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## Ecology of the threespine stickleback on the breeding grounds

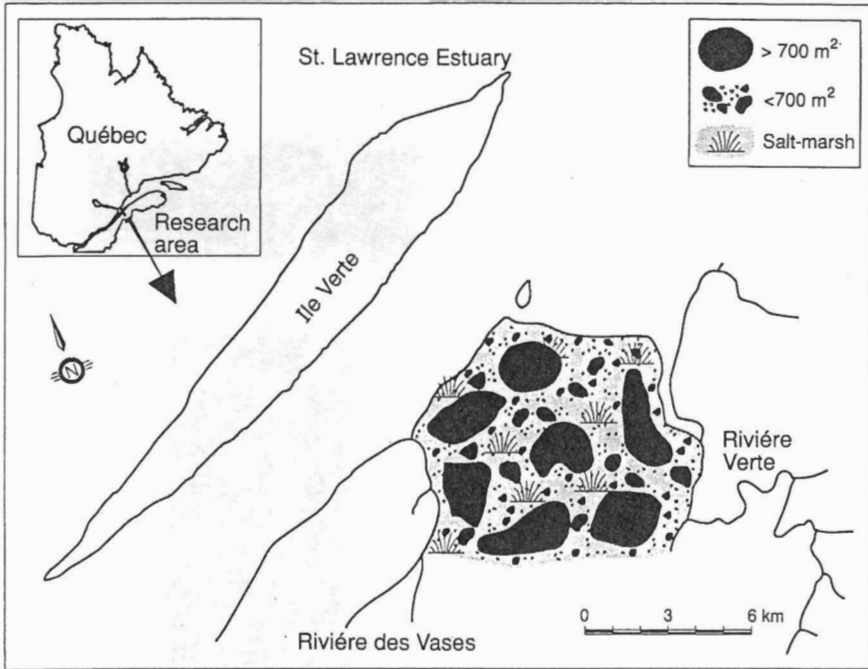
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A central theme of the behavioural ecology of reproduction of natural populations is the study of the factors causing variation in individual reproductive success (genetic contribution to future generations) (Clutton-Brock 1988). A knowledge of their relative importance is necessary to formulate predictions about the evolution of an animal's morphology or behaviour. Pertinent questions include: how widely does breeding success vary among individuals of each sex? How much variance in reproductive success is contributed by different components of reproductive success (survival to breeding age, reproductive life span, fecundity, mating success, and offspring survival)? To what extent does survival change with age? How do environmental, phenotypic, developmental, or genetic factors affect reproductive success in each sex?

Although only some of these questions have been adequately answered for the threespine stickleback, *Gasterosteus aculeatus*, this small fish is an excellent subject with which to address many important issues in behavioural ecology. Not only is this stickleback amenable to laboratory observations and manipulations, it can be readily observed *in situ* during the reproductive season. Males arrive on the breeding grounds in the spring, establish territories, look for materials with which to build nests, and court females to obtain eggs. During the spawning act, guardian males must prevent rival males from stealing fertilizations or eggs. Paternal care consists mainly of oxygenating the eggs during incubation by fanning currents of water over them with the pectoral fins, and removing dead or diseased eggs (reviewed by Wootton 1976; Rowland page 337 this volume). Males guard their eggs and fry against a variety of predators including conspecifics (see also Rowland page 339, Foster page 394 this volume). After the eggs are laid, the female has no additional role in rearing of the young.

The purpose of this review is to summarize what is known about the factors affecting some of the components of reproductive success, and, by indicating gaps in our knowledge, to provide suggestions for future work. Emphasis is placed on an anadromous population that breeds in salt-marsh tidepools along the St Lawrence Estuary near the village of Isle Verte,



**Fig. 7.1** Map of Isle Verte study site, showing series of tidepools where work on an anadromous population of threespine stickleback has been conducted since 1977. As there are about 887 tidepools at the site, this map is schematic and cannot depict all the smaller pools. For additional details see FitzGerald *et al.* (1992).

Quebec, Canada, (Fig. 7.1) because more ecological data have been collected at this site than at others. The numerous pools high in the intertidal zone of the Isle Verte salt-marsh offer abundant opportunities for field observation and experiment. This breeding habitat differs considerably from that used by freshwater populations of the threespine stickleback in that it experiences rapid and extreme fluctuations in the physical environment. Whenever possible, data are also presented from populations breeding in other habitats.

#### MEASURES OF REPRODUCTIVE SUCCESS

Field biologists are obliged for practical reasons to use measures that estimate reproductive success (indices). The indices used for male threespine stickleback have been the number of eggs in nests at the time of collection (e.g. Kynard 1978a; FitzGerald 1983) or the number of males hatching fry (Ward and FitzGerald 1988). These indices may under-estimate reproductive success because (1) it is possible that some of the males whose eggs were

collected would have completed additional breeding cycles within the same or in another breeding season (Kynard 1978*a*; FitzGerald *et al.* 1986), (2) the male might have fertilized eggs in the nests of other males (van den Assem 1967), and (3) some of the eggs fertilized by the male could have been stolen by a rival and reared successfully in his nest (van den Assem 1967; Whoriskey and FitzGerald 1985*a*). In other situations, egg or fry counts may over-estimate reproductive success because (1) the eggs collected might have failed to hatch because of predation or unfavourable environmental conditions, (2) some of the eggs in the nest of the male could have been fertilized by a rival male, and (3) some of the eggs in the nest of a male might have been stolen from the nest of another male after the other male had fertilized them.

Most examinations of reproductive success of threespine stickleback have been done in the laboratory (reviewed by Wootton 1976, 1984*a*; Rowland Chapter 11 this volume). More recently, field investigations of some of the factors affecting individual reproductive success have been conducted (e.g. Kynard 1978*a*, 1979*a*; FitzGerald 1983; Whoriskey and FitzGerald 1987; Ward and FitzGerald 1988). This chapter concentrates on summarizing these studies. Additional information on the breeding ecology of the threespine stickleback is given in Wootton (1976, 1984*a*), FitzGerald and Wootton (1986), and in the chapters of this volume by Baker, Foster, and Rowland.

Variation in male reproductive success is more thoroughly studied and is treated first in some detail. Then, because of the relative paucity of data, factors influencing variation in female reproductive success and the survival of independent juveniles are treated sequentially.

#### DURATION AND TIMING OF THE BREEDING SEASON

The length of the breeding season ranges from year-long in one Japanese population (Mori 1985) to about 50 d in southern Quebec (FitzGerald 1983) and southern France (Crivelli and Britton 1987). It is not known what factors determine its onset and length. Possible factors include changes in food, in water temperature, and in photoperiod. However, both the onset and the length of the breeding season can vary over short geographic distances. In tidepools on the southern shore of the St Lawrence Estuary, fish finish breeding at the end of June, whereas in Lac Gauthier, only 40 km to the north, fish breed well into August (FitzGerald, unpubl. data). The only pattern to emerge from a comparison of different populations is that the breeding season generally begins later in the spring in northern areas (Wootton 1984*a*; Baker page 155 this volume).

Differences in the time of breeding can occur for different forms of the threespine stickleback that breed in the same lake. In Lake Azabachije, Kamachatka (Russia), an anadromous completely plated form breeds much earlier than a resident low-plated form (Ziuganov and Bugayev 1988). It

seems that temperature and photoperiod are involved in determining the onset and termination of breeding, but the relative importance of these cues may vary among populations. In Lake Azabachije the anadromous populations bred at 5–6 °C whereas the resident population spawned at much higher temperatures. Mori (1985) suggested that the constant 15 °C temperature at his site in Japan allowed the fish to breed throughout the year. However, in southern France, breeding ceases with no noticeable environmental changes (Crivelli and Britton 1987; FitzGerald, pers. obs.). In this population it appears that endogenous factors (e.g. accelerated senescence associated with reproduction) cause fish to cease breeding.

Although laboratory studies indicate that photoperiod may influence the timing of breeding and the length of the breeding season (Wootton 1976, 1984a; Baker page 155 this volume), the situation is more complex in the field, as illustrated by the above example comparing the two Quebec populations.

#### BREEDING HABITAT

The threespine stickleback breeds in sloughs, ponds, rivers, lakes, drainage canals, freshwater and saltwater marshes, tidal creeks, and sublittoral zones of the sea. It is not known why certain areas within these habitats are chosen but other seemingly suitable areas are ignored. Warner (1988, 1990) has shown that both the physical characteristics of a site and a tradition to use the same spawning area determine where the bluehead wrasse, *Thalassoma bifasciatum*, spawns. The annual breeding cycle of most populations of the threespine stickleback makes it unlikely that cultural transmission plays a role in choosing a breeding site, although it is possible in biannual populations. It is not known whether this stickleback returns to its natal site to breed. The choice of a breeding area is probably determined principally by physical factors such as the presence of suitable nesting material and cover.

An anadromous population of threespine stickleback migrates from its overwintering areas in the middle St Lawrence Estuary to a coastal salt-marsh near Isle Verte, Quebec, where it breeds in tidepools in May and June (Picard *et al.* 1990). The fish enter the marsh with high spring tides. The pools are separated from one another and from the estuary during the two-week interflooding intervals. The choice of pool is critical for a fish because some pools will dry out, killing the adults and fry before they can return to the estuary (Whoriskey and FitzGerald 1989). Fish avoid those pools that will dry out, although it is not known how they do so. Unlike lizards (Stamps 1988), they evidently do not use conspecifics as a cue for habitat selection, because newly arriving fish were unaffected by the presence of fish already in the pools (Whoriskey and FitzGerald 1989).

Male threespine stickleback may form breeding 'aggregations' or colonies, as evidenced by the fact that nests are often clumped when seemingly suitable

habitat nearby is unused (e.g. Moodie 1972*a,b*; Kedney *et al.* 1987). There are advantages and disadvantages to coloniality. Whereas territorial males can combine efforts to defend their nests against raiding shoals of females and non-territorial males, the same males may have increased risks of egg stealing, courtship interruptions, and stolen fertilizations from rival territorial fish (e.g. Loiselle and Barlow 1978). The costs and benefits of coloniality in the threespine stickleback need to be investigated.

### Nest site characteristics

Males build nests at sites that differ in water depth, substrate type, amount and type of cover, and distance from the shore. The type of available materials used in nest construction may help conceal nests. Some nests are more difficult to locate than others because they blend well with the substrate (*pers. obs.*). Perhaps non-human predators also have difficulty in locating well-camouflaged nests. Nests are found at depths ranging from a few centimetres in tidepools (e.g. FitzGerald 1983) to 6 metres in lakes (Kynard 1978*a*). In shallow tidepools, nests are especially vulnerable when water levels recede because of evaporation (Poulin and FitzGerald 1989*a*). In lakes, nests in shallow water are vulnerable to waves during storms (Kynard 1978*a*), and in rivers they are vulnerable to fluctuations in water level (Wootton 1972*a*).

Male threespine stickleback build nests on different types of substrates, but the effects of this variation on reproductive success have not been studied. Nests are found on sand, mud, rocks, and detritus (reviewed in Wootton 1984*a*). Anadromous and stream-resident species of threespine stickleback in the Little Campbell River, British Columbia, Canada, nest on sand and mud surfaces, respectively (Hagen 1967, McPhail page 408 this volume). Although the threespine stickleback typically nests on a firm substrate, the 'white stickleback' (an undescribed threespine stickleback species characterized by white male nuptial coloration and divergent reproductive behaviour) nests above the substrate in plumes of algae. In the same location, the threespine stickleback nests on the bottom of the substrate (Blouw and Hagen 1990; Jamieson *et al.* 1992*a*).

Nest sites of the threespine stickleback also differ in the amount of concealment they afford the nest. Cover can be provided by rocks, fallen logs, vegetation, and virtually any other object. Within populations there can be considerable variation in nest concealment (Moodie 1972*a*; Kynard 1978*a*, 1979*a*), and in Enos Lake the benthic species nests mostly in vegetation whereas the limnetic species uses open areas (Ridgway and McPhail 1984, 1987; McPhail page 421 this volume). The nest of the white stickleback is partially concealed by the algae in which it nests, whereas the sympatric threespine stickleback nests in the open (Blouw and Hagen 1990; Jamieson *et al.* 1992*a*).

## VARIATION IN MALE REPRODUCTIVE SUCCESS

There is great variation in male reproductive success within and among populations. In some years at Isle Verte, only about 30 per cent of the male threespine stickleback obtain territories and nest sites, and of these only about 30 per cent obtain any eggs (FitzGerald 1983). In a sample of 150 nests collected at the site, egg numbers ranged from 0 to 2107 (Lachance 1990). Haglund (1981) also reported that only about 30 per cent of the territorial males in Sespe Creek, California, USA, had eggs in their nests at collection. Nests with eggs contained an average of 385 eggs (range 23–877).

Males can also differ in the number of reproductive cycles they complete during one or more breeding seasons. In the laboratory, males from a freshwater population in Wales can complete up to five reproductive cycles within a breeding season and live up to 5 yr (Wootton 1976). Individuals in other populations can complete more than one cycle in a breeding season (e.g. Kynard 1978*a*; Whoriskey *et al.* 1986). It is not known whether those individuals that breed in one season survive to breed in a subsequent one. In an anadromous population from southern France, individuals almost certainly breed only once (e.g. Crivelli and Britton 1987).

A high parental effort in an initial reproductive cycle is energetically costly, and this high cost may reduce a male's chances of surviving to a second breeding season (Chellappa *et al.* 1989; FitzGerald *et al.* 1989). Moreover, reproductive males may be more vulnerable to predation than non-reproductive ones (Whoriskey and FitzGerald 1985*b*). Increased vulnerability could occur because nesting males are brighter and hence more visible, and (or) activities associated with reproduction make them less wary and more visible. At sites where year-long breeding occurs, it is likely that different fish breed at different times, and not that the same fish breed continuously (Mori 1985).

Factors potentially causing variation in male reproductive success include intra- and interspecific competition for territories, nesting materials, nest sites, matings, and fertilizations.

### **Intraspecific competition for territories**

Competition occurs when animals of the same or different species interfere directly or indirectly with each other's use of resources. Territories are essential resources and may be in short supply in some habitats (Haglund 1981). One way to determine whether space limits the number of nesting males is to remove resident males and observe whether the vacated territories are refilled by other previously non-breeding males. Sometimes newly vacated territories are quickly filled (e.g. Black and Wootton 1970; Haglund 1981), but in Isle Verte tidepools, only 4 per cent of the emptied sites were reoccupied within 24 h (Whoriskey and FitzGerald 1985*a*). Furthermore, there were many seemingly suitable nest sites available in the pools.

A second test for competition for territories is to manipulate densities of adults and evaluate the effect upon male reproductive success. Manipulations showed that the percentage of males nesting, and the average territory size, decreased as fish densities increased in tidepools (Whoriskey and FitzGerald 1987; see also van den Assem 1967; Stanley and Wootton 1986). Many males failed to nest at low densities when seemingly suitable space was available. Furthermore, the median number of eggs obtained per male was unrelated to density, indicating that other unmeasured factors are more important determinants of reproductive success than competition for territories at this site.

Competition for nest sites was demonstrated in the laboratory by Sargent and Gebler (1980), who allowed males to compete for a limited number of flowerpots in wading pools. Males nesting in pots spawned earlier and more often, had a better hatching success, and suffered fewer stolen fertilizations, nest raids, and territorial encounters than males nesting outside the pots. It is still not known how important such competition is in nature.

When males compete for territories, the outcomes of interactions may be influenced by body size, age, male nuptial coloration, and aggressiveness (Rowland page 298; Bakker page 348 this volume). Because these characters are highly intercorrelated they are often difficult to discriminate, particularly in the field.

### **Interspecific competition for nest sites**

Male threespine stickleback may compete for nest sites with other species, although this phenomenon is little studied. Kynard (1979b) reported that a decline in the stickleback population of Wapato Lake (Washington, US) followed the introduction of the pumpkinseed sunfish, *Lepomis gibbosus*. He speculated that the threespine stickleback may have lost nesting space to the sunfish. The species may also compete with the mudminnow, *Novumbra hubbsi*, where the two coexist (Hagen *et al.* 1980). In tidepools, male threespine stickleback outcompete blackspotted stickleback, *G. wheatlandi*, for territories and nest sites (FitzGerald and Whoriskey 1985; Gaudreault and FitzGerald 1985). In laboratory studies of competition for territories and nest sites, the threespine stickleback outcompetes blackspotted (Rowland 1983a), fourspine, *Apeltes quadracus*, (Rowland 1983b), and ninespine stickleback, *Pungitius pungitius* (Ketele and Verheyen 1985).

Male threespine stickleback may also compete with salmonids for nesting sites, although this has not been observed directly. Gaudreault *et al.* (1986) found that breeding ninespine stickleback chased juvenile brook charr, *Salvelinus fontinalis*, from their feeding territories. The charr held feeding territories adjacent to the ninespine territories. Because the threespine stickleback is sympatric with several species of salmonids throughout its range, such interference competition may be common and should be investigated.

### Mating success

Mating success in threespine stickleback can be measured by the number of eggs a male obtains. This number depends upon the number and size of the females he can attract to spawn in his nest. Females may prefer to spawn with some males rather than others because of differences in male phenotype, degree of parasitism, and nest contents (Rowland page 313 this volume). For example, females responded more strongly to the larger of two dummy males (Rowland 1989c), indicating a possible preference for larger males in the wild. McLennan and McPhail (1989a,b) showed that those males that courted most intensively had the brightest nuptial colours, and Milinski and Bakker (1990) suggested that females choose the brightest males because these males are more likely to be free of parasites than duller males. However, breeding males of the Isle Verte population of threespine stickleback harbour few parasites, and there is no association between male nuptial colouration and parasites (FitzGerald *et al.* unpubl. data). Ward and FitzGerald (1987) studied female choice of Isle Verte threespine stickleback. In the laboratory, they found that females 'chose' males based upon their level of aggressiveness rather than their degree of nuptial coloration when territory size and quality were similar. Both highly aggressive males and very timid males were unsuccessful in getting mates. The most aggressive males broke off courtship prematurely to attack rivals, whereas the most timid males courted less often than other males. This finding supported FitzGerald's (1983) earlier field result that the most aggressive males obtained the fewest eggs.

Female choice may also be affected by nest and nest site characteristics. Although this idea has not been tested directly in the field, in the laboratory, males with concealed nests spawned earlier and more often than those with more exposed nests. They also suffered fewer stolen fertilizations, nest raids, and encounters with rivals (Sargent and Gebler 1980).

In the field, more eggs have been found in nests in deeper water (e.g. Moodie 1972b; Wootton 1972a; Kynard 1978a) and nests in or near cover (e.g. Moodie 1972b; Kynard 1978a; FitzGerald 1983), suggesting that these nest site characteristics affect female choice. Deep sites may be more attractive because they are less vulnerable to drying and wave action (Wootton 1972a, Kynard 1978a; Poulin and FitzGerald 1989a), and possibly because they are less vulnerable to predators. Concealed sites may be preferred because the young are less vulnerable to predators (e.g. Moodie 1972b).

Nest size may also be a factor in determining mating success. In the Isle Verte tidepools, the small one-year-old (1+) males build smaller nests than larger two-year-old (2+) males. Some large 2+ females were unable to enter the nests of the 1+ males (Lachance pers. comm.).

Nest contents evidently influence mating success because once a male obtains an initial clutch, he may become increasingly successful in obtaining

additional clutches. Ridley and Rechten (1981) concluded that female threespine stickleback prefer to spawn with males guarding eggs in preference to those with empty nests. Since their study, this finding has been confirmed with other species of fish (e.g. Marconato and Bisazza 1986; Unger and Sargent 1988; Peterson 1989; Sikkell 1989). However, Jamieson and Colgan (1989) criticized the experimental methodology and statistics of Ridley and Rechten, and concluded that it was not the presence of eggs but a more vigorous courtship by males with eggs that caused their greater mating success. In the above studies, females were presented with a choice between an empty nest and one with about one clutch of eggs. However, it is possible that females avoid nests having large numbers of eggs because of egg crowding. Belles-Isles *et al.* (1990) showed that female threespine stickleback prefer to spawn with males having one clutch rather than no eggs, but when females were given a choice between one and either two, three, or four clutches, they did not spawn in the nests with the most eggs, suggesting that egg crowding may occur. Another possibility is that males court less when they have more than one clutch. In nature, it is likely that all or some of these factors interact to determine male mating success.

### Stolen fertilizations

Male *G. aculeatus* may steal fertilizations from other males, thereby enhancing their own reproductive success and decreasing that of their rivals. This behaviour involves sneaking into a rival's territory while he is courting, and then following the female through the nest, fertilizing the eggs before the resident. The behaviour occurs both in the laboratory (van den Assem 1967) and in the field (Kynard 1978a). At Isle Verte, Rico *et al.* (1992) used DNA fingerprinting to assign paternity of embryos collected from nests in the wild. They found that two of the 17 nests examined contained eggs that had been fertilized by sneaker males. It would be interesting to know whether some males specialize in sneaking, and whether some individuals are more likely to be victimized than others. At Isle Verte the 1+ fish produce a greater volume of sperm, and have more viable sperm, than 2+ fish (de Fraipont pers. comm.). As the 1+ fish are less successful than 2+ fish in obtaining nest sites (Dufresne *et al.* 1990), it is possible that the 1+ fish specialize as sneakers in 'parasitizing' the mating success of the older fish.

### Egg stealing

Guardian males can lose eggs to rival males who take them back to their own nests (e.g. Wootton 1971a). Egg stealing occurs regularly in the laboratory after sneak spawnings (Jamieson pers. comm.), so perhaps the thief is simply recovering eggs that he had previously fertilized. However it is unclear why he should not let the cuckolded male raise his young. A useful study would be to determine under what circumstances egg stealing occurs in the field. Are stolen eggs raised to fry or are they eaten by the guardian

male? Perhaps a male steals eggs as a means of attracting females. Another possibility is that by adding foreign eggs to his own eggs, he decreases the risk that his own eggs will be stolen or eaten (dilution effect). Eggs and fry are vulnerable to a number of invertebrate and vertebrate predators (see below).

### **Paternal care**

After the eggs have been fertilized, the male drives the female from the territory and begins to care for the eggs. The principal activities during the egg stage are oxygenation ('fanning') and aggressive defence. Following hatching the male may guard the fry for up to 2 wk. He attempts to keep the fry together by retrieving strays and spitting them back into the centre of the brood. These activities are time-consuming, energetically costly (e.g. Chellappa *et al.* 1989; FitzGerald *et al.* 1989), and expose the male to risks of predation. As a consequence, the time a male spends with his current brood is probably inversely related to the time and energy he has for subsequent broods. The length of the parental phase depends upon how long it takes the eggs to hatch and how long before the fry are large enough to avoid the male's attempts at retrieval. From the time the male has fertilized eggs until he is ready to begin another cycle, three or more weeks may have elapsed.

### **Parental investment theory**

Predictions generated by parental investment theory (e.g. Trivers 1972; Pianka and Parker 1975; Carlisle 1982) can be effectively tested with paternal male threespine stickleback (e.g. Pressley 1981; Sargent and Gross 1986; Ukegbu and Huntingford 1988; Lachance and FitzGerald 1992). Parental investment (PI) is any material contribution or behaviour performed by a parent that increases the fitness of offspring while decreasing the parent's ability to produce future offspring. The pattern of investment should reflect a trade-off between the relative value of current broods versus future broods. The shape of the trade-off curve should be determined by the reproductive value of the parent (its chances of producing additional offspring) as determined by the age of the parent (Sargent and Gross 1986). Three key predictions of PI theory are that PI should increase with (1) the age of the parent, (2) the number of young in the current brood, and (3) the age of the brood. Each of these will be discussed below.

Two studies (Ukegbu and Huntingford 1988; Lachance and FitzGerald 1992) that have investigated the relationships between parental investment and male age in threespine stickleback failed to demonstrate the expected positive association. Ukegbu and Huntingford (1988) observed a seasonal decline in risk taking (a measure of PI) of parental males from an annual population, rather than the predicted increase, as the males aged over the course of the breeding season. They suggested that this behaviour was a

relic from an ancestral condition in which the population was biannual or that the behaviour was a laboratory artefact. However, Lachance and FitzGerald (1992) also failed to detect a positive association between male age and PI. He found no differences in risk taking over the breeding season or between the two age classes of males in the biannual salt-marsh population at Isle Verte, Quebec.

Pressley (1981) provided support for a positive relationship between PI and both brood size and brood age. He demonstrated that males from two lacustrine populations in which males live only 1 yr did accept increased risk in defence of the young as brood size and age increased. In contrast, males in the biannual population in the Isle Verte salt-marsh did not display increased levels of parental care when tending older and larger broods (FitzGerald and van Havre 1985; Lachance and FitzGerald 1992).

Lachance and FitzGerald (1992) argued that the differences in results between Pressley's (1981) study and his could be explained by habitat differences, because environmental conditions are more unpredictable in tidepools than in lakes. In the tidepools, extreme temperatures, low dissolved oxygen levels, and pool desiccation can kill parents or cause them to leave the salt-marsh before the eggs can hatch (FitzGerald *et al.* 1986; Whoriskey *et al.* 1986; Poulin and FitzGerald 1989a). In such extreme habitats, the best strategy may be to invest maximally in the current brood regardless of its size or age, because the probability of obtaining a second brood may be low, and high levels of investment may maximize the probability of hatching prior to the onset of adverse conditions. In lacustrine habitats, where risks to the parent and offspring are relatively low (e.g. Pressley 1981), changes in parental investment with changes in the reproductive value of the young may be greater and more readily detectable.

Although high levels of environmental uncertainty and individual variation in behaviour reduce the probability that differences in PI associated with differences in the reproductive value of parents or offspring will be detected (e.g. Pressley 1981), the absence of any detectable associations in the salt-marsh population suggests that PI is not adjusted to these factors in this population. The apparent differences in PI relative to brood value between the salt-marsh population (Lachance and FitzGerald 1992) and two lake populations (Pressley 1981) suggest that different selection pressures have produced adaptive interpopulation variation in this aspect of stickleback reproductive behaviour.

#### FEMALE REPRODUCTIVE SUCCESS

Little is known about the factors determining individual variation in female reproductive success in nature. Probably the best estimate of female reproductive success that field biologists can achieve is the total number of eggs produced in her lifetime. In the laboratory, the threespine stickleback can

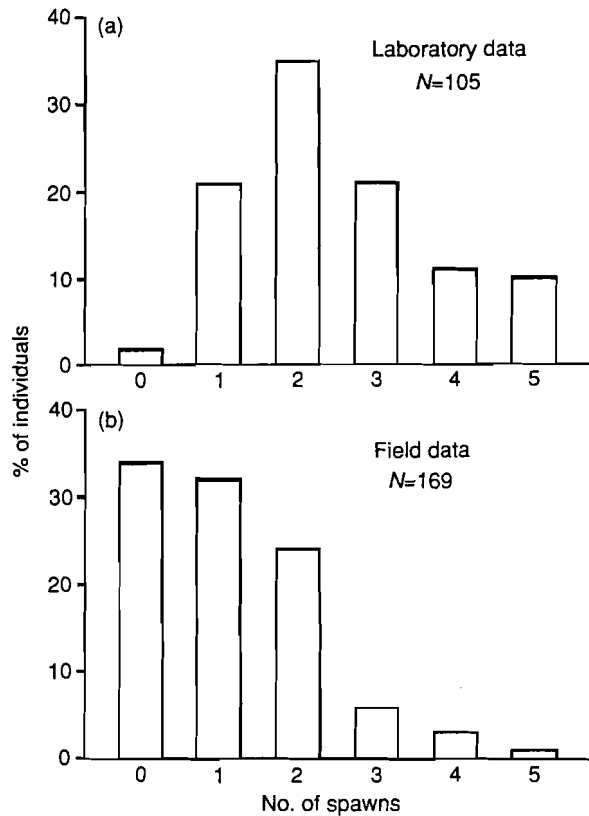
spawn a clutch of several hundred eggs every 3–5 d over a two to three month breeding season (Wootton 1976, page 135 this volume). If the breeding season is relatively short, females may spawn only once or twice in their lives (Crivelli and Britton 1987; Bolduc and FitzGerald 1989). When marked females in the Isle Verte tidepools were observed daily, they stayed on the breeding grounds for only about 2 wk (Whoriskey *et al.* 1986; Bolduc and FitzGerald 1989), about enough time to produce a single clutch at this site. In other habitats, females remain on the breeding grounds much longer, potentially producing many more clutches in a season (reviewed in Baker page 171 this volume).

Bolduc and FitzGerald (1989) compared the fecundity of females breeding in tidepools at Isle Verte with that of Isle Verte females breeding in the laboratory. They found that total seasonal egg production was higher in the laboratory, but that there was no significant difference in clutch size between the two groups. In the field, physicochemical factors (water temperature, levels of dissolved oxygen, pH, and salinity) explained a statistically significant but small amount of variation in the various measures of reproduction (i.e. daily egg production, total egg production, clutch size, interspawning interval).

Even temperature, which varies dramatically in the Isle Verte tidepools on a daily basis (McQuinn *et al.* 1983), had little effect on egg production when manipulated in the laboratory to mimic the natural temperature regime (Boulé and FitzGerald 1989). Females kept under fluctuating temperatures produced more eggs per clutch, but had longer interspawning intervals than fish kept at a constant 20 °C. Total seasonal egg production and egg size did not differ between the two groups, although fish kept in fluctuating conditions survived longer and were in better condition than those kept at 20 °C.

Bolduc and FitzGerald (1989) argued that the time spent on the breeding ground *per se* was the principal determinant of the number of spawnings an individual completed. We used some of Bolduc and FitzGerald's unpublished data to compare the patterns of individual variation in reproductive success in the laboratory and field during a single breeding season (Fig. 7.2). The field data were from individuals that survived on the breeding grounds at Isle Verte for periods ranging from 25 to 57 d. In the tidepools 34 per cent of the females never spawned and another 32 per cent produced only one clutch, whereas in the laboratory more than 77 per cent of the fish spawned twice or more over a comparable time period. These differences between laboratory and wild fish are highly significant ( $\chi^2 = 67.3$ , d.f. = 1,  $P < 0.001$ ). Hence, contrary to the conclusion of Bolduc and FitzGerald (1989), our analysis suggests that field conditions may limit reproductive output in some circumstances, but we have yet to determine the cause.

There are a number of reasons why females in nature are unlikely to achieve the same reproductive output as in the laboratory. Lower average temperatures in the field may reduce egg production if time for breeding



**Fig. 7.2** Multiple spawning by *Gasterosteus aculeatus* during a single breeding season in salt-marsh tidepools near Isle Verte, Quebec, Canada. The proportion (per cent) of females that spawned, one, two, three, four, or five times (a) in laboratory pools and (b) in tidepools is shown. See Bolduc and FitzGerald (1989) for details.

is limiting (e.g. Boulé and FitzGerald 1989). Females may be killed by predators, or the presence of predators and (or) parasites may reduce their food intake (Lima and Dill 1990) and hence egg production. Harsh physical conditions may also lead to a suppression of feeding activity (Whoriskey *et al.* 1985) with similar consequences for egg production (Wootton page 133 this volume). Furthermore, the availability of mates may limit spawning opportunities (Ward and FitzGerald 1988).

In contrast to that of males, the reproductive ecology of female threespine stickleback has received little attention, and this is clearly an area for additional research.

## ECOLOGY OF EGGS, FRY, AND JUVENILES

Mortality is usually great during the early life history stages of fish, and a small change in the daily or weekly rate of mortality can cause a severe effect so that an entire year class will be small or even non-existent (Wootton 1990). For a complete understanding of the factors affecting the population dynamics and ecology of threespine stickleback, it is essential to know the relative importance of biotic and abiotic factors in determining the survival of the early life history stages.

Although paternal care presumably evolved to minimize the effects of predation upon the eggs and fry and to provide adequate oxygenation to the eggs (Potts 1984), such care may not always be sufficient to ensure a high success. If the male dies before the eggs hatch (e.g. killed by a predator; Whoriskey and FitzGerald 1985*b*), they may all die, either because of predation or owing to suffocation.

### **Survival of embryos and fry**

#### Abiotic factors

High water temperatures, low levels of dissolved oxygen, and siltation may affect egg survival. In extreme cases, the water bodies may dry out before the eggs hatch or the fry can escape to deeper water (Wootton 1972*a*; Poulin and FitzGerald 1989*a*). Abiotic conditions may directly and indirectly affect the survival and growth of fry. Poulin and FitzGerald (1989*a*) compared the growth rates of threespine stickleback fry in a physically harsh tidepool habitat with those in a more benign river. Growth rates were higher for river than for tidepool fish. This difference may have been caused by differences in food supplies between the sites, although the tidepools are a productive habitat (e.g. Castonguay and FitzGerald 1990). A more likely possibility is that the higher pool temperatures combined with low levels of dissolved oxygen may have added higher physiological cost(s) for the rapidly growing tidepool fry compared with cost(s) encountered in the river.

In tidepools, threespine stickleback first nested near the pool banks and used the middle areas only when near-shore sites were taken (Gaudreault and FitzGerald 1985). FitzGerald *et al.* (1992) showed that nests farthest from the banks were most vulnerable to raids by conspecifics trying to attack the eggs.

It is likely that nest site characteristics are closely coupled with male care in ensuring successful rearing of the brood. Whoriskey and FitzGerald (1985*a*) removed males from their nests and compared the fate of the nest contents during the next 24 h. There was no relationship between the likelihood that a nest would be raided for nests differing in distance from the shore, per cent cover, depth, nearest neighbour distance, species of nearest (stickleback) neighbours, and material used in nest construction. The impact of environmental factors may be more pronounced in some years than in

others in highly unstable environments such as tidepools, but less variable in milder and more stable habitats such as rivers and lakes.

#### Predators and parasites

Paternal care is probably essential for the survival of the offspring. When 58 males were removed from their nests before the young had hatched, only 11 nests survived the first 24 h (Whoriskey and FitzGerald 1985a). Frequent causes of adult mortality include predators (Riemchen Chapter 9 this volume), parasites (Wootton 1976), and, in some habitats, suffocation (e.g. Poulin and FitzGerald 1989a). However, male defence of young is not perfect, and several predators, including the prickly sculpin, *Cottus asper* (Foster and Ploch 1990), the leech, *Haemopsis marmorata* (Moodie 1972a), and possibly large predatory aquatic insects (Benzie 1965), prey on embryos and fry in the nests of males.

It is not known for any population what proportion of the eggs and fry are lost to predators, but intraspecific predation (cannibalism) appears to be a major source of mortality in many populations (Whoriskey and FitzGerald 1985c; Hyatt and Ringler 1989a,b, Foster page 395 this volume). Rival territorial males, non-territorial males, and females are all potential cannibals.

Filial cannibalism (eating of kin) is of particular interest to evolutionary biologists. Rohwer (1978) suggested that guardian males eat some of the eggs in their nests in order to maintain themselves in sufficient condition to raise present and future broods. This might occur because males might not be able to obtain enough other food while caring for their young. However, filial cannibalism in the threespine stickleback occurs in habitats with abundant food supplies (e.g. Whoriskey and FitzGerald 1985c) and when males are well fed (Belles-Isles and FitzGerald 1991). The adaptive significance of male filial cannibalism in fish remains to be elucidated (FitzGerald 1992a; FitzGerald and Whoriskey 1992).

Females are also frequent egg cannibals in some populations of threespine stickleback (Whoriskey and FitzGerald 1985c, 1987; FitzGerald and van Havre 1987; Foster 1988; Foster *et al.* 1988; Ridgway and McPhail 1988; Hyatt and Ringler 1989a,b). In these populations, females form shoals of a few to several hundred individuals to attack nests guarded by males. Although males can defend nests effectively against solitary males, they cannot do so against large groups (e.g. Foster 1988). Thus, group foraging enables cannibalistic females to overwhelm the defensive abilities of males, a phenomenon similar to that described for several species of coral reef fishes (e.g. Barlow 1974; Robertson *et al.* 1976; Foster 1985a,b, 1987). As shown for two species of group-foraging coral reef fish (Foster 1985a,b, 1987), large shoals of threespine sticklebacks may be more effective than smaller shoals. At Isle Verte, large pools contain more adult threespine stickleback than do smaller pools, and the shoals formed in large pools are larger. As expected, males in large pools are less successful at defending their nests

from shoals of cannibalistic fish than are males in small pools (FitzGerald *et al.* 1992).

Eggs may be superior to alternative prey because they are more easily digestible or contain some essential nutrient not found in other foods (Belles-Isles and FitzGerald 1991). In support of this possibility, female threespine stickleback prefer conspecific eggs to blackspotted stickleback eggs, even though the same numbers of eggs were offered (FitzGerald 1992b).

It would be extremely useful to know the proportion of eggs lost to the different types of cannibalism and to different predators, in order to predict what antipredator tactics the parents and young would be expected to evolve (see Huntingford *et al.* Chapter 10 this volume). It is likely that the relative importance of cannibalism and interspecific predation on the young stages varies among populations and perhaps even within populations.

### Competition

Although not systematically investigated, there is a possibility that competition can occur at the egg and (or) early fry stages. Eggs could compete for oxygen in nests having high egg density (Reebs *et al.* 1984). In tidepools at high temperatures, oxygen levels can be below 1 ppm for several hours, and the males are forced to abandon oxygenation of their eggs to seek shelter in cooler waters. In these cases, eggs may suffer sublethal effects of oxygen deprivation. Eggs that have been laid first and covered by subsequent clutches may suffer greater oxygen deprivation than eggs on the perimeter of the egg mass, with consequent effects on egg survival, time to hatching, and morphology of the developing embryo (Ali and Lindsey 1974).

In the Isle Verte threespine stickleback population, bigger females produce larger eggs (Wootton and Whoriskey unpubl. data; but see Baker page 164 this volume). As males may mate with multiple females, their nests can contain eggs of different sizes. If competition for oxygen occurs, there may be longer-term effects on the behaviour, growth, and survival of fry. For example, large eggs may hatch sooner and produce faster-growing fry, which are better able to resist stresses, such as high temperatures and low oxygen conditions (Ware 1975).

### Survival of independent juveniles

The juvenile stage is the period in which the immature young are independent of their father. Little is known about the ecology of this stage for threespine stickleback, although it is likely that mortality is due to both biotic and abiotic factors. Juveniles are probably less vulnerable to deteriorating environmental conditions than eggs and fry because of their greater mobility. Juvenile stickleback can probably avoid unfavourable temperatures and salinity conditions as can adults (FitzGerald and Wootton 1986), although this has not been studied in juveniles.

Juveniles are vulnerable to predators and parasites. The predators that

feed on juveniles are diverse, including several species of fish, birds, and insects (Reimchen Table 9.1 this volume). Crivelli and Britton (1987) reported that egrets, *Egretta garzetta*, and grey herons, *Ardea cinera*, fed large numbers of juvenile threespine stickleback to their nestlings. Adult conspecifics are among the piscivorous fish that feed on juvenile threespine stickleback, although their impact is difficult to measure (Foster *et al.* 1988). As is the case for juveniles of other prey fishes (e.g. Werner and Gilliam 1984), predators can affect habitat use by juveniles. In particular, small juveniles vulnerable to cannibalism are confined to vegetation until large enough to be invulnerable to this form of predation. In contrast, insects that perch on weeds and ambush juveniles can cause them to leave the vegetation (Foster *et al.* 1988).

Parasites may also affect the growth and survival of juveniles. Although little is known about the effects of endoparasites, some recent experiments have shown that juveniles with a heavy infestation of the blood-sucking fish louse, *Argulus canadensis*, were less likely to survive than uninfected fish (Poulin and FitzGerald 1987, 1988, 1989*b,c*). The parasites rest on the pool substrate and attach themselves to fish that pass near by. In pools with parasites, fish swam near the pool surface, whereas in pools without parasites, fish swam near the bottom and stayed near vegetation. As there were no other 'predators' of juveniles in the pools, the observed differences in microhabitat use were probably caused by the parasites. It is unlikely that differences in microhabitat used were caused by differences in the kinds and distributions of food, as all juveniles were feeding upon zooplankton in the open waters of the pools (Poulin and FitzGerald 1989*a*; Castonguay and FitzGerald 1990).

There is little evidence that competition is a major factor affecting the growth or survival of juvenile threespine stickleback. Delbeek and Williams (1987*a*) and Poulin and FitzGerald (1989*a*) examined the food habits of sympatric sticklebacks (threespine, blackspotted, ninespine, and fourspine stickleback) in eastern North America. At both sites, food supplies were abundant and there was strong overlap in diet among juveniles of the species present. Poulin and FitzGerald (1989*a*) manipulated densities of sympatric and allopatric populations of juvenile sticklebacks in tidepools and found no consistent effects of either intraspecific or interspecific competition in these experiments. Although their results must be considered preliminary, as only a limited range of densities was used, the evidence to date indicates that competition for food is unlikely to be important for juvenile sticklebacks in highly productive coastal environments. Similar data have not been collected in other habitats.

## CONCLUSIONS

Our goal was to review some of the factors important in determining reproductive success of threespine stickleback upon the breeding grounds.

Many basic questions remain to be answered with respect to those factors. Much work on stickleback biology has been done in the laboratory, and while such studies will continue to be useful in helping to explain variation in reproductive success of the threespine stickleback, it is clear to us that more field studies are needed. The field studies that do exist are relatively few in number, of limited duration, and are usually descriptive. More field experimentation would be valuable. This should be possible in habitats such as tidepools, backwaters of small streams, and in some small lakes. In order to make generalizations about the selective pressures acting to shape morphology and behaviour, researchers must study more than one population of threespine stickleback, as different populations are influenced by different selection pressures. Only by addressing the same questions with the same methodology in different populations will progress be made in determining how a suspected selection pressure has acted to determine morphology and behaviour.

Some basic questions concerning the reproductive ecology of male threespine stickleback that remain to be answered include: How many times does an individual breed over his lifetime? Does an individual that reproduces in his first year of life reduce his chances of reproduction in future years? What proportion of the males actually fertilize eggs? Any attempt to predict individual reproductive success based on phenotype and (or) nest site characteristics will fail if the eggs have been fertilized by a rival male.

For females, field work is needed to determine what proportion of the females contribute to the gene pool. How often do females spawn and how many eggs do they produce over their lifetime? It is likely that the reproductive potential of females differs among populations as a consequence of variation in fish size and longevity, the intensity of competition for food, numbers of predators and parasites, and the severity of the abiotic environment.

More research is needed on early life history stages as very little is known about events affecting the survival of young. The breeding season is only a short part of a threespine stickleback's life, yet we know little about factors affecting the survivorship of adults and their progeny outside the breeding season. Is there any correlation between the number of eggs an individual produces or fertilizes and the number of its progeny surviving to reproduction? If not, the usefulness of much of the current work on stickleback ethology and behavioural ecology for an understanding of the ecology of this species is problematic. Much of the work reviewed in this chapter has attempted to link phenotypic characteristics (e.g. body size, nuptial coloration, territory size) to variation in measures (indices) of reproductive success (e.g. number of spawnings, number of eggs in nests, whether or not fry hatch). Even in these short-term studies, however, our ability to predict individual reproductive success is poor. Why some males are obvious 'winners' and others obvious 'losers' still eludes us in most cases. The importance of nest raiding and group behaviours have received little attention

in past studies, and these factors clearly affect individual fitness (Foster page 394 this volume).

#### ACKNOWLEDGEMENTS

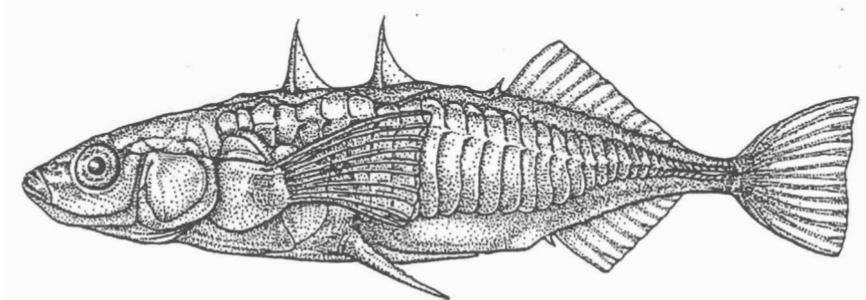
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