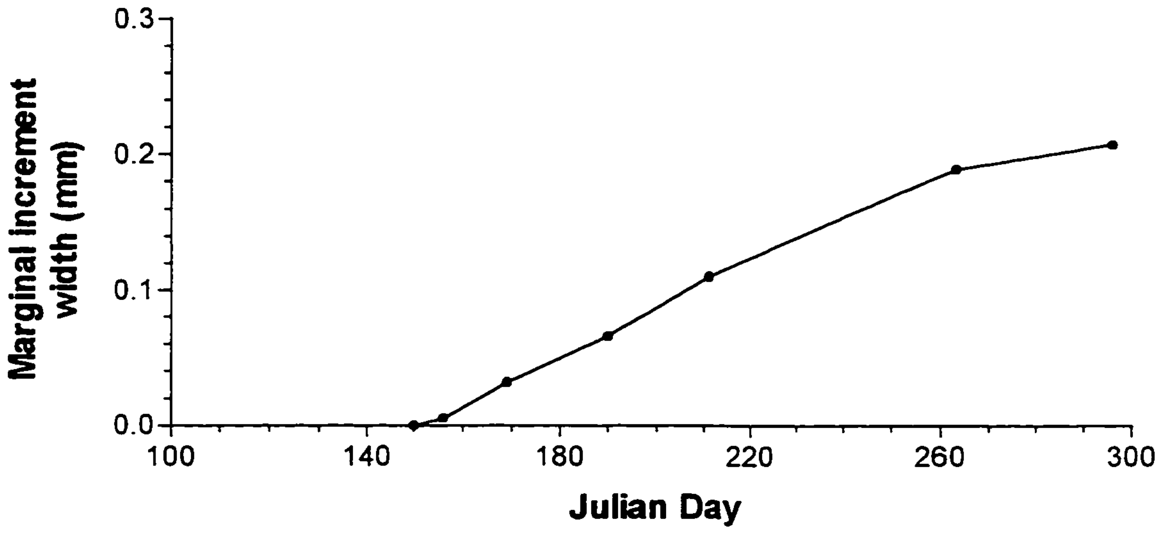


Figure 1.9 The otolith marginal increment plotted by sample date for age 1 gobies collected in 1996. Data points correspond to collections from May 29, June 4, June 17, July 8, July 29, September 19, and October 22.

were visible in the otoliths. This was likely a result of poor growth of the gobies due to a poor diet or from overcrowding in the lab or a combination of both factors. Gobies marked with OTC did not experience any mortality while immersed in the OTC solution and almost zero mortality afterwards. Strong marks were produced in the otoliths by OTC but it was not possible to determine the number of daily rings in the otoliths as a number of the fish (approximately 55-62 mm SL) which were assumed to be YOY were actually yearlings and the growth increments were too narrow to be counted accurately. In YOY fish, growth increments after marking were also quite narrow and difficult to resolve.

Round gobies representing four age classes were collected over the season and at least two age groups were present on each sample date (Figures 1.10 and 1.11). Individuals of age 1 were usually the most common age class collected followed by age 2 fish. Age 3 fish were uncommon with only 3 individuals being collected over the entire sampling period. Age 0 fish did not appear until the July 29 sample when a single individual was caught. Age 0 and age 1 fish were the only age classes represented in the September and October samples. Age 1, 2, and 3 fish were present in the May 29 sample and there was little or no overlap in the sizes of the three classes, although age 1 gobies exhibited a large size range. On all subsequent sample dates when age 2 fish are present, there was size overlap with age 1 fish. This is particularly true of the July 29 sample where age 1 fish of up to 80 mm SL were present while the distribution of age 2 fishes range from the 65 mm to 100 mm size classes (Figure 1.11). There was some overlap between the age 0 and age 1 classes on both September 19 and October 22 (Figure 1.10). The smallest age 1 individuals increased in length by approximately 20 mm over the season and

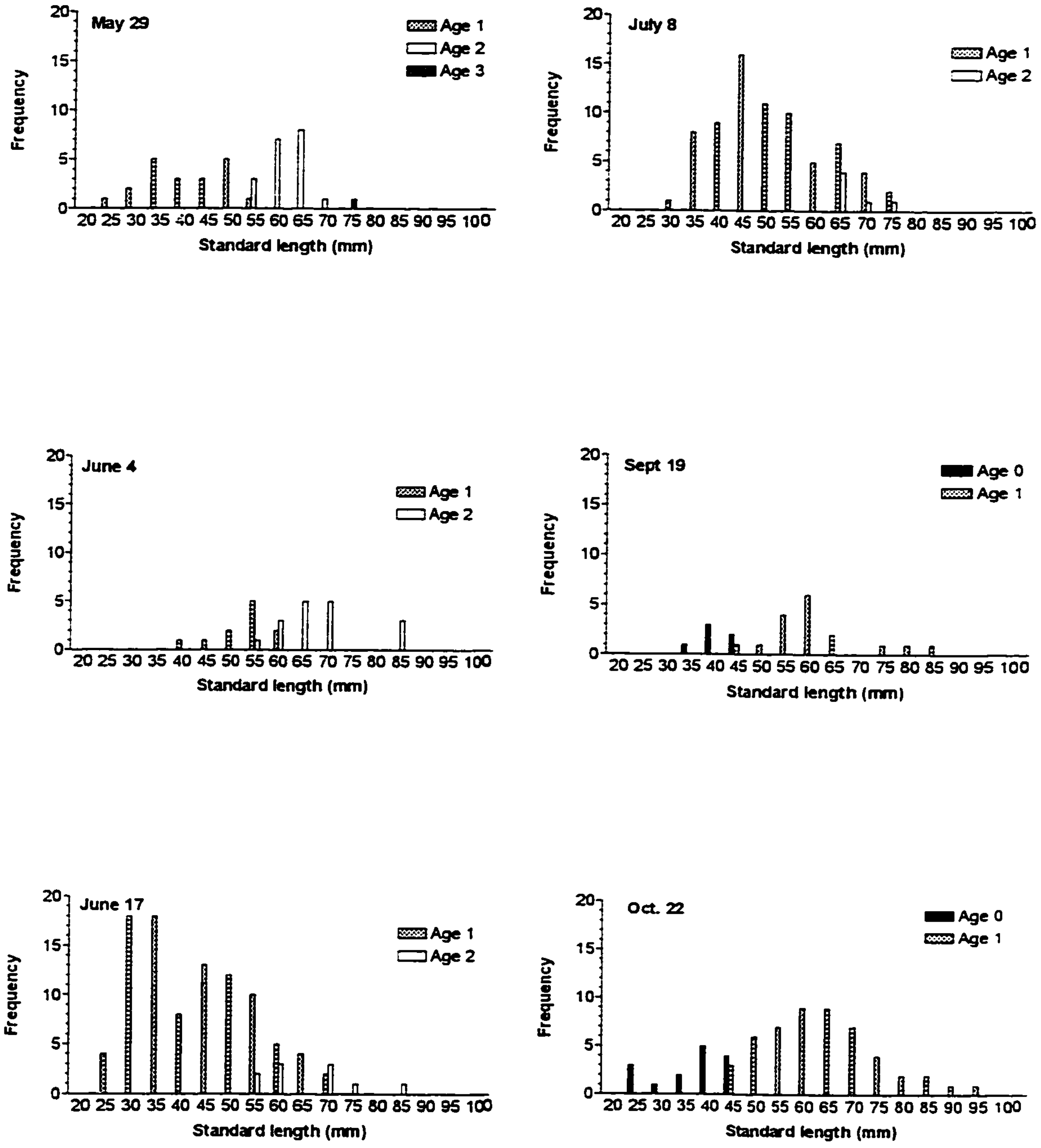


Figure 1.10 The size-frequency distributions by age for each sample date where gobies were collected by trawling during 1996.

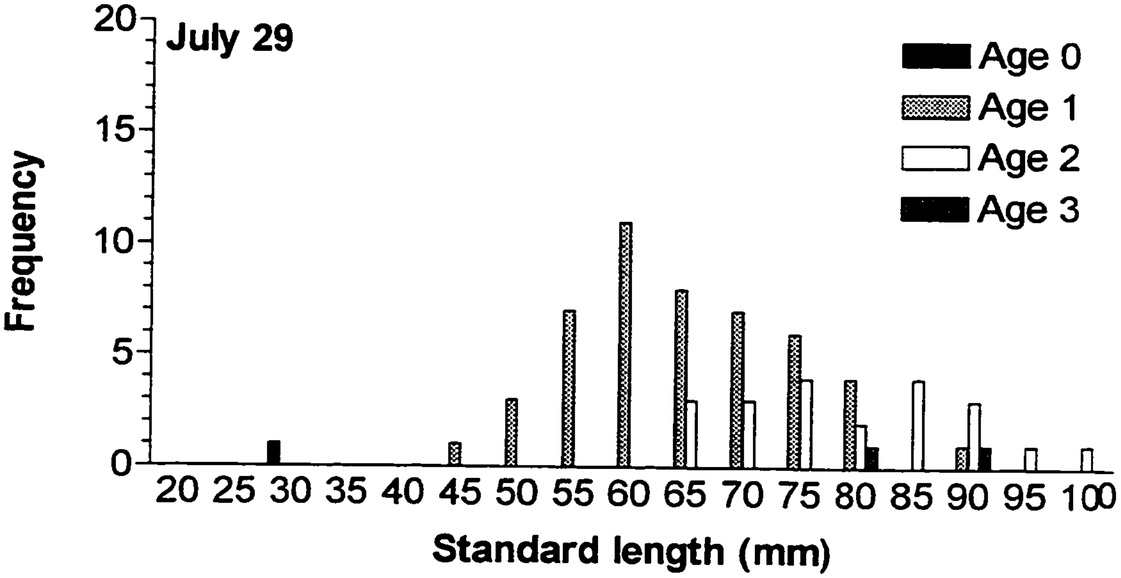


Figure 1.11 The size-frequency distributions by age for gobies collected on July 29, 1996 by hook and line.

this assumed that the smallest individuals of the age 1 class were collected in the May 29 sample. The majority of the age 1 individuals appeared to be immature based on comparison with the corresponding length and sex distributions for each sample date. Apparently, several age 1 individuals matured over the season based upon the sex and age distributions for October 22 (Figure 1.4 and 1.10).

The age in days for the 20 age 0 fish ranged from 67 to 144 and the corresponding hatch dates for these fish ranged from May 23 to August 5. Although standard length was a good predictor of otolith radius for these fish ($r^2 = 0.70$, $p < 0.0001$) otolith radius was not as good a predictor of the age in days ($r^2 = 0.49$, $p < 0.001$).

Back-calculation of size:

The relationship between fish size (SL) and otolith radius in mm according to the SPH was significant ($r^2 = 0.74$, $p < 0.0001$) and showed the typical trend of increasing scatter with increasing fish size (Figure 1.12). The same was true for the relation according to the BPH, although this relationship was represented by a different equation. The relationship in Figure 1.12 also appears that it may be non-linear and following $\log_{10}$ transformation of the variables, a better fit of the regression line was observed ($r^2 = 0.78$, $p < 0.0001$) (Figure 1.13). The values for each of the parameters for the back calculation formulas are listed in Table 1.1.

The results of back calculation varied depending on the model used and the age back-calculated to (Table 1.2). The overall error for the non-linear models was higher than observed for the linear models based on the mean size. The calculated error for the linear and non-linear models were 5.83 mm and 9.77 mm respectively for age 1 fish and 1.99

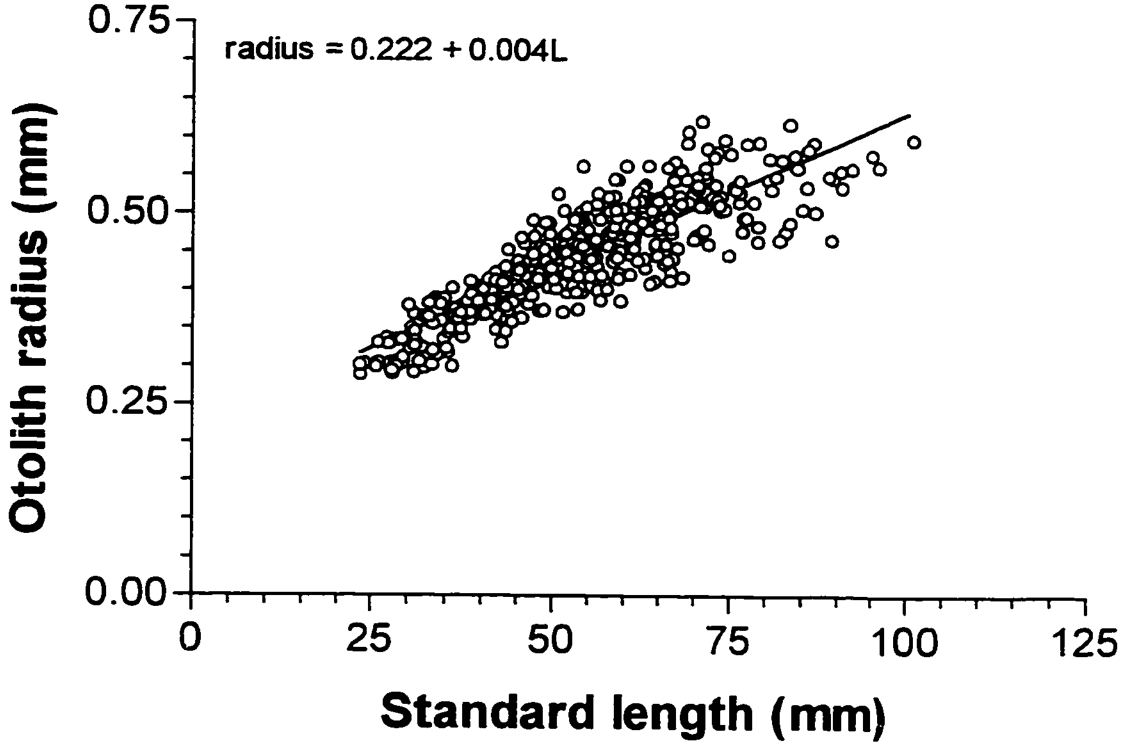


Figure 1.12 The relationship between standard length and otolith radius ($r^2 = 0.74$, $p < 0.0001$) for 413 round gobies collected during 1996.

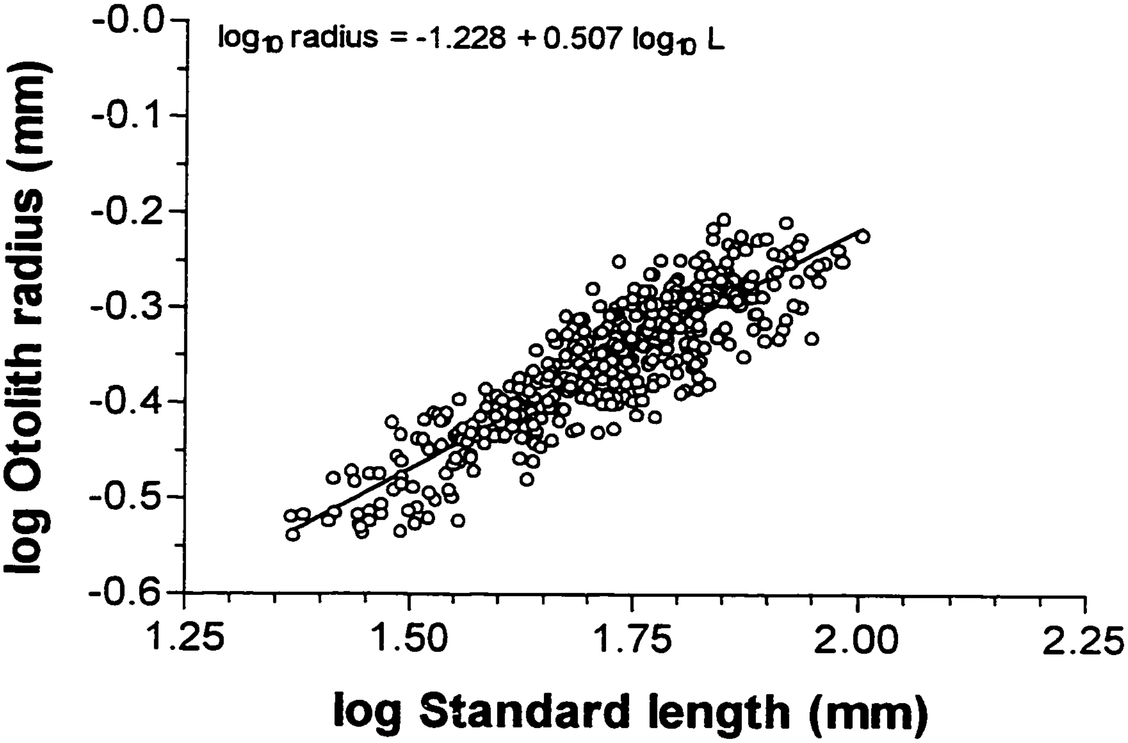


Figure 1.13 The relationship between log standard length and log otolith radius ($r^2 = 0.78$, $p < 0.0001$) for 413 round gobies collected during 1996.

Table 1.1 The parameters used in the four back-calculation formulas determined from their respective regression equations.

	Parameter					
Formula	a	b	c	d	u	v
LSPH	0.222	0.004				
LBPH			-25.569	180.057		
NLSPH					0.507	
NLBPH						1.544

Table 1.2 The sizes at age 1 and 2 determined by back-calculation using of the four formulas compared to the sizes observed in the field at the time of annulus formation. All sizes are in millimetres.

	Mean	S.E.	Minimum	Maximum	Range
Age 1					
LSPH	31.49	0.915	-5.71	63.60	69.31
LBPH	37.32	0.748	12.79	66.15	53.36
NLSPH	47.42	0.718	22.27	81.05	58.78
NLBPH	37.65	0.694	15.28	65.15	49.87
Field	45.00	0.582	24.08	61.54	37.46
Age 2					
LSPH	65.33	0.561	49.84	84.19	34.352
LBPH	67.32	0.540	53.04	85.12	32.07
NLSPH	72.36	0.587	56.73	94.64	37.91
NLBPH	66.51	0.532	52.38	84.19	31.38
Field	64.45	0.464	51.52	85.60	34.08

mm and 5.85 mm respectively for age 2 fish. However, when the range, and minimum and maximum sizes for each formula are compared directly to the observed data, considerable differences are evident. For back-calculated sizes at age 2, all the formulas are relatively similar, but greater differences are observed for back-calculated sizes at age 1. The most notable differences are from the LSPH where negative sizes at age one are calculated and from NLSPH which calculated larger sizes than were actually observed. The NLBPH was chosen as the best back-calculation formula based on the higher r^2 value from the regression of the $\log_{10}$ transformed variables and that its calculated sizes at age 1 best fit the observed data. Lee's phenomenon was observed in adult females and immature males (two sample t-test; $t = 1.980$, $p < 0.05$ and $t = 1.989$, $p < 0.01$). It may also occur in adult males as the mean back-calculated size at age for age 1 males was 42.21 mm SL and 33.86 mm SL for age 2 males, however the sample size was quite low with only six age 1 males and five age 2 males.

Growth:

The back-calculated sizes from NLBPH for all fish which had two or more back-calculated sizes were used to generate the Walford plot in Figure 1.14. Although the regression was significant, the model only explained about half of the variance ($r^2 = 0.48$, $p < 0.0001$). The Walford plot for females shows a much better fit ($r^2 = 0.66$, $p < 0.0001$) (Figure 1.14) while the plot generated for males was similar to the overall plot with the modell explaining about half of the variance ($r^2 = 0.49$, $p < 0.0001$) (Figure 1.14). The estimated values for L_∞ and k determined from these Walford plots are listed in Table 1.3. Starting from these initial values a curve of best fit was determined for the combined field

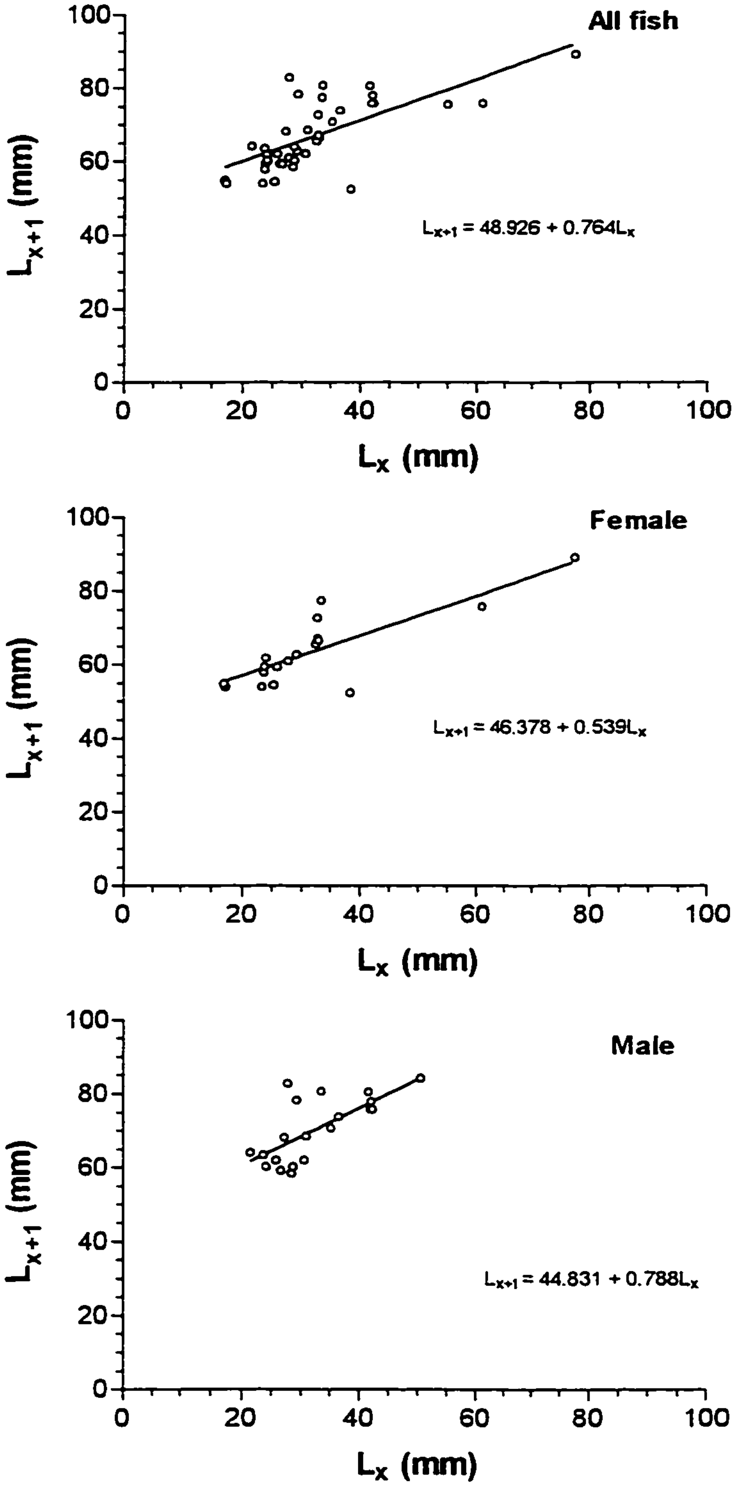


Figure 1.14 The Walford plots generated from the back-calculated sizes of 39 round gobies and from the back-calculated sizes of 18 female and 20 male round gobies.

Table 1.3 The estimates of the parameters for the von Bertalanffy growth function determined from Walford plot analysis.

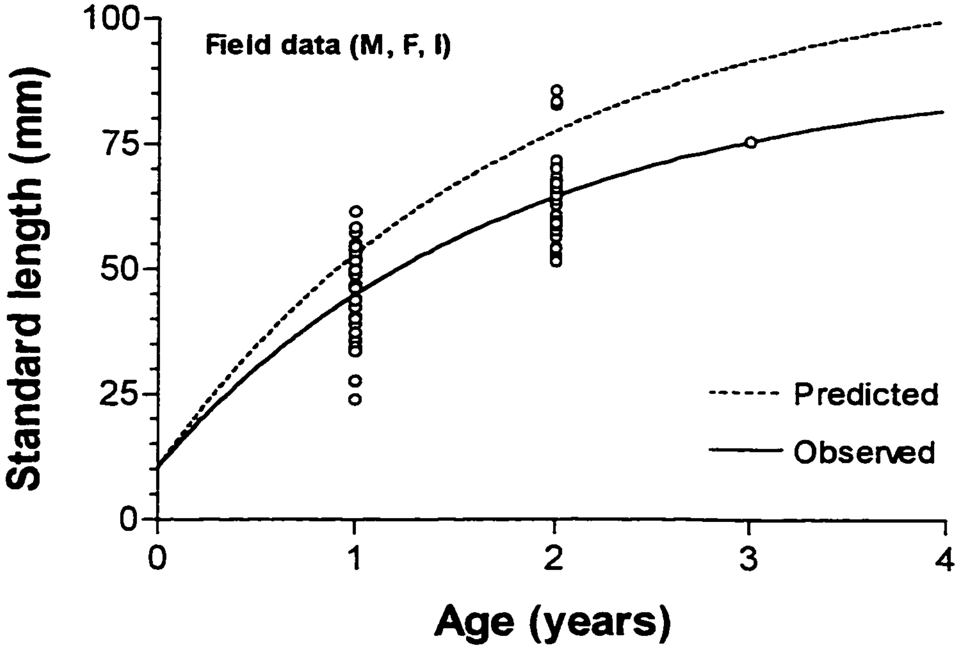
	Parameter	
	L	k
Curve		
All fish	175.945	0.764
Males	211.374	0.788
Females	115.398	0.618

collections from May 29 and June 4. All back-calculated sizes and separate curves were also estimated for the males and females from both of these groups. Each of these curves also was plotted with a curve generated using the predicted values for that group as constants. The estimated values of L_∞ , k and t_0 and their standard errors are listed in Table 1.4. Because of the large standard error of the parameters estimated from non-linear regression, no statistical comparisons were conducted on the observed and predicted curves. It is unlikely that any differences would be observed since the values for the Walford plot estimated parameters fall within the confidence intervals for the parameters estimated by non-linear regression.

For the overall growth curves, both the predicted and observed growth curves are relatively similar although the predicted curves are elevated compared to the best-fit curve (Figure 1.15). The R^2 values for the best fit curves for the field data and back-calculated data are 0.57 and 0.41 respectively. The lower value for the back-calculated curve is likely a result of the wider range in size at age 1 (Figure 1.15). The R^2 values for the curve predicted from the Walford plot are low, being -0.15 and -0.86 for the field data and back-calculated data, respectively. The predicted and observed curves for the males were the most divergent with the predicted curves not passing through the data at all (Figure 1.16). However, the confidence limits for the best fit curves were very high and because of the limited amount of data for older males it is unlikely that these curves are a true representation of growth in male round gobies. The highest R^2 values for the predicted (0.43) and observed (0.59) curves were for field collected females (Figure 1.17). This is the only case where a positive R^2 was obtained for the predicted curve. The difference

Table1.4 The parameter values for the von Bertalanffy growth function determined from non-linear regression of both the back-calculated sizes and the sizes of fish collected in the field at the time of annulus formation.

	Parameter					
	L	S.E.	k	S.E.	t	S.E.
Back-calculated						
All fish	101.820	38.4292	0.612	0.5105	0.278	0.22651
Males	175.934	3.81E+08	0.246	7.97E+05	-0.130	8.42E+05
Females	344.537	1.53E+03	0.080	0.4184	-0.399	0.7658
Field						
All fish	89.851	47.5471	0.569	0.8271	-0.222	0.861
Males	175.898	4.13E+05	0.222	759.033	-0.189	873.9584
Females	99.249	72.9064	0.419	0.7065	-0.407	0.9893



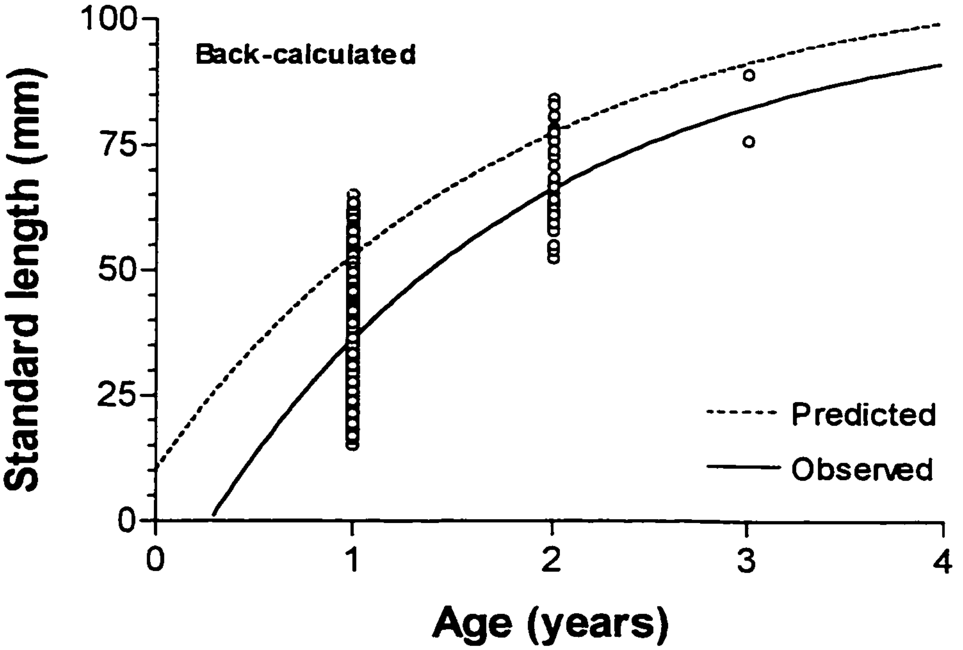


Figure 1.15 The predicted and observed von Bertalanffy growth curves for all fish (male, female, and immature) collected in the field (n = 68) at the time of annulus formation (May 29 and June 4) and for all back-calculated sizes (n = 400).

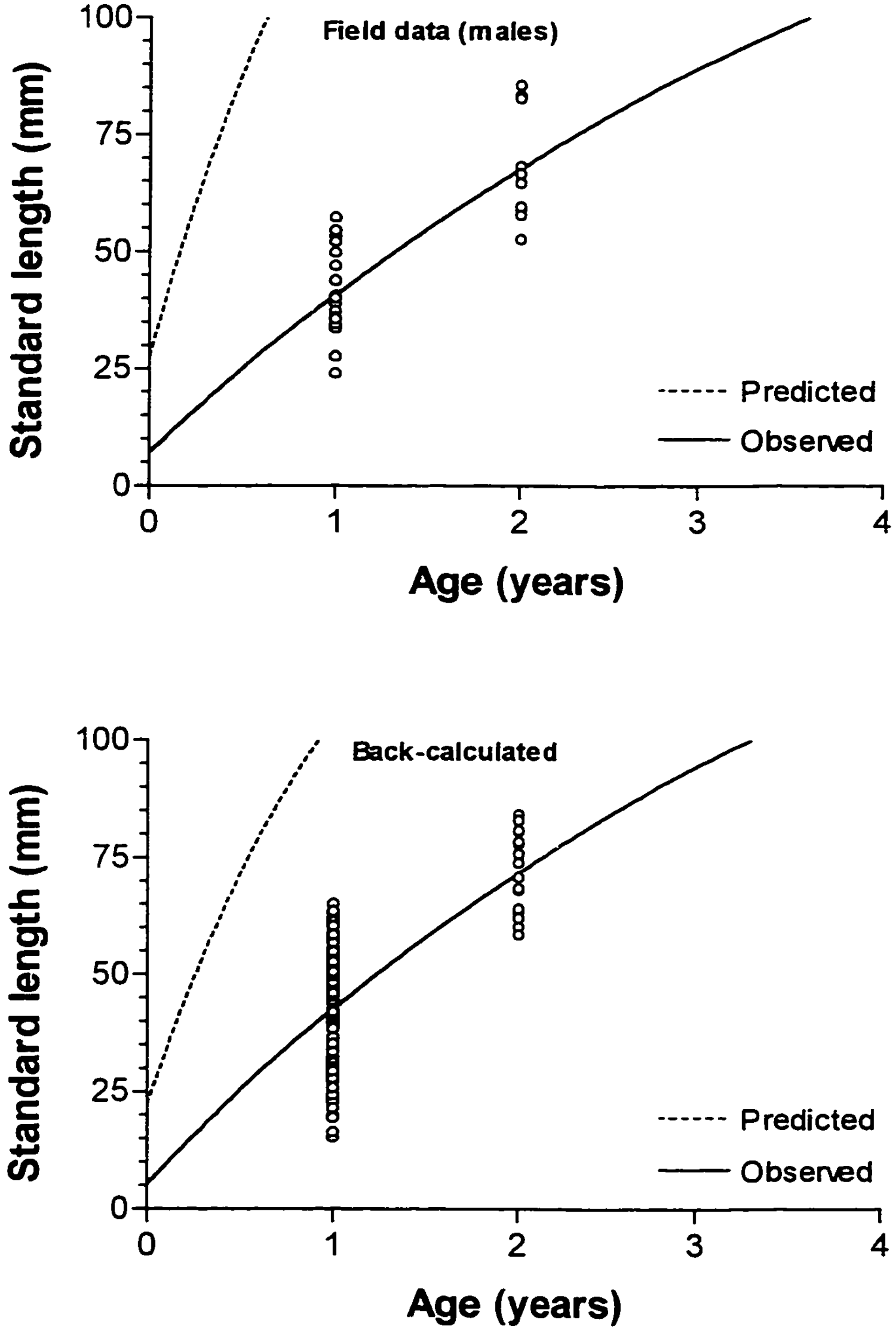


Figure 1.16 The predicted and observed von Bertalanffy growth curves for all male gobies (adult and immature) collected in the field (n = 29) at the time of annulus formation (May 29 and June 4) and for male back-calculated sizes (n = 123).

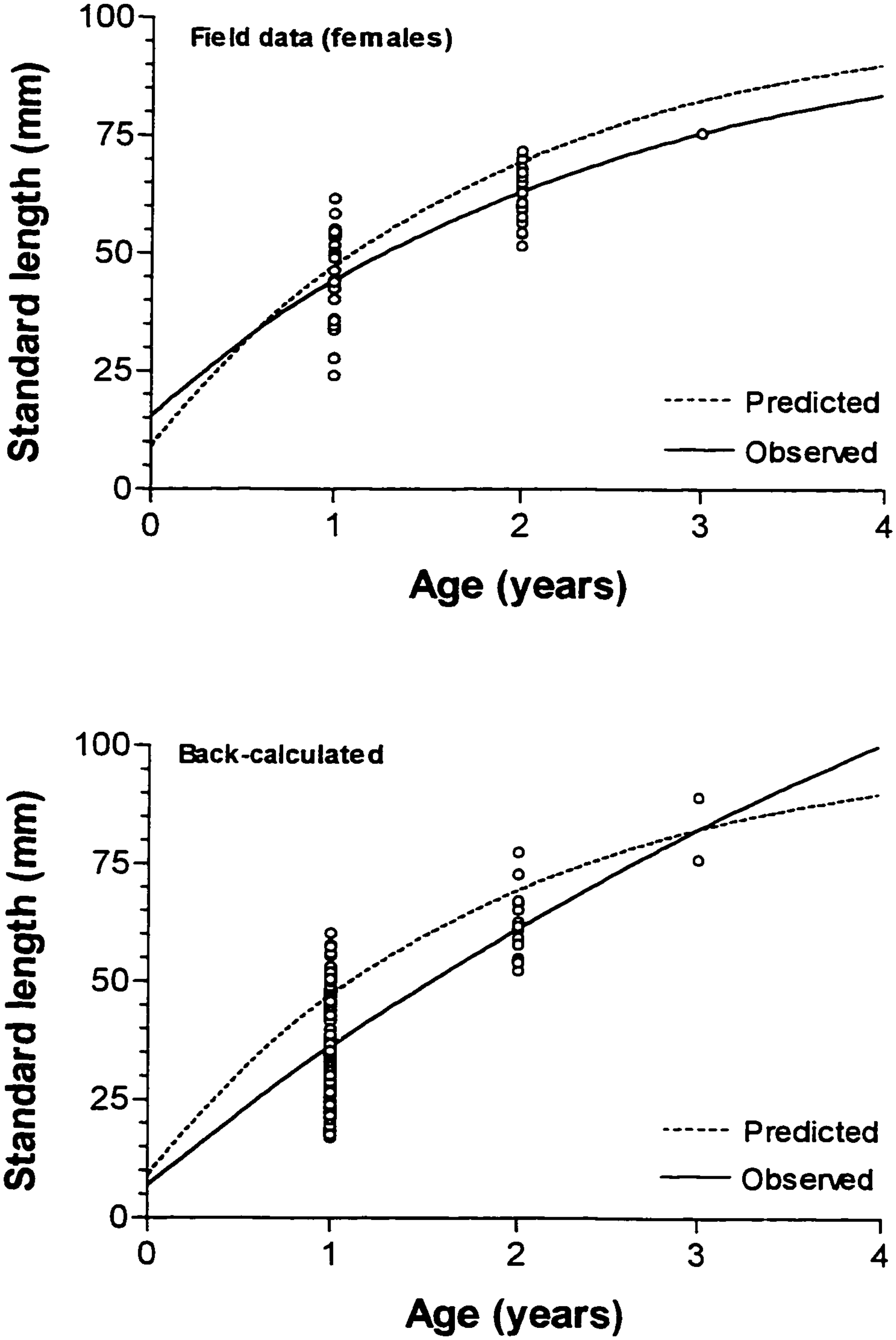


Figure 1.17 The predicted and observed von Bertalanffy growth curves for all female gobies (adult and immature) collected in the field (n = 49) at the time of annulus formation and for female back-calculated sizes (n = 156).

between the two curves for the back-calculated females was greater with the observed curve going to a much higher maximum than the predicted curve (Figure 1.17). The R^2 values for the predicted and observed curves are -0.14 and 0.41, respectively. As in the overall data, the poorer fit to the back-calculated data is likely a result of the greater size range for age 1 fish.

Discussion

The results from trawling suggest that the population dynamics of the round goby in North America are similar to the dynamics in its native range, although overall sizes are somewhat smaller. In its native range, the commercial catch is predominately of age 2 fish (Kovtun *et al.* 1976 cited in Marsden *et al.* 1996) and the size range was 130-160 mm for males and 110-150 mm for females (Berg 1949) in the Sea of Azov. Commercially caught round gobies from their native range are also over 30 g in weight (S. Rudnika, personal communication). The size of round gobies captured in the Detroit River was considerably smaller with the largest male collected having a total length of 124 mm and a weight of 28.53 g. The largest female collected had a total length of 112 mm and a weight of 17.5 g. The age 1 and age 2 size classes were also the most commonly collected age classes with age 1 fish being the most common class. This is similar to the mean age range of 0.73 to 1.47 years of the commercial catch from the Sea of Azov for 1968-1970 (Marsden *et al.* 1996).

The lack of representation of large adult male round gobies is not at all surprising at least for the spring and summer trawl collections. Since these males would be guarding nests under rocks and other objects and within burrows, they would be out of reach of the trawl net. The few adult males that were collected were 1-2 years of age which is younger age at maturity than expected for adult males based upon the European literature (Miller 1986). These may represent males that were just maturing or were too small to successfully obtain and defend a nest. Female gobies in other genera (*Padogobius martensi* and *Pomatoschistus minutus*) generally prefer to spawn in the nests of larger males (Bisazza *et al.* 1989, Magnhagen and Kvarnemo 1989). It is likely that the abundances of all round gobies were under-estimated in the trawl due the decreased efficiency of trawl nets over uneven bottoms (Hayes 1993) and the fact that trawls tend to underestimate the abundance of small cylinder-shaped bottom fishes (Adams *et al.* 1995). However, with the exception of large adult males the relative abundances of the gobies would be representative. The abundance and size distribution of age 0 (YOY) fish may also be under-estimated as these fish may be too small to be caught by the net or they may be present in different habitats than were sampled. Seining was also ineffective at collecting juvenile gobies in 1996.

Although the relative abundance of adult males was low, the abundance of immature males was considerably higher than the abundance of immature females. Whether or not all these males become nest guarders needs to be assessed. At least some males have an alternative reproductive strategy and become sneak spawners (Gross 1991). It is possible that immature males experience higher mortality rates than do immature females. In the Black Sea, adult males move inshore earlier than in the spring than do females and can be subject to selective fishing pressure during this time. A similar situation does exist in the Detroit River where gobies are regularly caught by anglers fishing for other species (personal observation). Immature males made up the majority of the catch from the July 29 hook and line collections. Thus, immature males may be subject to higher mortalities from fishing, but this may be only a localized influence.

These males may also be subject to greater predation pressure due to their apparently more aggressive nature and greater activity rate. Of several potential predatory species examined by Jude *et al.* (1995) walleye, smallmouth bass, rock bass, and yellow perch had all eaten round gobies. These species are common in the Detroit river and both yellow perch (21%) and rock bass (22%) were common (>15% numerically) in trawls. Rock bass in particular may be a major predator of the round goby. The rock bass population in the Detroit River appears to be thriving based on collections of an estimated 200-300 YOY (approximately 20 - 40 mm TL) in each of two trawls on September 19. Mortality rates of males need to be examined in detail as the ratio of adult males to females is a strong predictor of year class strength in the round goby (Kovtun 1980). In the Sea of Azov, the survival of juveniles to underyearlings is reduced considerably when the number of males is less than the number of females.

Adult males are assumed to die after a single spawning season because they do not feed while guarding a nest (Miller 1984). No adult males older than age 1 were collected in the October 22 sample, which is presumably after the breeding season, suggesting indirect evidence for this phenomenon. No age 2 females were collected in the October 22 sample either. Thus, there may be a movement of the older fish away from shallow water breeding habitats during the fall. In their native range round gobies migrate to deeper water in the winter (Miller 1986). However, this trend was not observed by Jude *et al.* (1995) in the St. Clair River. The reason for the appearance of large numbers of small age 1 gobies in the June 17 sample is unknown. It may be a result of an inshore migration of these gobies, which have been observed to migrate offshore as YOY at fall turnover in the central basin of Lake Erie (Knight 1996).

Based on the size and age distributions observed in the Detroit River, size frequency distributions are inappropriate for determining the age of round gobies. It appears possible to separate most of the age 0 fish based on length in the late fall and most of these same fish as age 1 individuals in the early spring. It is not possible to separate the older classes because of the high degree of overlap in size between age classes. Ageing of round gobies using the lapilli was very effective. Growth in the lapilli was much more uniform regardless of fish age with clear annual increments always present. Examination of whole and partially sectioned sagittae showed multiple growth zones and no clear annuli. To produce transverse sections of the sagittae would have been inefficient due to their greater size and thickness than the lapilli. Annulus formation in the Detroit River occurred slightly later than in the Sea of Azov where annulus formation occurred during April or May (Kostjuchenko 1961, cited in Marsden *et al.* 1996). Interestingly, in the St. Clair River, annulus formation appears to occur in August based on ageing with the sagittae (D. Jude, University of Michigan, personal communication). This may be a result of the cooler thermal regime in the St. Clair River as annulus formation has been shown to be affected by temperature for both cold and warm water species (Lentsch and Griffith 1987, Samuel *et al.* 1987). The date of annulus formation the Detroit River may vary somewhat depending on the year and the environmental conditions. It may also be more difficult to detect annuli at the time of their formation in whole otoliths.

The relationship between fish size and otolith size was not as strong as expected, but increasing scatter with fish size is common in many fishes (Francis 1990). Some of the variability may be accounted for by measurement error caused by asymmetric growth in the otolith. All measurements were carried out on the same straight line axis but the best approach may be to measure on a curve from the nucleus (Campana 1992). Some of the variation may also have been caused by changes in the otolith growth pattern which can change with the sexual maturity and age of the fish.

The non-linear BPH was selected as the most appropriate hypothesis for back-calculation of size in the round goby. Linear models were rejected as a better fit of the regression line was obtained following log transformation of the data. Non-linear SPH was rejected upon examination of the size-frequency distribution for back-calculated size at age 1 which showed back-calculated sizes that were 20 mm larger than those observed in field captured fish. This size of fish was well within the size range of fish captured while trawling, but they were not observed in the field collections. The smaller sizes, calculated by the NLBPH formula, were considered more likely to occur since they were below the effective capture size of the trawl. The June 17 sample age-frequency distribution had a similar shape to that of the NLBPH distribution although the minimum size of fish is larger. The June 17 sample was obtained after annulus formation, and growth in length would have occurred over that period. Smedstad and Holm (1996) validated a number of back-calculation formulas for cod otoliths by following the growth of individual groups of fish over time. They indicated that the BPH was the more appropriate hypothesis and that the non-linear form yielded the best results.

A second explanation for the smaller back-calculated sizes may be Lee's phenomenon, whereby the back-calculated length at age 1 decreases as the length of the fish used increases (Francis 1990). This phenomenon is generally attributed to higher mortality of the larger, faster growing individuals (Ricker 1975). Bil'ko (1971) observed that mature male gobies of age 1+ had a greater back-calculated size at age 1 than did immature males of age 1+. The mature males would die at the end of the spawning season. Bil'ko (1971) also noted the same phenomenon to occur in female round gobies and attributed it to post spawning season mortality as well.

Lee's phenomenon may also partially explain the poor fits of the von Bertalanffy growth function to the back-calculated data. The major reason is the high degree of scatter in the data because the high degree of variability in size at age. The large number of gobies with a size of less than 30 mm SL had a major effect on the size range at age 1 and the shape of the regression line for both the overall and female back-calculated growth curves. The poor curve fits for the males are likely a result of the limited data (n = 29), especially for age 2 and older males. A second problem for male round gobies may be that the growth rate of males changes with age (Bil'ko 1971). During their first year of life male gobies have a similar growth rate to females, but in the next year of life the growth rate of males increases. With this change in growth rate, the growth curve for males may be better described by the Gompertz growth function which includes an inflection point (Moreau 1987). A second solution may be to generate two separate growth curves, one for the fast growing, early maturing individuals and a second for the slower growing later maturing individuals.

Size-selective winter mortality appears not to be a big factor in determining the abundance of age 1 round gobies. The large numbers of age 1 gobies under 35 mm SL length from the June 17 sample clearly demonstrates this. The back-calculation of smaller sizes than observed in the field at age 1 provides additional evidence. There is a significant loss of condition over the winter which is probably related to low feeding rates. Some individuals from both sexes are maturing at an earlier age than was expected with both males and females maturing at age 1 based on the ages determined from mature round gobies in the field collections. Based on the field collections and the growth curves it appears that females likely reach a maximum standard length of slightly more than 100 mm and a maximum age of 3. The maximum age for males is unknown based on the very low numbers captured and the absence of any individuals older than age 2. The maximum age for males is at least age 3 as immature males of age 2 were collected on July 29 and September 19.

A rapid growth rate and early maturity appear to be two of the mechanisms contributing to the success of the round goby in the Great Lakes. Both Ehrlich (1989) and Leach (1995) state that a short generation time is one of the characteristics which makes a non-indigenous species a successful colonizer. Although overall growth rates were quite rapid it was not possible to determine if male and female growth rates differed because of the limited number of adult male round gobies collected. Little dimorphism in size between male and female round gobies was observed in the field collections although the largest goby collected was an age 2 immature male indicating that it does occur. Overall, the fit of the von Bertalanffy growth curves was relatively poor because of the high variability of size at age. A more effective approach may be to fit two separate curves, one for fast growing individuals and one for slow growing individuals. Identification of the fast and slow growing individuals is important to understanding the population dynamics of the round goby as the slower growing individuals live longer (Bil'ko 1971). Size-selective winter mortality of YOY round gobies is not evident and if present does not have any effect on year class strength.

Chapter 2: Reproductive Biology

Introduction

Most gobiid fishes have a reproductive strategy characterized by male parental care of the eggs (Miller 1984). The demersal eggs are deposited on a fixed overhead surface within a cavity of some type. Reese (1964) divided the gobiid reproduction pattern into five stages: establishment of a territory, nest preparation, courtship behaviour, spawning and parental care of the eggs. This type of reproductive strategy affects a number of life history variables. Generally fecundity is lower in fishes with this type of reproductive strategy, but the bestowal (bestowal: amount of female reproductive effort per offspring) per offspring is higher leading to larger offspring at hatching and lower mortality of young fish.

The round goby is a multiple spawner (abbreviate iteroparous) with an extended reproductive season (Miller 1986). The length of the reproductive season varies considerably depending on the locality. In the Black and Caspian Seas spawning may begin as early as April and continue until the end of June (Romania) or July (Sea of Azov) or as late as September (Varna, Bulgaria) (Miller 1986). Spawning occurs at water temperatures from 9-26°C at a depth of 0.2 - 1.5 m (Marsden et al. 1996). Male gobies will construct nests in a variety of locations including under stones, logs, crayfish burrows or inside cans (Marsden et al. 1996). The general nest requirements are for a hard, immobile overhead surface and a single opening to the cavity (Miller 1984; S. Rudnika, personal communication).

In the round goby sexual dimorphism is more pronounced than in other gobioid fishes. The adult males being characterized by larger size at maturity, enlarged cheeks, and all-over dark colouration (dark grey to black) (Nikol'skii 1963, Miller 1984). In their native range, male round gobies also mature at age 3-4, a year later than females which mature at age 2-3 (Bil'ko 1971, Miller 1986). Males also show a faster growth rate than females and do not feed while guarding the nest (Miller 1984). Both of these factors are thought to contribute to the death of males after a single breeding season while females may spawn in more than one season. In addition to the guarding males, an alternative male reproductive strategy has been observed in the round goby (C. Murphy, University of Alberta, personal communication). These sneaker or satellite males are identified by their small size, distended abdomens, and lack of male secondary sex characters other than an enlarged genital papilla.

The round goby shows one of the highest levels of bestowal among all gobiid fishes, and accordingly its young do not have a planktonic stage (Miller 1984). The number of eggs produced by a single female during one reproductive season can range from 328 - 5221 (Kovtun 1978). Compared to many fish this is relatively low. Another goby, *Sicyopterus japonicus*, has a fecundity of about 225,000 at 105 mm in length, where as a round goby of the same size has a fecundity of about 1,600 (Miller 1984). A trend of increasing fecundity within a single year class has been linked to decreased bestowal in several species of gobies, including the round goby (Miller 1984). A trend towards decreased bestowal would manifest itself as a smaller egg size, and declines in egg size have been recorded in many species with extended spawning seasons (Bagenal 1971). In many fish species, older fish tend to spawn earlier in the season (Bagenal 1957, 1971).

While an increase in egg size is associated with decreased fecundity, the size of young at hatching and their subsequent survival also increases. This may be an important reason for the success of the round goby in the Great Lakes. An unrelated goby, *Acanthogobius flavimanus*, which has successfully become established in San Francisco Bay (Brittan *et al.* 1970) and New South Wales, Australia (Hoese 1973) also exhibits relatively high levels of bestowal (Miller 1984).

The number of eggs spawned in a round goby nest can be as high as 10,000 representing the spawning efforts of from 4-6 females. Fertilization rates in the round goby can be up to 95% and a male can hatch up to 95% of the eggs in his nest (Marsden *et al.* 1996). Survival rates of the young are unknown. Although there are no data 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 also are 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 in round gobies and to examine seasonal variation in reproductive effort. Female round gobies from the Detroit River were expected to be maturing at age 2, the same as in their native range. It also was expected that fecundity would be similar with a trend to increasing fecundity with female size and age. The gonadosomatic index, which expressed the weight of the gonads as a percentage of body weight, was used to determine the length of the reproductive season which was expected to extend from early May until early September. A second measure of reproductive seasonality was variation in the size (number of eggs) and density of round goby nests. Differences in nest density and size between cobble substrate and sand substrate sites also were tested using artificial nests. It was expected that the number of eggs per nest would be greater on the cobble substrate as that is the preferred habitat of the round goby. The number of nests occupied was expected to be greatest on the sand substrate as natural nest sites would be limiting.

Methods

Fecundity and spawning season:

To determine fecundity, female round gobies were collected every three weeks during the summer and fall of 1996 from the upper Detroit River and western Lake St. Clair (Figure 2.1) using a small otter trawl. The trawl was equipped with 'rockhopper' foot gear and the dimensions of the net opening were 4 m wide by 1 m high. The mesh size of the net was 40 mm stretch measure on the body of the net with 10 mm stretch measure mesh in the cod end. Trawling was conducted from a 23' boat with twin 70 hp outboard engines and the net was operated by hand. The net was towed at an average speed of 2 knots for 10 minutes per haul. Round gobies were collected on May 29, June 4 and 17, July 8 and 29, September 19, and October 22 of 1996. No fish were collected during August as no trawl net was available at this time.

The species and number of all fish captured in each trawl was recorded. All gobies were sexed by examination of the genital papilla (Miller 1984). Female gobies were transferred to aerated coolers for transport back to the lab. At the lab gobies were euthanized with CO_2 and individually frozen. Frozen gobies were then stored in

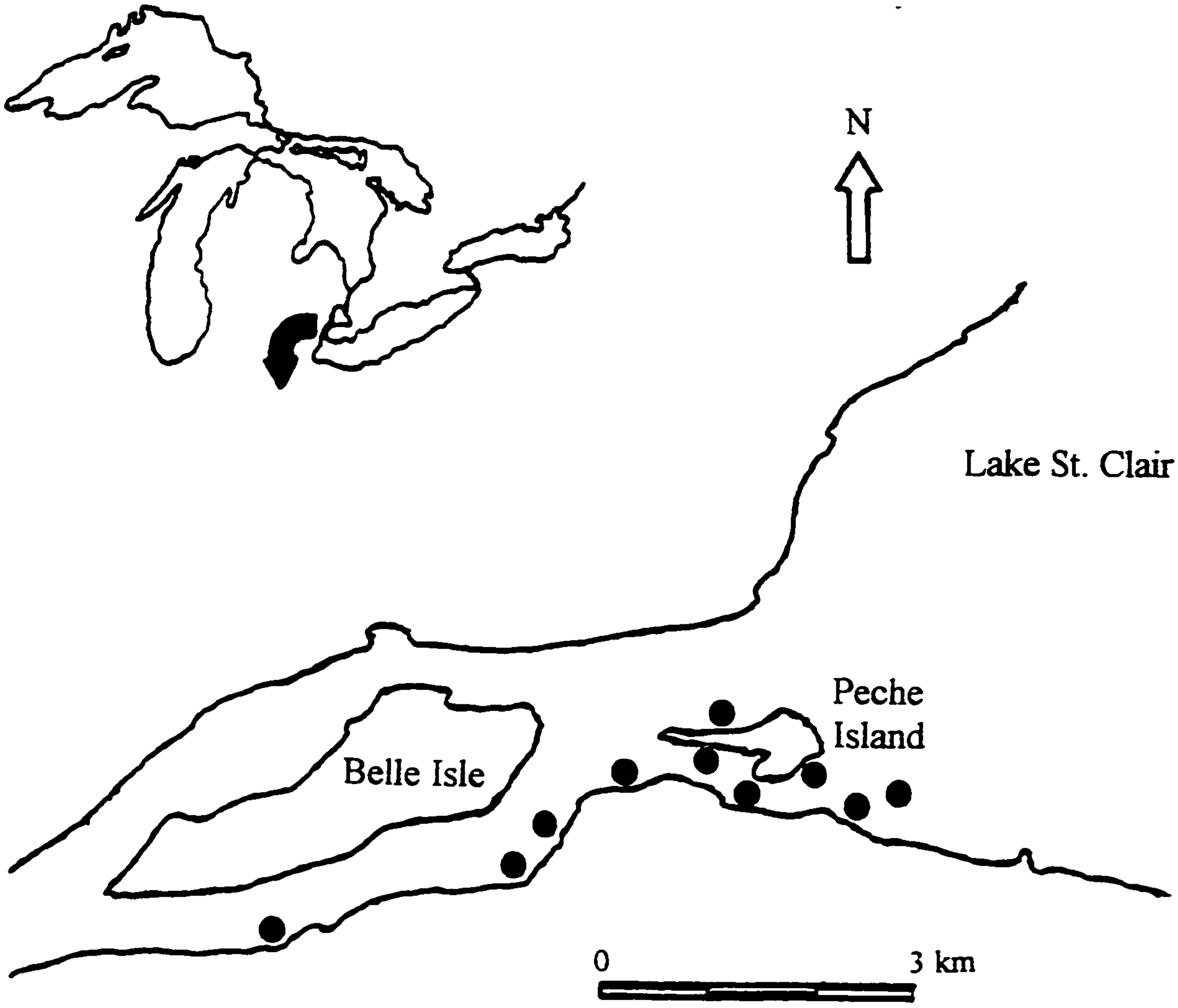


Figure 2.1 The upper Detroit River and southwestern Lake St. Clair showing the locations where round gobies were collected by trawling.

Whirlpacks® until lengths and weights could be recorded and the ovaries removed. Standard lengths were measured to the nearest 0.01 mm using digital calipers and total weights determined to the nearest 0.001 g using an analytical balance. Ovaries were removed, weighed to the nearest 0.001g on an analytical balance, and then preserved in a 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 since it preserves and hardens the eggs while breaking down the ovarian tissue (Snyder 1983). Ages were determined as in Chapter 1.

Using the total and ovarian weights a standard gonadosomatic index (GSI) was calculated. The GSI expresses the ovarian weight as a percentage of body weight and is used to determine the general reproductive status of individual females as well as that of the population (Nikol'skii, 1963, Snyder 1983). This index assumes the relationship between gonad weight and body weight is linear with a zero Y-intercept and the coefficient of variation is the same for all body weights (de Vlaming *et al.* 1982). Egg counts were conducted by first separating the eggs from the remaining ovarian tissue and then counting them by hand with the aid of a stereomicroscope. Only ovaries with mature, yolked and unovulated eggs were used to avoid underestimation of fecundity due to some proportion of the eggs having been spawned or lost during handling of the fish (Heins and Baker 1993). Following completion of egg counts the percentage of ripe females was calculated for each sample date. Seasonal trends in fish size and GSI were tested using one-way analysis of variance (ANOVA). Differences in egg number between age classes were tested using a two sample t-test.

Artificial nest experiment:

The artificial nests (15 cm long × 10 cm wide × 5 cm high) were composed of two pieces and had one open end. The top, sides, and single end were ceramic tile cemented together with silicone. The removable lower portion of the nest was a half section of PVC pipe. A total of 36 nests were placed in a 6 m × 6 m grid at each of the six sites with the nest opening randomly oriented to one of the four cardinal directions. The six (3 cobble substrate and 3 sand substrate) study sites were located in the upper Detroit River and western Lake St. Clair (Figure 2.2). The actual number of sites was reduced to four as two of the sites could not be relocated because of poor visibility and macrophyte growth. Initial SCUBA surveys were used to select sites for this experiment.

The first set of nests were placed in the field on June 1, 1996 at the east end of Peche Island (sand). The next two sets of nests were placed at St. Rose Beach (cobble) and Goose Bay (sand) on June 10, 1996. The final three sets of nests were placed in Lake St. Clair at Stop 26 Beach (sand) and north east of Peche Island (cobble) and in the Detroit River on the north side of Peche Island (cobble) on June 22. No data was collected from the sites east or north east of Peche Island. The water depth was between 1.5 and 2 m at all sites. All nests were placed in the field using SCUBA and SCUBA was used on return visits to the nest sites as well. Beginning on June 17 nests sites were visited on a weekly basis. On each date nests were either examined visually for the presence/ absence of goby eggs or recorded on video for later analysis in the lab. Video recordings were made using a black and white CCD camera in a water housing connected by cable to a monitor and VCR on the dive boat. The video recordings were made at the 24 hr setting

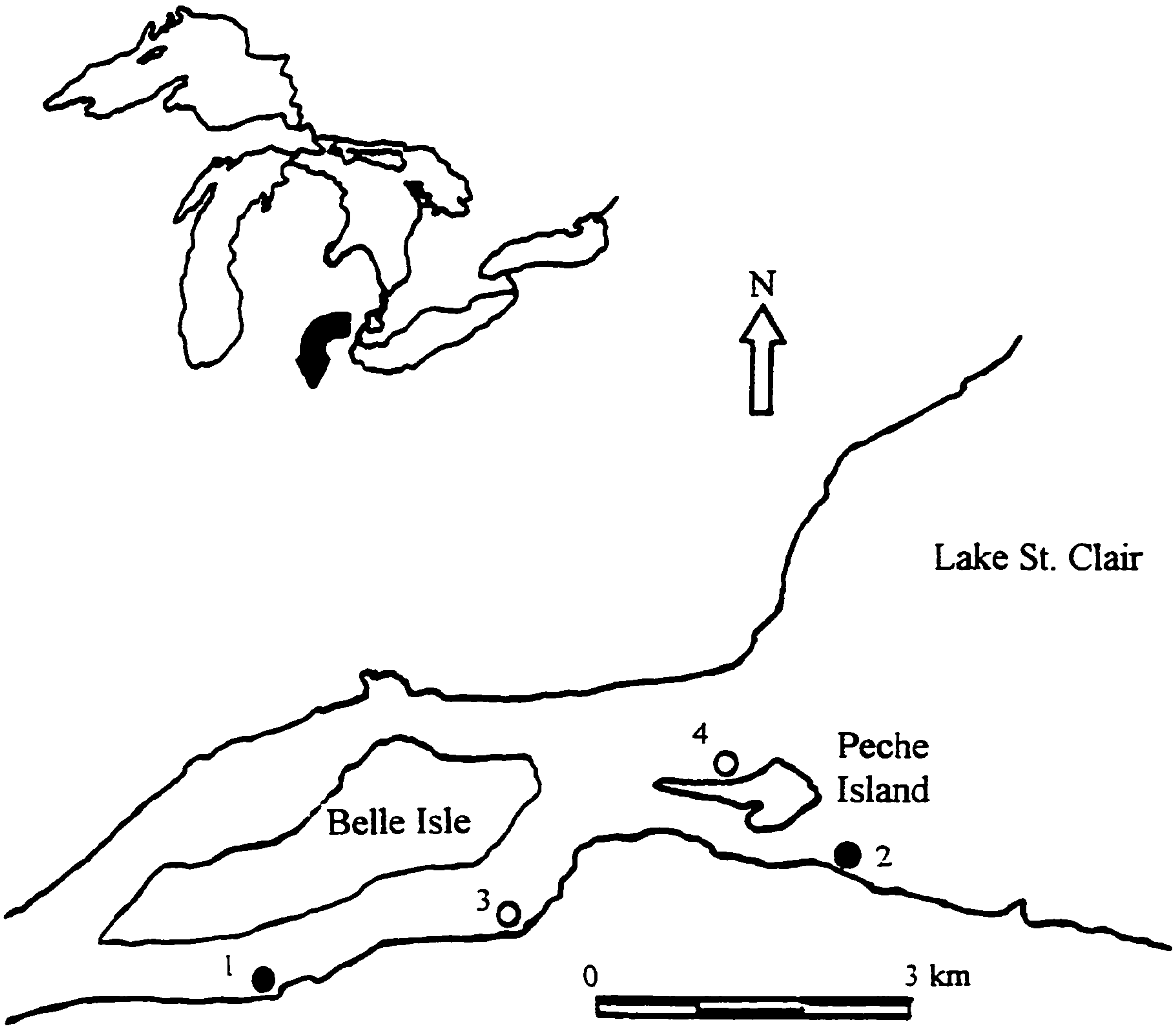


Figure 2.2 The upper Detroit River and southwestern Lake St. Clair showing the sites where artificial nests were placed. The two additional sites where no data was obtained are not indicated. Open circles indicate cobble substrate sites and closed circles indicate sand substrate sites. (1=Goose Bay, 2=Stop 26 Beach, 3=St. Rose Beach, 4=North side of Peche Island).

on the VCR using a professional quality videocassette.

The videotape was then analyzed in the lab using computer image analysis (Mocha System, Jandel 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. 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 then measured using image analysis and the number of eggs per unit area calculated.

Results

Fecundity and spawning season:

The mean length of female round gobies collected varied significantly depending on date of capture (one-way ANOVA, $p < 0.001$, df = 5, 115, $F = 5.635$) although there was no seasonal trend apparent (Figure 2.3). The mean fish size of individuals captured on July 29 by hook and line was significantly higher than the greatest mean size of females collected by trawling (two sample t-test, $t = 2.023$, $p < 0.005$). Age 1 fish were the most abundant age class of females followed by age 2 females, represented by 83 and 41 individuals respectively. Only three, age 3 females were caught during the field season. Fish size (SL) at age was highly variable with a great deal of overlap between age classes (Figure 2.4 and 2.5). Similar overlap in size occurred on all sample dates. The size range of mature females was 42.42 mm to 92.02 mm SL with a mean (±S.E.) size of 60.75 (± 0.808) mm SL ($n = 136$). Examination of age-length frequency distributions showed that

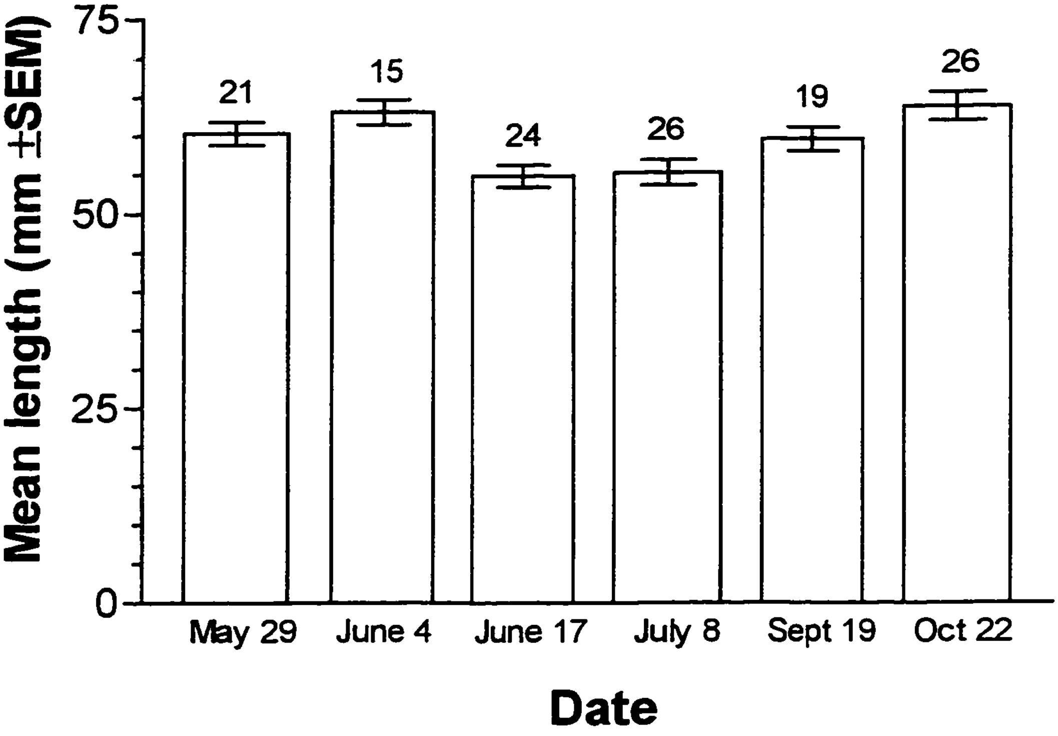


Figure 2.3 Mean lengths of mature females collected during 1996. The numbers above the bars are the sample size on each date.

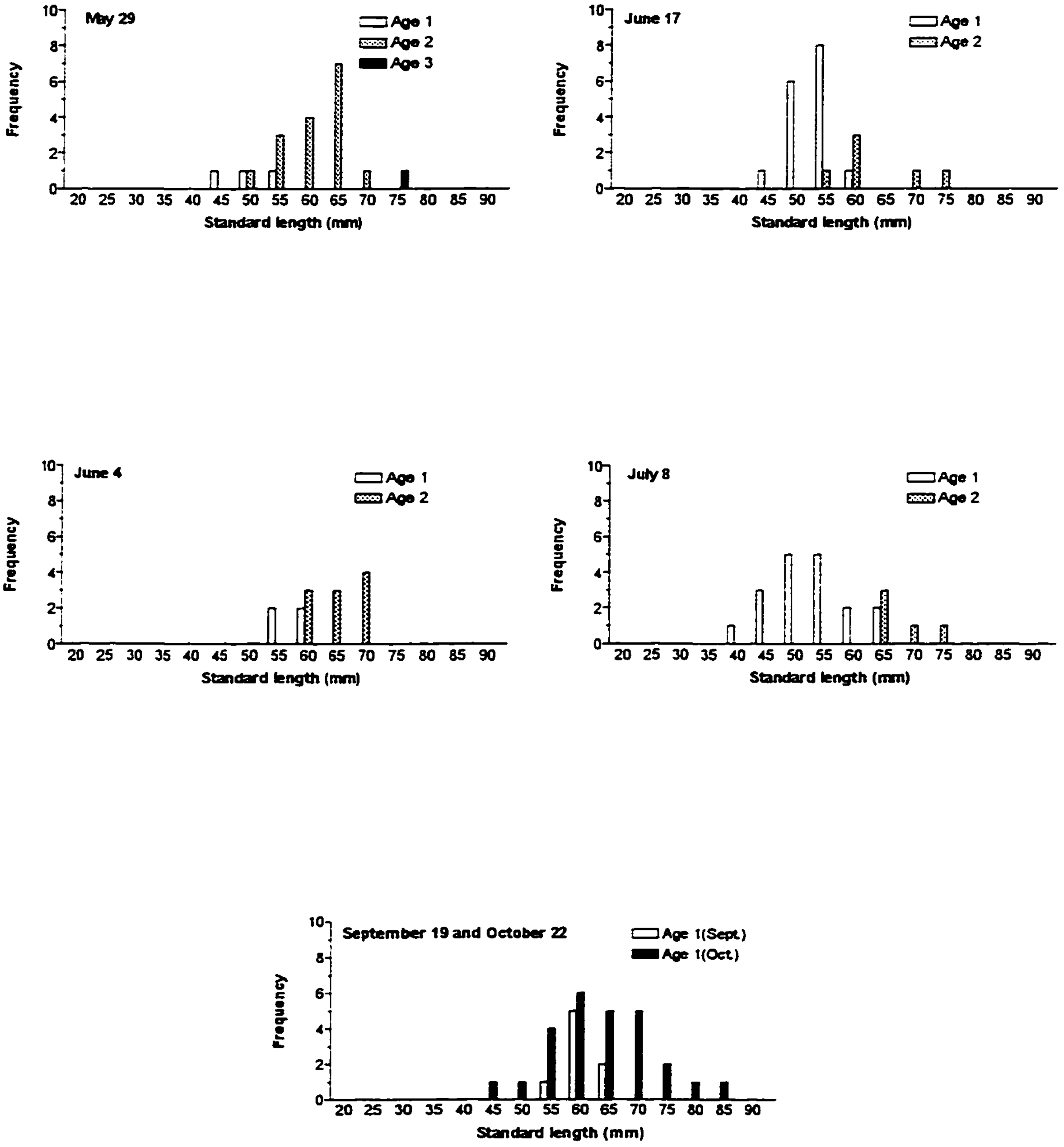


Figure 2.4 The size frequency distributions by age of adult females only for each sample date where gobies were collected by trawling during 1996.

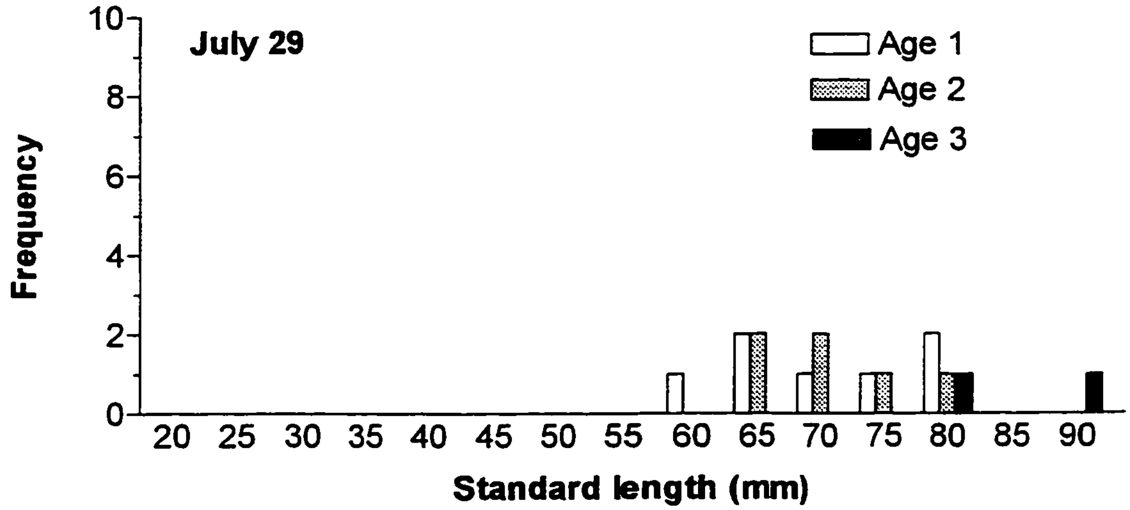


Figure 2.5 The size-frequency distributions by age for female gobies collected on July 29, 1996 by hook and line.

age 2 females were more abundant in the May 29 and June 4 collections. In the June 17 and July 8 collections age 1 females were considerably more abundant than age 2 females and in the September and October samples only age 1 females were present. Age 1, 2, and 3 individuals were represented in the May 29 and July 29 samples.

The modified Gilson's fluid used for preserving the ovaries only hardened eggs which had begun to accumulate yolk and only ovaries containing hardened eggs were used in the egg counts. Individual fecundity ranged from 84 - 606 eggs and was significantly correlated to both standard length ($r^2 = 0.76$, $p < 0.0001$) and weight ($r^2 = 0.76$, $p < 0.0001$) (Figure 2.6 and 2.7). The relationship between egg number and standard length may be non-linear indicating an allometric relationship between these characters. In order to elucidate this relationship more females greater than 75 mm SL would be required. The mean (± S.E.) number of eggs for age 2 (218.3 ± 16.33) fish was significantly higher than for age 1 (163.7 ± 9.24) fish (2 sample t-test, t(2-tailed) = 0.004, $p < 0.005$).

The percentage of ripe females varied significantly depending on sample date (one-way ANOVA, $p < 0.001$). For this calculation all females used in the egg counts were classified as ripe. The percentage of ripe females declined beginning on July 29 and none or few were found on subsequent sample dates. (Figure 2.8). The data do not meet the first assumption for the GSI as there is no relationship between gonad weight and body weight ($r^2 = 0.02$, $p > 0.05$) (Figure 2.9). However, the GSI and the percentage of ripe females show similar seasonal trends (Figure 2.10), indicating the spawning season in the Detroit River may extend from sometime in May until early August. The mean number of

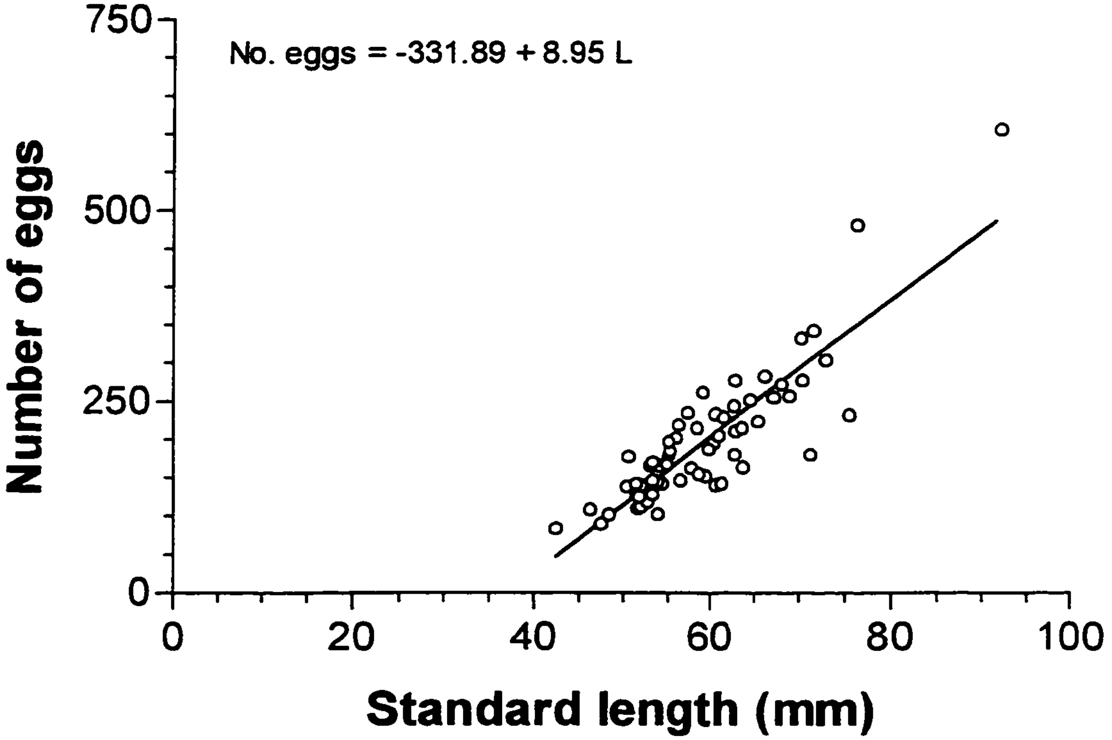


Figure 2.6 Relationship between standard length and number of eggs ($r^2 = 0.76$, $p < 0.0001$) for 63 female round gobies.

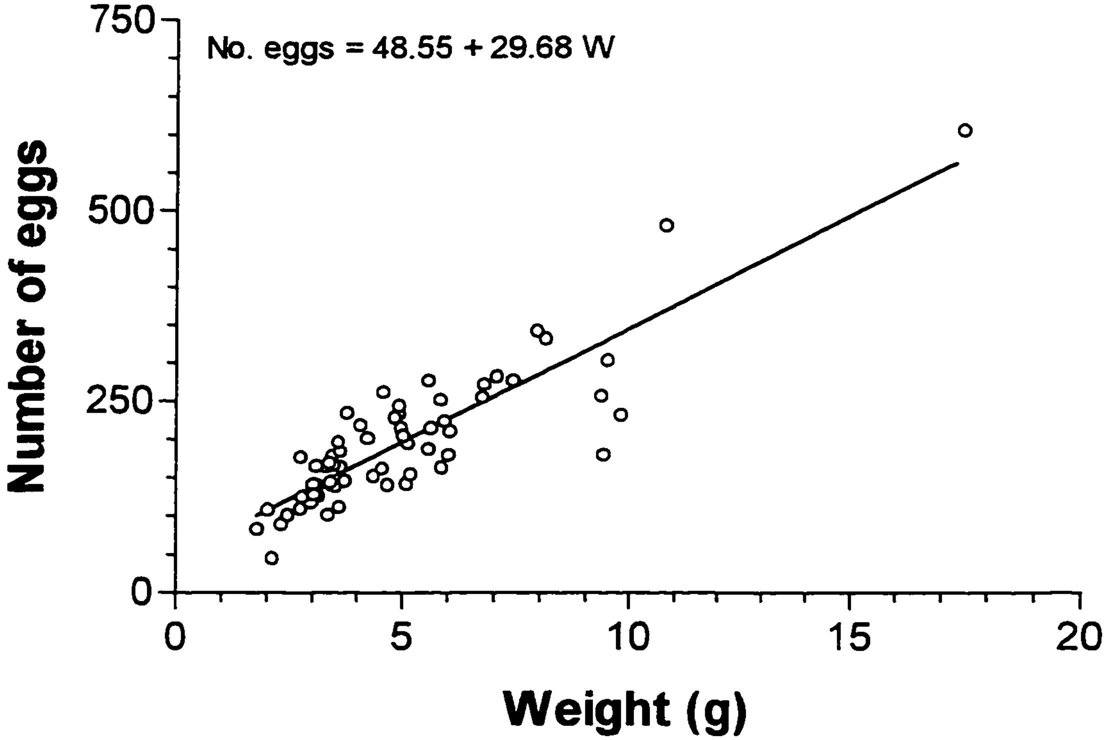


Figure 2.7 Relationship between total weight and number of eggs ($r^2 = 0.76$, $p < 0.0001$) for 63 female round gobies.

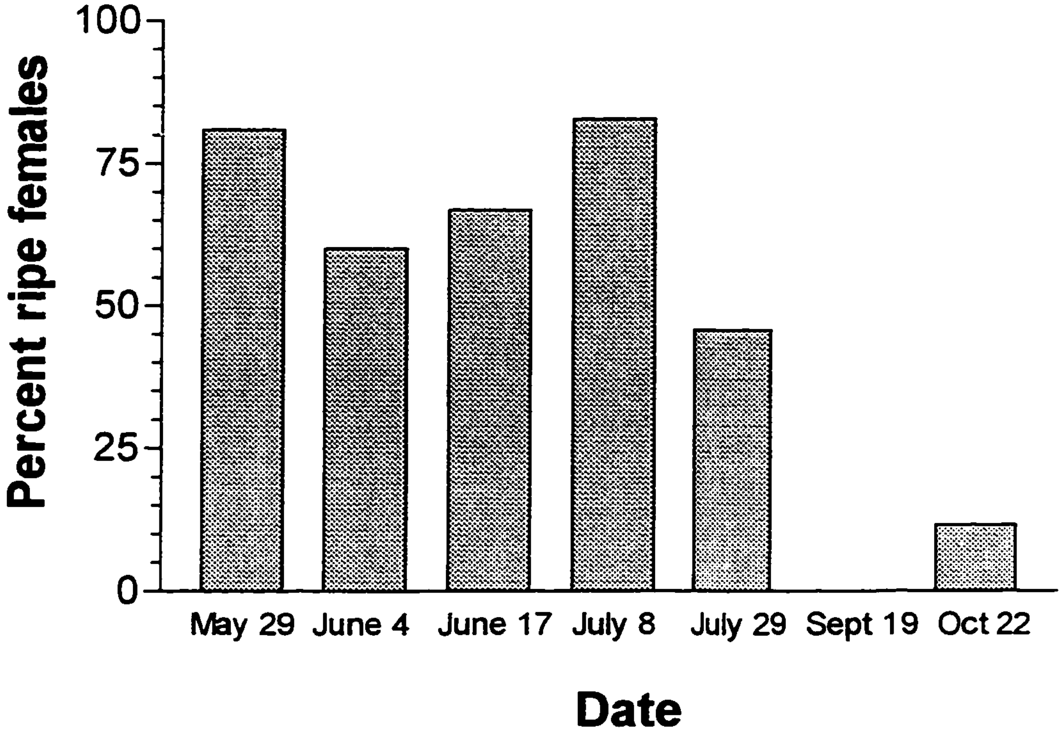


Figure 2.8 The percent of ripe females in the total catch of mature females on each collection date.

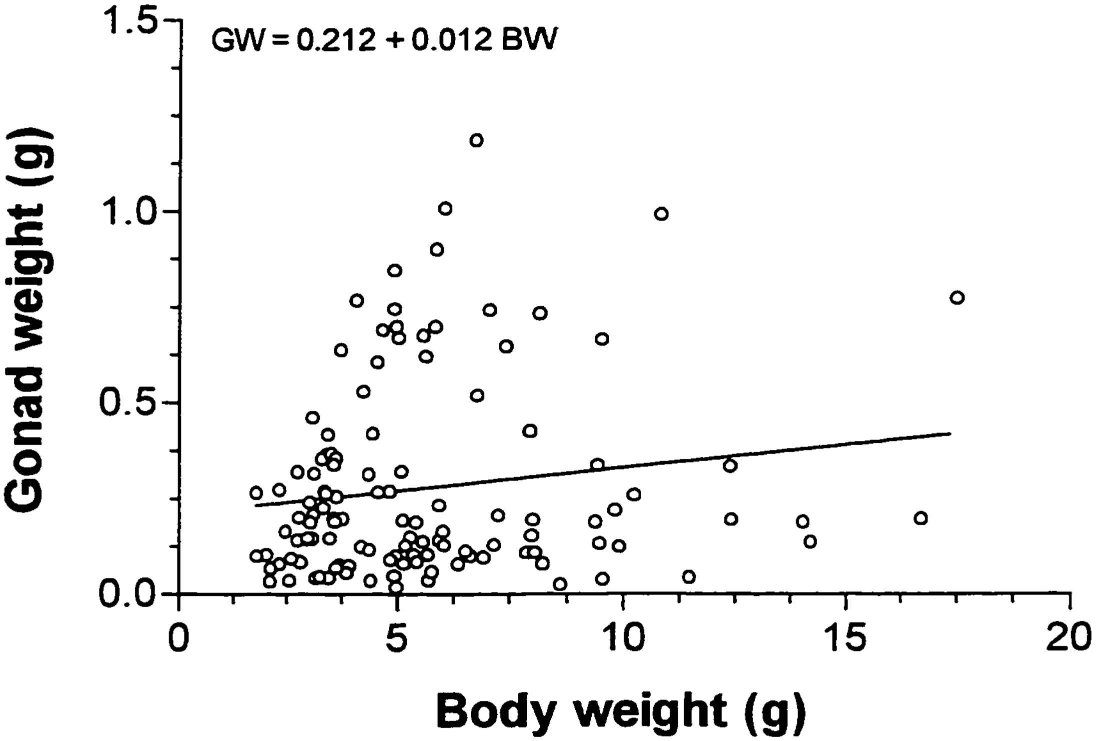


Figure 2.9 The relationship between body weight and gonad weight ($r^2 = 0.02$, $p > 0.05$) for the 118 mature females collected during 1996.

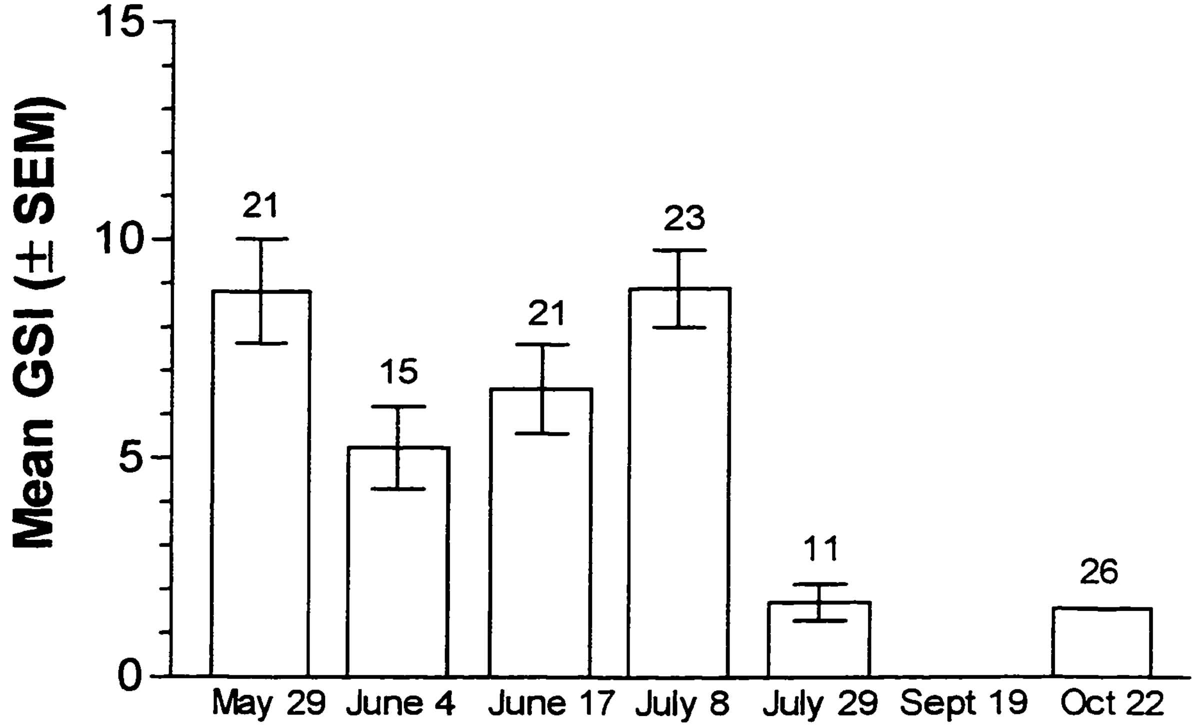


Figure 2.10 The mean gonadosomatic index (GSI) on each collection date for all mature females captured. The numbers above the bars are the sample size on each date.

eggs per individual did not vary significantly with season (one-way ANOVA, p =0.6, df = 5, 60, F = 0.73).

Artificial nest experiment:

Although the original design of this experiment had three cobble substrate sites and three sand substrate sites, the number of sites was reduced to four (2 cobble and 2 sand) because of poor visibility (< 0.5 m), heavy macrophyte growth (particularly *Cladophora*), camera malfunctions, and vandalism (stolen buoys).

The number of nests which contained eggs varied considerably between sites with the highest occupation rate at Goose Bay and the lowest at Stop 26, both of which are sandy sites (Figure 2.11). The two cobble sites, Peche Island and St. Rose Beach, had intermediate number of nest occupied (Figure 2.11). Only the St. Rose site had goby eggs present on August 13. However, the presence of egg scars in a nest at Stop 26, which did not contain eggs previously, indicates the nest was occupied between the July 24 and August 13 sample dates (Table 2.1).

In the nests which 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 the nest. On only one occasion was a second, partial egg layer present covering only 3.8 cm^2. In all nests, the egg layer was essentially continuous with the only irregularities occurring at the edges of the egg mass. The density of eggs within a nest was 39.97 eggs/ cm^2 and the estimated number of eggs within a nest ranged from 644 - 9462 eggs. For the large nest this could mean about 15 females would have spawned in this nest if all females had the maximum fecundity of 606 eggs reported here. There was no clear trend in egg number

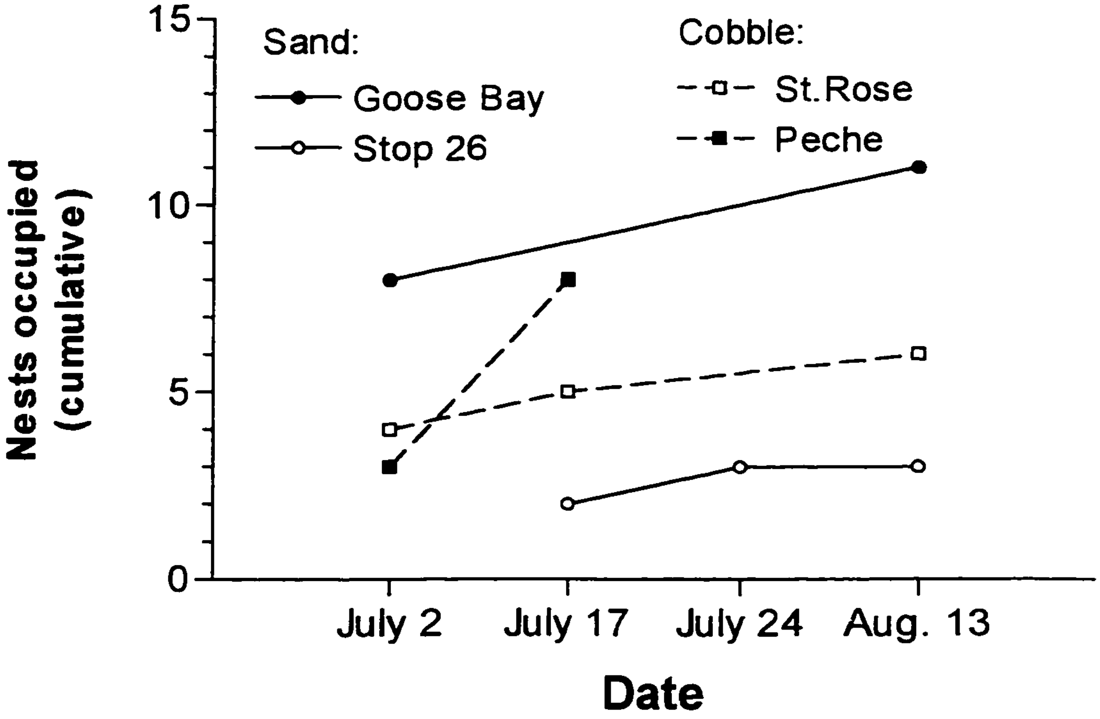


Figure 2.11 The cumulative number of artificial nests occupied at each of the four sites. The dashed lines represent the cobble substrate sites and the solid lines represent the sand substrate sites.

Table 2.1 The number of artificial nests at each of the four sites which contained either goby eggs (E) or egg scars (S) on each sample date. (St. Rose and Peche = cobble substrate, Goose Bay and Stop 26 = sand substrate; ND = no data)

	Date							
	July 2		July 17		July 24		August 13	
Site	E	S	E	S	E	S	E	S
Cobble:								
St. Rose	4	-	4	1	ND	ND	1	5
Peche	3	-	4	4	ND	ND	ND	ND
Sand:								
Goose Bay	8	-	ND	ND	ND	ND	-	11
Stop 26	ND	ND	1	1	-	3	-	3

between the sites (Figure 2.12). Nests where egg number was determined from measurement of the area of egg scars were excluded from this mean. Although nests were placed one metre apart it was not unusual for adjacent nests to be occupied by gobies even though very few of the nests at a given site were occupied (Figure 2.13).

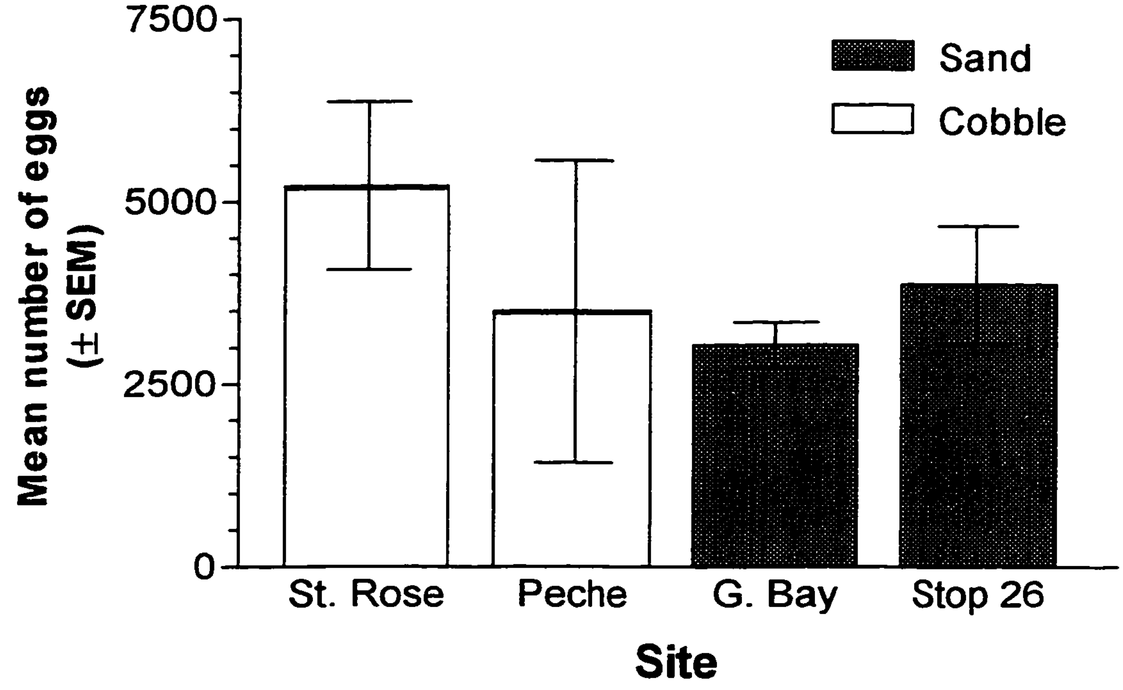


Figure 2.12 The mean number eggs per artificial nest at each of the four sites. St. Rose and Peche are the cobble substrate sites and Goose Bay and Stop 26 are the sand substrate sites.

Cobble Substrate

		X			
X		X			X
					X
					X

St. Rose

	X				
		X	X		X
X			X		
		X			X
X					

Peche

Sand Substrate

			X		X
	X			X	
		X	X	X	
		X	X	X	X
		X		X	

Goose Bay

	X	X			
			X		
		X			

Stop 26

Figure 2.13 The spatial distribution of nests occupied by round gobies for the four sites. All nests which had contained goby eggs or scars are included.

Discussion

It has been assumed that the round goby has a similar reproductive life history in the Great Lakes as in its native European range. This can be a dangerous assumption as there can be considerable variation in life history characters between fish populations even over relatively small geographic distances (Baker and Heins 1994). The round goby could have considerably different life history characters in the Great Lakes particularly given the differences in habitat (especially salinity) and possible differences in the thermal regime.

In their native range, female round gobies mature primarily at age 2 although some will mature at age 3 (Miller 1986). In the Detroit River, most female round gobies are maturing at age one and possibly some at age 2. I captured mature females < 45 mm SL that are considerably smaller than mature female round gobies in Europe. In an examination of the fecundity of round gobies from the Sea of Azov, Kovtun (1978) counted all gobies of less than 7 cm body length as a single size class suggesting mature females of this size are relatively uncommon. He also reported that some round gobies in the Sea of Azov mature at age 1. The Detroit River goby population is maturing earlier and at a smaller size and this could be important to population dynamics.

Evidence from the percentage of ripe females captured and GSI indicate that the major spawning season of the round goby in the Detroit River extends from mid May until early August. Some spawning may occur after this as the presence of eggs was observed in an artificial nest on August 13, 1996. The length of the reproduction season is 3 months, although some annual variation depending on temperature regime may exist. Round goby spawning can occur at temperatures as low as 10°C but is more prevalent at warmer temperatures (S. Rudnika, personal communication). The GSI was a good indicator of the length of the spawning season in the round goby and its results corresponded to a second measure of reproductive success, the percentage of ripe females. The GSI also has been used in other gobiid fishes for determination of reproductive season successfully (Kanabashira *et al.* 1980, Arruda *et al.* 1993). Kanabashira *et al.* (1980) found that the seasonal change in the GSI corresponded to the abundance of egg-containing nests in the field. Although nest data in this study are limited it does correspond to the decline seen in the GSI and the percentage of ripe females at the end of July. However, the results of the GSI are weakened somewhat as the relationship between body weight and gonad weight was not linear, a linear relationship between these variables is the first assumption of the GSI (de Vlaming *et al.* 1982). As the first assumption was not met, it was not possible to test the validity of the other assumptions for the GSI.

In the artificial nest experiment the amount of spawning activity did vary depending on the site but no real conclusions can be drawn given the limited amount of data available. The high number of nests occupied at the Goose Bay site was expected since it had a sand substrate and the number of natural nest sites available would be limited. The number of nests occupied at the two cobble substrate sites was lower as expected since more natural nest sites would be available. The Stop 26 site (sand substrate) had the lowest numbers of nest occupied overall which was not expected. Although it is not possible to draw conclusions from only one site, this result may be caused by higher predation rates on round gobies at Stop 26. Little cover is available to the gobies at this site and visibility was always much better than at Goose Bay , the other sand substrate site. A second possibility is that the difference is a result of the physical differences between the river and lake sites. The upper Detroit River is deeper than Lake St. Clair and has considerably less shallow water habitat available than Lake St. Clair. Round gobies prefer to spawn in water depths from 0.2 to 1.5 m (Marsden *et al.* 1996). The preferred distance between nests ranges from 5 to 10 m but this will decline if suitable nest sites are limited (S. Rudnika, pers. comm). Since there is a greater area of shallow water habitat present at Stop 26 the number of nests may tend toward the preferred density, while in the Detroit River the area of shallow water habitat is considerably less and may increase the nest density. Further research is required to determine the density and depth distribution of goby nests in the Great Lakes.

There was no apparent trend in the mean number of eggs per nest among the sites except that St. Rose, a cobble site, was slightly higher than the remaining three sites. The numbers of eggs at Goose Bay may have been underestimated as the poor visibility at this site greatly affected the quality of the video image. In their European range, a goby nest may contain up to 10,000 eggs representing the clutches of 4-6 females (Marsden *et al.* 1996). A similar range in the number of eggs per nest was observed in this study but the number of females contributing to a single nest appears to considerably higher given the lower fecundity of the round goby in the Great Lakes. Female gobies appear to prefer to spawn in nests already containing eggs which is common among nest guarding fishes (Forsgren *et al.* 1996, Kraak and Weissing 1996). Also the largest males usually are guarding the nests with the most eggs (Bisazza *et al.* 1989). It was not possible to determine this trend for the round goby as the male would disappear as soon as the upper portion of the nest was removed in order to record the eggs on videotape. Interestingly, Kovtun (1980) did note that large nests (8,000 - 10,000 eggs) are more susceptible to predation and tend to be more poorly aerated.

Egg number was significantly correlated to body size in an apparent linear relationship with number of eggs increasing with body size. The number of eggs per female as measured here is simply a measure of the batch fecundity. In the ovaries two classes of eggs were present, those which were ripening and accumulating yolk and a group of much smaller atretic eggs which were not hardened by the preservative. Of the mature and ripening eggs present within the ovary, there was no difference in size between the eggs indicating that the eggs would be spawned as a single batch. Potentially there were other eggs present in pre-yolk stages but this could not be determined as histological examinations of the ovaries were not conducted. Round gobies have been known to spawn up to 6 times every 18-20 days in captivity (Rashcheperin 1964, cited by Kovtun 1978) and in intensive culture a female can spawn up to 10 batches per season (S. Rudnika, personal communication) In the wild it is more normal for a female to spawn from 2-4 batches per season (Kovtun 1978, S. Rudnika, personal communication).

Using an estimate of 3 batches per season it is possible to estimate the absolute annual fecundity of individual females. Batch fecundity ranged from 84 - 606 eggs per individual and the corresponding absolute fecundity ranged from 252 - 1818 eggs. This falls below and within the lower end of the range reported by Kovtun (1978) of 328 - 5221 eggs. Age class fecundities range from 252 - 849 eggs and 384 - 1818 eggs for age 1 and 2 females respectively in the Detroit River. In the Sea of Azov the absolute fecundities of age 1 and age 2 round gobies are 988 - 4221 and 1665 - 5221, respectively. It is not possible to compare age 3 females as I only have egg counts from 2 individuals. The absolute fecundities for these two individuals fall in the middle of the range for age 2 gobies.

A number of other Great Lakes fishes exhibit a similar reproductive life history pattern to the round goby. Four such species are the mottled sculpin (Cottidae: *Cottus bairdi*), the johnny darter (Percidae: *Etheostoma nigrum*), the northern madtom (Ictaluridae: *Noturus stigmosus*) and the brindled madtom (Ictaluridae: *N. miurus*) (Scott and Crossman 1973). These four fishes are cavity nesters with male parental care of the eggs and therefore may compete directly with the round goby for nesting sites. Individual fecundities for these species range from an average of 257 in the mottled sculpin (Bailey 1952) to about 40 eggs in the brindled madtom (Scott and Crossman 1973). The madtoms are perhaps the least vulnerable of these species as their spawning season occurs near the end of the round goby spawning season when goby reproduction has declined (Taylor 1969; MacInnis 1997, ms submitted). The madtoms also have the additional defense of pectoral spines and a venomous dorsal spine (Scott and Crossman 1973). The mottled sculpin is definitely vulnerable and has experienced severe declines in the St. Clair River and southern Lake Michigan following introduction of the round goby (Jude *et al.* 1995). The johnny darter has a similar reproductive strategy to the mottled sculpin and may also decline as the round goby spreads throughout the Great Lakes basin.

One reason for the decline of the sculpin may be the aggressive nature of the round goby which could push the mottled sculpin out of optimal spawning habitat (Jude *et al.* 1995). In the lab the round goby has been shown to drive resident mottled sculpins out of a shelter (Dubs and Corkum 1996). Another possible reason for the decline of the mottled sculpin may be the large difference in reproductive capacity between these two fishes since the round goby has an extended reproductive season and spawns more than once while the mottled sculpin spawns only once early in May. Male round gobies are the first to appear in spawning habitat early in the spring and set up territories prior to the arrival of females (Kovtun 1980). These gobies could then disrupt nesting sculpins by driving them from the nest or consuming the eggs causing year class failure in the sculpins (Jude *et al.* 1995). A similar scenario could very likely occur in the johnny darter as well.

A potentially high reproductive capacity appears to be one of the mechanisms by which the round goby population is thriving in the Great Lakes and will ensure its continued range expansion. Its extended reproductive season will minimize interannual variation in year class strength as it will be less vulnerable to nest destruction by a single event like a storm. The fecundity of this exotic fish is at least as high as many similar Great Lakes fish with the advantage of an extended reproductive season. Female round gobies mature rapidly and begin reproducing after their first winter. The number of batches produced by a single female during the season is unknown but a reasonable estimate would be 3 batches per season. For a female with an average fecundity of 198 eggs per clutch this could lead to a lifetime fecundity of 1782 eggs. Although this estimate does not account for increases in fecundity with fish size and age, it still represents a very high reproductive capacity given that fertilization rates in the round goby are high (~ 95%) and successful males can hatch up 95 % of the eggs in their nest (Marsden *et al.* 1996).

General Discussion

Since their first discovery in the St. Clair River in 1990 (Jude *et al.* 1992, Crossman *et al.* 1992), round gobies have been reported from all of the Great Lakes. The largest and best-established populations are in the Huron-Erie corridor, south-central Lake Erie, and southern Lake Michigan and populations established elsewhere are expanding rapidly (Marsden *et al.* 1996). Several mechanisms as to why the round goby is such a successful invader have been proposed and include the aggressive nature and large size of the round goby compared to native benthic fishes, competition for food between YOY gobies and native fishes, and an apparently high reproductive rate (Jude *et al.* 1995). Round gobies are also potential predators of many native benthic fishes. To date the round goby has only been documented to detrimentally affect a single species, the mottled sculpin, but effects on other species have been hypothesized (Jude *et al.* 1995, Marsden *et al.* 1996). The life history of the round goby in the Great Lakes is poorly understood but this information is crucial to management of this exotic fish and to minimizing any negative effects it may have on the native fish community.

In the Detroit River, the goby seems to have similar population dynamics as in its home range although maturation occurs earlier and at a smaller size. There is some reference to individuals maturing at small sizes and at age 1 by both Bil'ko (1971) and Kovtun (1978). Round gobies in North America also seem to be less rotund than their European counterparts (S. Rudnika, personal communication). The overall size of individuals in the Detroit River also appears to be smaller than in the St. Clair River where gobies up to 180 mm TL have been collected and individuals of 250 mm TL have been observed (Jude *et al.* 1995). The largest individual collected in the Detroit River during 1996 was 124 mm TL. The apparent lack of older larger individuals in the Detroit River is probably because the Detroit River population is younger than the St. Clair River population and therefore there are few large individuals in the population yet. The size of individuals within in a population also varies considerably depending on geographic location in their native range (Marsden *et al.* 1996).

Adult males were noticeably absent from the trawls and in hook and line collections since they were guarding nests and were uncatchable using the trawl. A few age 1 and age 2 males were collected and these are likely individuals that had just matured or were unsuccessful in obtaining or defending a nest. Males following an alternative reproductive strategy also were observed. These sneaker males did not exhibit any secondary sex characters other than a large genital papilla, were relatively small (~50 mm SL), and had very large testes (similar in size to the testes of larger parental males). The mesorchial glands, which are believed to secrete female attractant hormones, are reduced in sneaker males compared with parental males (C. Murphy, personal communication). With the exception of an enlarged genital papilla, sneaker males appear to be gravid females and therefore may utilize a sneaker spawning strategy (Gross 1991). Sneaker males also have been observed to adopt the satellite spawning strategy (C. Murphy, personal communication). Further research is required on the dynamics of both types of male gobies and into the contribution of sneaker males to the population.

Size-frequency distributions should not be used as a method of determining the age of round gobies due to the large overlap in size between age classes. The only case where they may be applicable is in separating some of the YOY gobies from the remainder of the catch in late fall collections. Based on the small number of YOY gobies collected on October 22, 1996 all gobies under 40 mm SL are YOY. For accurate determination of the age in years for round gobies, the lapilli were very effective although care should be taken not to grind through the edge since the growth pattern of the otolith does not follow a perfect sagittal axis.

It was not possible to validate the occurrence of daily rings in the lapilli of YOY gobies, but there is a strong increment pattern that does suggest daily rings. Daily rings have been shown to occur in many temperate fishes (Brothers *et al.* 1975). If daily rings are to be validated for YOY gobies the fish should be collected as early in the year as possible and certainly before the end of August. The back-calculation formula following a non-linear body proportional hypothesis appears to be the most appropriate for round gobies but should be applied with care until it is properly validated by following individual fish through time. The support for this hypothesis would also be strengthened by collections of more gobies of less than 25 mm SL at the time of annulus formation or in the fall prior to annulus formation. The trawl net used in this study was relatively ineffective at collecting gobies in this size range. Seining does tend to collect smaller fish but its effectiveness in collecting round gobies is highly variable.

The von Bertalanffy growth function accurately described the growth for only 40 - 60% of the round gobies collected in the field and fits to the data were lower for the back-calculated sizes. The poor fit of the growth function to the data is a result of the wide range in size at age for round gobies due to their extended spawning season. Another reason for the poor fit is that the growth rates of individuals within a cohort may vary. Some individuals have faster growth rates and reach maturity earlier while other individuals have slower growth rates and reach maturity later (Bil'ko 1971). If this is the case then perhaps fitting two separate growth curves to the data may be more appropriate. Further research is required into this phenomenon to identify the slow and fast growing individuals. More data are required on older males to accurately determine their growth curve but the Gompertz growth function (Moreau 1987) may be more appropriate than the von Bertalanffy since it includes an inflection point. The inflection point would account for the reported increase in the growth rate of males after their first year (Bil'ko 1971).

Female round gobies in the Detroit River are maturing predominately at age 1 although some individuals were maturing at age 2 based on ages determined for mature individuals. Although age at maturity was relatively constant, the size of mature females was highly variable. Female fecundity was significantly related to body size with larger fish having more eggs. The number of eggs per clutch was similar in number to the mottled sculpin (Bailey 1952), but since round gobies may spawn 2-4 clutches per season their overall fecundity is much higher than the sculpin. Higher fecundity coupled with an extended spawning season with multiple clutches of young gives the round goby a much higher reproductive rate than any other small benthic fish in the Great Lakes. Otolith investigations may provide insight into the number of clutches per female if spawning checks can be identified in the otolith. It may then be possible to estimate the life time fecundity for individual fish and determine which females make the greatest contribution to the population.

Male round gobies also appear to have a fairly high reproductive success based on the large numbers of eggs found in the artificial nests. How successful individual males are at hatching all of the eggs in their defended nest remains to be determined. Large nests may experience a higher predation rate and lower survival rate of the eggs due to poor aeration (Kovtun 1980). The number of eggs in the nest is positively correlated with the size of the male in a number of fish species with male parental care (Bisazza *et al.* 1989, Kraak and Weissing 1996) and a similar situation may exist in the round goby. However, the large number of eggs per nest observed in this study may be an artifact caused by the artificial nests being particularly large and attractive to a goby. Natural nest sites should be observed to determine an appropriate size and shape for future artificial nest studies. There is no conclusive evidence for differences in nest densities between substrate in this study but it does suggest that nest densities may be lower in Lake St. Clair than in the Detroit River.

In summary, it appears the rapid expansion of the round goby in the Great Lakes is related to its life history characteristics. The rapid growth rate ensures that much of the population begins reproducing early. This coupled with the high fecundity and extended spawning season with apparently high reproductive success gives the round goby a high rate of population increase. These factors will ensure the continued expansion of the round goby throughout the Great Lakes.

Future Research Needs

In this study, I presented the results of the first study on the life history of the round goby in the Great Lakes. Although this study does answer a number of questions about the population structure, age, growth, and reproductive biology of the round goby it also indicates some directions for future research.

Trawling was an effective method of collecting round gobies in this study though in the future a stratified random design for trawling could be used so that the abundance of gobies could be estimated quantitatively. Further investigation is needed into effective ways of estimating the abundance of both adult males and YOY since these two groups were under-represented in the trawls. The most effective way to estimate the abundance of adult males would be to utilize SCUBA surveys using quadrats to locate the nest guarding males. The mesh size on the trawl was likely too large to collect many of the YOY round gobies so a trap or a finer mesh liner in the cod end of the trawl may be more effective for collecting YOY. The habitats where YOY are present in greatest abundance also needs to be identified.

Otoliths proved to effective for ageing round gobies and the occurrence of annual increments in the otoliths was validated, but it was not possible to complete the validation of the occurrence of daily rings. Validation of the occurrence of daily rings and the date of first ring formation in the otoliths would be a priority in future work. I would follow the same design as is presented in this study except that I would collect YOY as early as possible in the season so that otolith increments would be of greater width than in the fish used in this study which were collected late in the fall. The use of transverse sections of the sagittae for ageing gobies is also worth investigation. The sagittae are larger than the lapilli therefore the daily increments would be wider and easier to detect in YOY and it may be possible to detect spawning checks in the sagittae from adult females.

Following completion of age validation for YOY, gobies it will be possible to accurately determine hatch dates and further verify the length of the spawning season in the Detroit River. With a large enough sample size of YOY it should be possible to determine hatch dates for fish of age 1 and greater on the basis of otolith radius at the first annulus. YOY round gobies also may hold the most promise for determining the fast and slow growing individuals in the population. Detection of these individuals would be important to obtaining better fits for the von Bertalanffy growth function. Determining growth rates in YOY would also allow for better determination of whether the von Bertalanffy model or the Gompertz model, which includes an inflection point, is more appropriate for describing the growth of round gobies.

The work on fecundity is essentially complete but examination of egg size would be interesting to see if there is a decline in the egg size over the reproductive season. If such a trend does occur it is possible that the smallest eggs hatched at the end of the season would have the fastest development rate and potentially these could be the fastest growing fish in the population. Even though the nest experiment in this study produced few results, it is worth repeating although an effective method of marking the location of the sites is needed. The nest design should be changed to minimize disturbance of the guarding male. One possible solution would be constructing the nests with a clear plexiglass top with a single tile over it as a cover. Any study using artificial nests should also be coupled with a survey of natural nests in the field to determine densities and average size (number of eggs). Both the artificial nest study and the survey of natural nests should be designed so that it could be determined if round gobies in the Great Lakes spawn at depths greater than 2 metres and what the distribution by depth is. An artificial nest study could also be used to follow the reproductive success of individual males over the season to determine if it is related to male size.

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Vita Auctoris

Name: Andrew J. MacInnis

Place of Birth: Charlottetown, Prince Edward Island

Date of Birth: September 16, 1972

Education: Charlottetown Rural High School, Charlottetown, P.E.I.
1987-1990

University of Prince Edward Island, Charlottetown, P.E.I.
1990-1995 B.Sc. (honours)

Univerity of Windsor, Windsor, Ontario
1995-1997 M.Sc.

IMAGE EVALUATION
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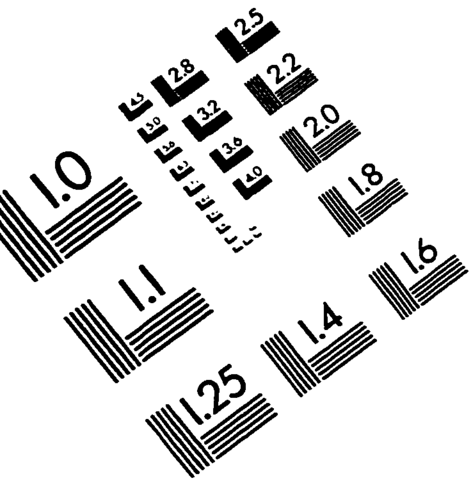

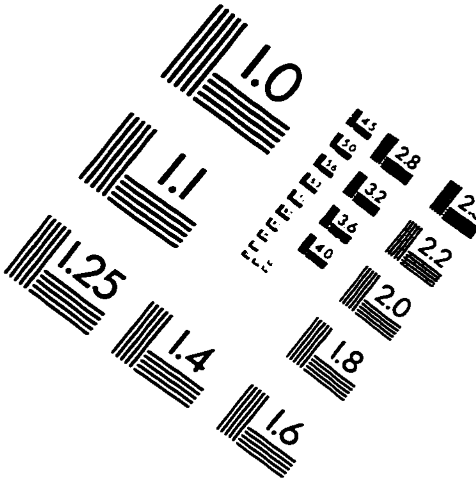

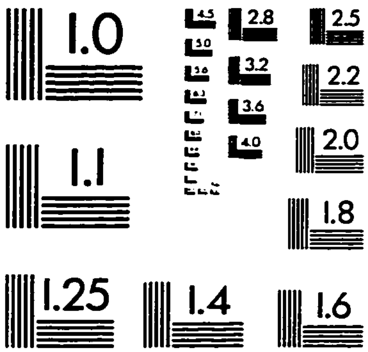

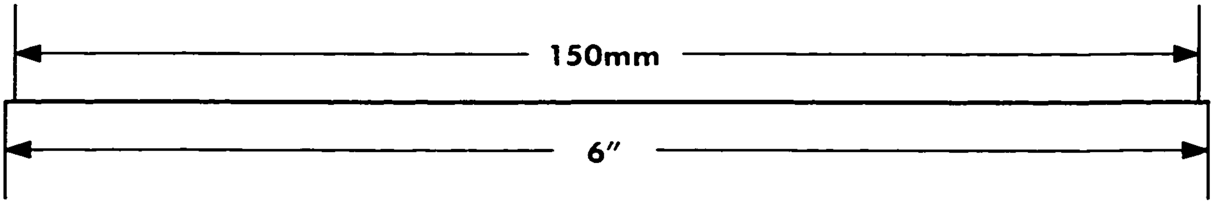

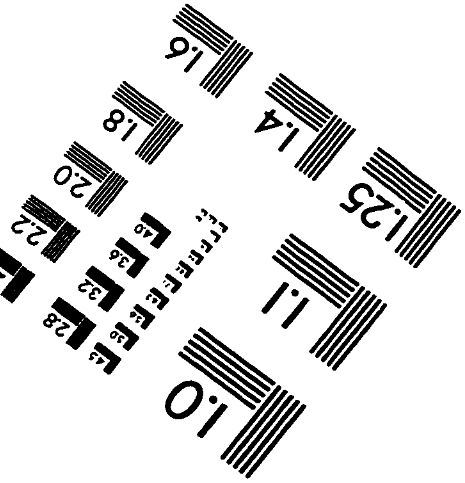

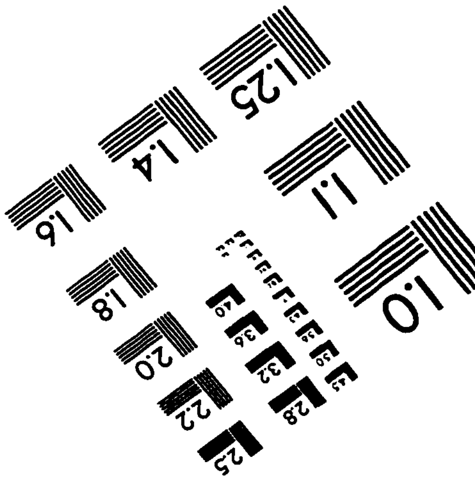

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Rochester, NY 14609 USA
Phone: 716/482-0300
Fax: 716/288-5989