

Predators and morphological evolution in threespine stickleback

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The wealth of investigations on threespine stickleback during the last half-century has established the species as a model organism for evaluating population differentiation. Stickleback are particularly attractive for these studies because they exhibit extensive variability within and among populations and occurs in a diversity of habitats, from open oceanic waters to isolated bog ponds. Differences in predation levels, which are an underlying theme in diverse studies of prey defences (Curio 1976; Endler 1986; Vermeij 1987; Greene 1988), are also suspected of occurring among stickleback populations and are associated with increased expression of spines, bony armour, and escape responses (Hagen and Gilbertson 1972; Moodie and Reimchen 1976a; Gross 1977; Giles and Huntingford 1984; reviews in Wootton 1976 and Bell 1984a).

In this chapter, I focus primarily on predation as an ecological component in the biology of stickleback, and secondarily on some of the evolutionary implications of predation to morphology (behavioural aspects of defences against predators are treated in detail by Huntingford *et al.*, Chapter 10 this volume). Despite the diversity of studies on stickleback, there is not yet a detailed assessment of the age-specific causes and amounts of mortality within the life history of any stickleback population. Such an assessment would seem fundamental to evaluating morphology, behaviour and variability. To this end, I present results from a long-term investigation on sources of mortality among insular populations of stickleback from the Queen Charlotte Islands, western North America. Some of the data provide insight into the broader issues of predation levels, predator foraging efficiencies, and selection intensities in natural populations.

PREDATOR DIVERSITY OVER THE GEOGRAPHICAL RANGE OF STICKLEBACK

Although the large dorsal and pelvic spines of threespine stickleback are a substantive deterrent to gape-limited piscivores (Hoogland *et al.* 1957), this prey has been found in the diet of a remarkable array of species.

Common predatory fish such as perch, *Perca* spp., pike, *Esox* spp., and salmonids, *Salmo* spp. and *Oncorhynchus* spp., regularly consume stickleback (Hartley 1948; Frost 1954; Greenbank and Nelson 1959) and were the focus for initial experimental and field investigations of stickleback functional morphology (Hoogland *et al.* 1957; Moodie 1972a; Moodie *et al.* 1973; Hagen and Gilbertson 1973b; Moodie and Reimchen 1976a). Avian piscivores, including loon, grebe, merganser, heron, and kingfisher are widely distributed and prey on stickleback (Munro and Clemens 1937; Penczak 1968; Bengtson 1971; Huntingford 1976a; Gross 1978; Reimchen 1980; FitzGerald and Dutil 1981; Giles 1981; Giles and Huntingford 1984; Whoriskey and FitzGerald 1985b). As well, some of the macroinvertebrates found in stickleback habitats, such as leeches, dragonfly naiads, bugs, and beetles are piscivorous (Moodie 1972a; Reimchen 1980; Foster *et al.* 1988). Conspecific predation on eggs and fry may be prevalent (Greenbank and Nelson 1959; Foster 1988; Foster *et al.* 1988; Hyatt and Ringler 1989b).

Predators of stickleback vary in size from 0.3 g backswimmers (Hemiptera) to 300 kg fur seals (Pinnipedia) and comprise at least 68 species (Table 9.1) from seven major taxa: Cnidaria (1 sp.), Hirudinea (1 sp.), Insecta (4 spp.), Pisces (22 spp.), Reptilia (1 sp.), Aves (34 spp.), and Mammalia (5 spp.). The diets of marine species are least well known and one presumes that the list of stickleback predators will expand as the diets of other species are examined. Even the extinct great auk, *Pinguinus impennis*, is known to have preyed on threespine stickleback (Olson *et al.* 1979), so it seems probable that many pelagic avian piscivores could exploit this prey. The regular utilization of tidepools by juvenile stickleback (Weeks 1985b; Whoriskey and FitzGerald Chapter 7 this volume) offers unexplored associations.

Such a broadly based predation regime for a single species is the consequence of several factors. The small body size of stickleback (7–110 mm), their slow swimming speed, and their abundance would make them potentially suitable for a variety of predators, but more importantly, stickleback occur in a greater diversity of habitats than most fish. They are found in muskeg ponds, littoral, limnetic, and benthic lake habitats, streams, rivers, marine estuaries, tidepool habitats, subtidal pelagic habitats, and recently, stickleback have also been observed in open oceanic waters 100 km from the continental coastline (Williams and Delbeek 1989; Cowen *et al.* 1991). Clearly, there would be a broad range of vertebrate and invertebrate piscivores over these habitats and geographical distances.

The relative importance of each group of predators in different habitats and in different geographical areas is poorly known. Predatory fishes are dominant sources of mortality in several European and North American populations where detailed diet analyses have been made (Frost 1954; Moodie 1972a; Hagen and Gilbertson 1973b; Reimchen 1990). These fishes may be less frequent at the southern edges of the freshwater distribution of stickleback in Europe (Gross 1978), and they are commonly absent from

northern ponds in Europe and North America where limnological conditions are unsuitable or where access is restricted. Avian piscivores, because of their mobility, probably occur in more stickleback localities than any other single group of predators. In some localities, stickleback are the primary prey for mergansers, terns, and kingfishers (Sjoberg 1985, 1989; Raven 1986). Rad (1980) noted that the nesting areas of red-breasted merganser in Norway closely track the distribution of threespine stickleback on which adult and pre-fledged birds feed. Stickleback harbour a diversity of parasites that require birds as definitive hosts (see Wootton 1976 for review), attesting to the general utilization of this prey by avian piscivores. Although birds are seldom as numerically abundant as predatory fish, they have much higher metabolic rates and eat approximately 18 per cent of their body weight in fish per day (Nilsson and Nilsson 1976), as compared with 1-3 per cent for predatory fish (Elliott 1976). Their contribution to total mortality in any single population could be substantial (Reimchen 1980; Whoriskey and FitzGerald 1985b).

Predation on stickleback by mammalian piscivores has not been extensively investigated. River otter consume stickleback (Erlinge and Jensen 1981), as do mink (Gerell 1968, cited in Wootton 1976). Water shrews, *Sorex palustris*, regularly take brook stickleback, *Culaea inconstans*, in central North America (Roberts pers. comm.), but have not been reported as predators on threespine stickleback in Europe where the ranges overlap. Fur seals captured 60 km off the coast of British Columbia had stomachs filled with stickleback (Biggs pers. comm.). Human exploitation of anadromous stickleback has been reported in northern Europe (Berg 1965, cited in Gross 1978).

Freshwater macroinvertebrates including odonates, hemipterans, and coelopterans are found in most stickleback habitats and occasionally consume stickleback fry (Reimchen 1980; Reist 1980b; Foster *et al.* 1988). Their importance might be greater in localities where predatory fish are absent or where macrophytes and submerged debris provide the appropriate foraging substrates for these predators (Reimchen 1980). Leeches are also widely distributed and prey on stickleback eggs (Moodie 1972a). Leeches capture and consume adult stickleback confined in fish traps (Reimchen unpubl. obs.), but the importance of this in nature is unknown. Marine invertebrates have not been evaluated for their contribution to stickleback mortality. There is evidence for passive consumption by jellyfish (Rasmussen 1973).

PREDATOR DIVERSITY WITHIN LOCALITIES

Multiple predator species can occur in a single locality. In one of the few systematic studies of predation in a stickleback population, Moodie (1972a) observed that leeches ate eggs from nests, prickly sculpin ate eggs and small stickleback, whereas cutthroat trout ate subadult and adult stickleback.

Table 9.1 Taxonomic diversity of predators on threespine stickleback. Citations are limited to studies where direct evidence of predation was observed (stomach contents or visual observations).

Group	Species	Reference ^a
Cnidaria	Jellyfish <i>Aurelia</i> sp.	1
Oligochaeta	Leech <i>Haemopsis marmorata</i>	2
Insecta	Dragonfly <i>Aeshna palmata</i>	3
	Water scorpion <i>Ranatra</i> sp.	4
	Backswimmer <i>Notonecta</i> spp.	4
	Giant water bug <i>Lethoceros americanus</i>	4
Pisces	Dolly Varden <i>Salvelinus malma</i>	2
	Arctic charr <i>Salvelinus alpinus</i>	5
	Atlantic salmon <i>Salmo salar</i>	6
	Rainbow trout <i>Oncorhynchus mykiss</i>	7
	Cutthroat trout <i>Oncorhynchus clarki</i>	2,8-10
	Coho salmon <i>Oncorhynchus kisutch</i>	11,45
	Herring <i>Clupea harengus</i>	12
	Sea scorpion <i>Taurulus bubalis</i>	12
	Eel <i>Anguilla anguilla</i>	13
	Cod <i>Gadus morhua</i>	12
	Coalfish <i>Pollachius virens</i>	12
	Garfish <i>Belone belone</i>	12
	Pike <i>Esox lucius</i>	13,14
	Perch <i>Perca fluviatilis</i>	12
	Pikeperch <i>Stizostedion lucioperca</i>	12
	Western mudminnow <i>Novumbra hubbsi</i>	15
	Bass <i>Morone labrax</i>	12
	Chub <i>Leuciscus cephalus</i>	12
	Northern squawfish <i>Ptychocheilus oregonensis</i>	16
Prickly sculpin <i>Cottus asper</i>	2,44	
Aleutian sculpin <i>Cottus aleuticus</i>	17	
Threespine stickleback <i>Gasterosteus aculeatus</i>	4,5,18-22	
Two-striped garter snake <i>Thamnophis couchi</i>	23	
Aves	Red-throated loon <i>Gavia stellata</i>	24,25
	Arctic loon <i>G. arctica</i>	24
	Pacific loon <i>G. pacifica</i>	26
	Common loon <i>G. immer</i>	25
	Pied-billed grebe <i>Podilymbus podiceps</i>	11
	Horned grebe <i>Podiceps auritus</i>	11
	Red-necked grebe <i>Podiceps grisegena</i>	11
	Great-crested grebe <i>Podiceps cristatus</i>	27
	Western grebe <i>Aechmophorus occidentalis</i>	26
	Double-crested cormorant <i>Phalacrocorax auritus</i>	11
	Grey heron <i>Ardea cinerea</i>	12,28
	Great blue heron <i>A. herodias</i>	11,26,29
	Black-crowned night heron <i>Nycticorax nycticorax</i>	30
	Scaup <i>Aythya marila</i>	31
	Scaup <i>Aythya</i> sp.	11,26
Tufted duck <i>A. fuligula</i>	31	

Table 9.1 (Cont)

Group	Species	Reference ^a
	Oldsquaw <i>Clangula hyemalis</i>	11,26,31
	Bufflehead <i>Bucephala albeola</i>	11,26
	Barrow's goldeneye <i>B. islandica</i>	31
	Hooded merganser <i>Lophodytes cucullatus</i>	11,26
	Common merganser <i>Merganser merganser</i>	11,26,32
	Merganser <i>M. serrator</i>	27,31,33,34
	Gull <i>Larus ridibundus</i>	35
	Gull <i>L. canus</i>	35
	Herring gull <i>L. argentatus</i>	29
	Ring-billed gull <i>L. delawarensis</i>	29
	Common tern <i>Sterna hirundo</i>	36,37
	Arctic tern <i>S. paradisaea</i>	36
	Greater yellow legs <i>Totanus melanoleucus</i>	29
	Lesser yellow legs <i>T. flavipes</i>	29
	American crow <i>Corvus branchyrhynchus</i>	29
	Bronzed grackle <i>Quiscalus quiscula</i>	29
	Kingfisher <i>Alcedo atthis</i>	38,39
	Belted kingfisher <i>Ceryle alcyon</i>	11,26
Mammalia	North American river otter <i>Lutra canadensis</i>	11
	European river otter <i>L. lutra</i>	40
	Mink <i>Mustela vison</i>	41
	Fur seal <i>Callorhinus ursinus</i>	42
	Human <i>Homo sapiens</i>	43

^aReferences: 1, Rasmussen (1973), cited in 12; 2, Moodie (1972a); 3, Reimchen (1980); 4, Foster *et al.* (1988); 5, Greenbank and Nelson (1959); 6, Jakobsen *et al.* (1988); 7, Hagen and Gilbertson (1973b); 8, Armstrong (1971); 9, Nilsson and Northcote (1981); 10, Reimchen (1990); 11, present study; 12, Gross (1978); 13, Hartley (1948); 14, Frost (1954); 15, McPhail (1969); 16, Hagen and Gilbertson (1972); 17, Baxter (1956), cited in 5; 18, Semler (1971); 19, Wootton (1979a); 20, Kynard (1978a); 21, Whoriskey and FitzGerald (1985c); 22, Hyatt and Ringler (1989b); 23, Bell and Haglund (1978); 24, Madsen (1957); 25, Reimchen and Douglas (1980); 26, Reimchen and Douglas (1984a); 27, Giles (1984b); 28, Giles (1981); 29, Whoriskey and FitzGerald (1985b); 30, FitzGerald and Dutil (1981); 31, Bengtson (1971); 32, Munro and Clemens (1937); 33, Sjoberg (1985); 34, Sjoberg (1989); 35, Giles and Huntingford (1984); 36, Lemmetyinen (1973); 37, Becker *et al.* (1987); 38, Eastman (1969); 39, Raven (1986); 40, Jenkins *et al.* (1979); 41, Gerell (1968), cited in Wootton (1976); 42, Biggs pers. comm.; 43, Berg (1965); 44, Pressley (1981); 45, Zorbidi (1977).

Consequently, stickleback are exposed to different predatory regimes during their ontogeny. In a spine-deficient stickleback population without sympatric predatory fish, odonate naiads took juvenile stickleback while seven species of avian piscivores (common loon, red-necked grebe, horned grebe, common merganser, red-breasted merganser, hooded merganser, and belted kingfisher) took subadults and adults (Reimchen 1980). Mortality in an estuarine population of stickleback in Quebec was due to at least eight species (great blue heron, black-crowned night heron, herring gull, ring-billed gull, greater yellow legs, lesser yellow legs, American crow, and bronzed grackle) (Whoriskey and FitzGerald 1985b). Up to six species of avian piscivores have been observed in lakes in the Outer Hebrides

(Giles 1987c). Therefore, any differences in spatial or temporal components to foraging activity by different predators might be expected to influence the phenotypic distribution within the prey population (Reimchen 1980).

QUANTIFYING MORTALITY AND PREDATION INTENSITY

Several methods have been employed to estimate predation intensity on stickleback populations. During some of the first such studies in western North America, presence or absence of predatory salmonids was equated with presence or absence of predation (Hagen and Gilbertson 1972; Moodie and Reimchen 1976a). Although crude, this method yielded predictive differences in morphological traits including body size, lateral plate number, and relative spine length of the stickleback. This method was improved by examining stomach contents of trout and measuring the proportion of trout containing stickleback among different populations (McPhail 1977).

Gross (1977, 1978), working on European populations of stickleback, undertook a more rigorous assessment of predation intensity. He compiled a list of known or probable predators on stickleback that included 15 species of fish and five bird species. Using distributional records for each species and some site-specific information on importance of stickleback in the diet of the piscivores, he classified localities into one of three predation levels: none, low, or high. There were significant associations between predation level and a diversity of morphological traits, including relative spine length and number of lateral plates. Although diet was not directly examined for most of the predatory species in his studies, and macro-invertebrates were not considered as a source of mortality, the study by Gross clearly emphasized the predictive value of such predation indices and demonstrated the complexity of predator associations operating on stickleback populations.

Seasonal differences in predation intensity have been addressed. The highest proportion of trout stomachs containing stickleback occurred in winter and the lowest proportion occurred in spring and summer (Moodie 1972a; Hagen and Gilbertson 1973b). Trout collected during winter also had more stickleback per stomach than those collected during spring, further suggesting increased predation levels during winter (Hagen and Gilbertson 1973b). Using estimates on metabolic rates and daily food consumption, Reimchen (1990) concluded that predation levels were highest in summer and that the increased proportion of trout stomachs containing stickleback during winter was the result of reduced stomach evacuation rates during cold temperatures, rather than increased predation. Avian piscivores such as red-breasted merganser and common loon typically prey most intensively on stickleback in spring and summer (Rad 1980; Reimchen and Douglas 1984a; Sjoberg 1989), and within these periods can exhibit a narrow pulse of activity when most predation occurs (Reimchen and Douglas 1980).

EVIDENCE FOR PREDATORS AS SELECTION AGENTS ON STICKLEBACK

Differential predation on phenotypes appears to be a common theme in studies of stickleback morphology, yet direct evidence for this remains limited. Loss of the typical, red nuptial coloration of threespine stickleback has occurred in a number of populations. In two cases, this loss has been interpreted as a consequence of strong selection against conspicuous red males by predatory salmonids (Semler 1971; Moodie 1972*a*). This interpretation has recently been questioned, however, because a geographical survey of populations in the Queen Charlotte Islands, British Columbia, Canada, detected no association between predation regime and extent of nuptial colour (Reimchen 1989). In Washington State, USA, males with black, rather than red, nuptial colour, occur in association with the western mudminnow *Novumbra hubbsi*. Originally, predation by the mudminnow on fry was thought to have favoured the black nuptial phenotype (McPhail 1969), but subsequent work (Hagen and Moodie 1979) failed to find field evidence of fry predation by the mudminnow. Thus, evidence that predation has favoured loss of red nuptial colour is equivocal at best.

Highly divergent adult body sizes of stickleback occur in some populations and are associated with extensive trout predation. Large size may provide a size refuge against these gape-limited predators (Moodie 1972*a*; Reimchen 1988, 1990, 1991*a*) while small adult size may represent selection for early reproduction if opportunity for escape from predators is small (McPhail 1977). However, there is no empirical evidence for predator-mediated selection on adult size that has partitioned out the numerous additional factors such as gravity and longevity that could also influence selection on body size.

There is stronger evidence that predation has influenced selection of spine lengths. In Mayer Lake in the Queen Charlotte Islands, the stomachs of cutthroat trout contained stickleback which had proportionately shorter spines than did those in the population, suggesting that long-spined stickleback had an advantage against predatory fish (Moodie 1972*a*). Geographical surveys in north-western North America (Hagen and Gilbertson 1972) and Europe (Gross 1978) have documented positive associations between predation by vertebrates and spine length, as would be expected if long spines provided defence against gape-limited piscivores.

In contrast, predation by macroinvertebrate piscivores such as odonate naiads could favour the loss of spines if spines facilitate the capture and manipulation of stickleback by these predators (Reimchen 1980). Although this is an intriguing possibility, preliminary experiments in this study detected no difference in escape probabilities among spined and non-spined phenotypes. Reist (1980*b*, 1983) detected differential predation by aquatic insects on spine phenotypes of brook stickleback, *Culaea inconstans*, but this was

a consequence of differential avoidance of capture, rather than escape after capture. Postcapture escapes from predatory invertebrates were infrequent in each of these experiments, and as a consequence, the specific importance of spine loss during manipulation has not yet been effectively addressed.

Analyses of stomach contents of piscivorous fish also provide evidence of differential predation on lateral plate phenotypes. Hagen and Gilbertson (1973*b*) found that in rainbow trout, stickleback with seven lateral plates were eaten less frequently than expected in each of three years. This phenotype had a 7 per cent to 40 per cent reduction in predation levels relative to other plate phenotypes, and the greatest increase in frequency in the population occurred during the season when predation appeared to be most intense. In Mayer Lake, stickleback with eight lateral plates were marginally but significantly more common in the stomachs of cutthroat trout than were other phenotypes (Moodie 1972*a*). In contrast with these results from predatory fish, stickleback with five lateral plates appear to be less vulnerable to predation by two-stripe garter snake than are other plate phenotypes (Bell and Haglund 1978), demonstrating that predators can differ in their effect on lateral plate phenotypes.

Geographical surveys indicate additional evidence for selection on lateral plate phenotypes. In north-western North America, a mode of seven lateral plates occurred where predatory fish were present and a lower mode where these were absent (Hagen and Gilbertson 1972; Moodie and Reimchen 1976*a*). In Europe, modes of five to seven plates were found where pike and perch were abundant, whereas modes were lower outside the distribution of these predators (Gross 1978). Apart from number of lateral plates, there is evidence for decreased variance and decreased asymmetry in lateral plates where predatory fish were present, suggesting increased normalizing selection on these traits (Moodie and Reimchen 1976*a*).

The causes of the differential vulnerability of lateral plate phenotypes are unknown. Because lateral plate phenotypes display different evasive responses to predatory fish, this differential vulnerability may arise from genetic linkage between loci influencing behavioural and lateral plate expression (Moodie *et al.* 1973). Aggression levels and lateral plate phenotype are correlated, and this correlation could alter susceptibility to predators (Moodie 1972*b*; Huntingford 1981). It is also possible that the characteristic plate modes and plate positions observed in populations is directly functional if phenotypes differ in escape rate during manipulation by predators (Reimchen 1983, 1992*b*). The relative importance of either behavioural or morphological attributes to predator defence awaits more detailed study.

Predatory fish can have a selective influence on vertebral expression in stickleback. Stickleback fry which were variable in both total vertebral number and in the ratios of abdominal to caudal vertebrae had non-random survival when exposed to predation by pumpkinseed sunfish, *Lepomis gibbosus* (Swain and Lindsey 1984; Swain 1986). Differences in burst

swimming velocity of fry occur among vertebral phenotypes, and may account for the differential survival observed in experiments and the temporal changes in frequencies of phenotypes in wild-captured fry (Swain 1992a,b). Such differences during early periods of the life history might explain the spatial differences in vertebral phenotypes within lakes, but would not readily account for seasonal changes in vertebral number of adult stickleback (Reimchen and Nelson 1987).

PREDATORS AND MORPHOLOGY IN QUEEN CHARLOTTE ISLAND STICKLEBACK

Morphological diversity

Threespine stickleback of the Queen Charlotte Islands exhibit a remarkable degree of morphological diversity among populations (Moodie and Reimchen 1976a; Reimchen 1983; Reimchen *et al.* 1985). The size of gravid females ranges from 27 mm SL to 110 mm in different lakes. The pelvis is absent in two populations, while dorsal and anal spines are deficient in these and four additional populations. Lateral plates vary concomitantly with spine expression. Where spines are long, the lateral plates which buttress the spines are generally well developed (Fig. 9.1(a)), but where spines are reduced in length or number, lateral plates are weakly expressed and frequently absent (Fig. 9.1(c),(d)) (Reimchen 1983, 1984).

Substantial morphological differentiation also exists over small geographical distances. Populations with robust spines and plates occur within several kilometres of those in which spines and plates are absent. Within a watershed, mean vertebral number is as variable as that found throughout the circumboreal distribution of the species (Reimchen *et al.* 1985). Between parapatric populations at stream-lake boundaries, where there is major opportunity for gene flow, morphologically discrete forms occur with adult body size of the lake form being twice that of the stream species (Moodie 1972a; Reimchen *et al.* 1985). These and other data on overlapping populations indicate speciation (McPhail page 411 this volume).

Evolutionary causes of this variation within and between populations may be very diverse. None of the divergent traits such as gigantism or spine reduction is unique to the Queen Charlotte Island populations; they may also occur in scattered localities throughout the distribution of stickleback (Larson 1976; Moodie and Reimchen 1976b; Campbell 1979; McPhail Chapter 14 this volume). The situation observed on the Queen Charlotte Islands is exceptional primarily in that the variation in this small geographic area encompasses the complete range of variation found throughout the circumboreal distribution of the species. Previous investigations (Moodie and Reimchen 1976a) concluded that differences in predation intensities, defined as the presence or absence of predatory fish, were a major factor in the morphological variability among populations. More recent research

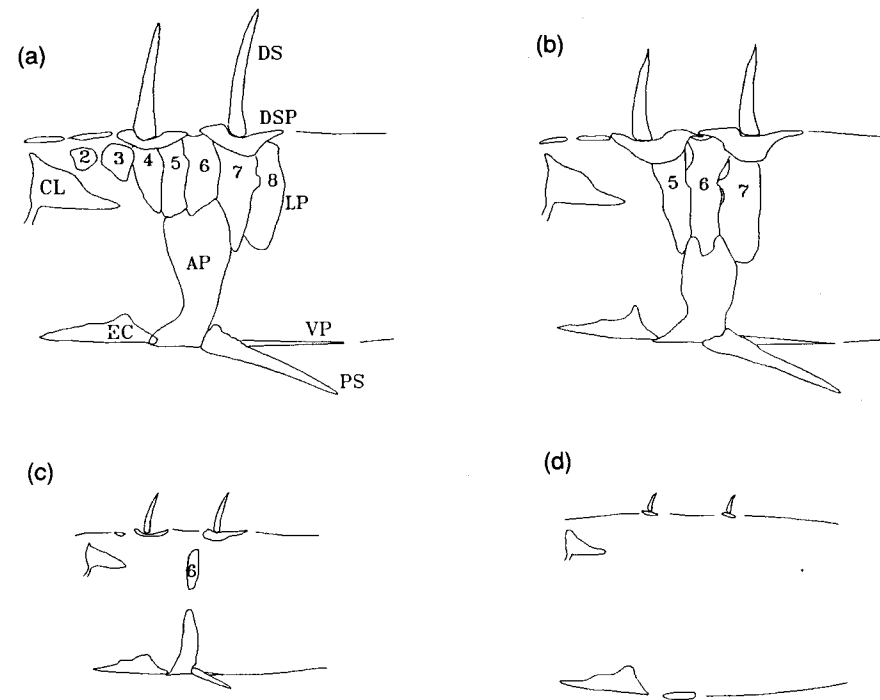
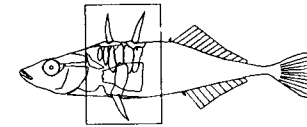


Fig. 9.1 Variation of lateral plate and spine expression among Queen Charlotte Island stickleback populations: (a) Eden Lake, (b) Hickey Lake, (c) Solstice Lake, (d) Serendipity Lake. Abbreviations: AP, ascending process; CL, cleithrum; DS, dorsal spine; DSP, dorsal spine process; EC, ectocoracoid; LP, lateral plate (position shown by number); PS, pelvic spine, VP, ventral plate.

has demonstrated that avian piscivores and macroinvertebrates could also be significant predators in some of these localities (Reimchen 1980). These initial studies involved collections from 25 localities, less than 10 per cent of potentially habitable lakes in the archipelago. From 1975 to 1988, I made collections at all lakes in the archipelago to expand the analysis of the relationship between stickleback morphology and predation regime.

Evaluating predator occurrence

Distributional data on piscivores was obtained during the geographical surveys of stickleback. The presence of predatory fish was determined by

gill netting, trapping, or rod-and-line fishing. Absence of large fish from some lakes was usually associated with poor drainage or extremes in water chemistry such as pH values near 4.0. However, even these localities may have occasional occupancy by anadromous salmonids that move into the upper reaches of most watersheds during periods of high run-off. Habitat occupation by avian piscivores was difficult to classify. These are often solitary or occur in pairs, and may readily be overlooked in sheltered habitats and on large lakes. Some species such as common merganser are absent from lakes during the day but occur near dusk and dawn (Reimchen and Douglas 1984a). Others such as grebes are only present during autumn and winter (Reimchen 1980). Consequently, some lakes were revisited at different times of the year and in different years. Macroinvertebrate abundance was also logistically difficult to ascertain because they were not regularly seen in visual surveys and were unpredictable in traps. Their occurrence was often detected by examining submerged debris. Several representative lakes were monitored weekly throughout the year for predators (Reimchen 1980; Reimchen and Douglas 1984a, see section below on Drizzle Lake).

Predator assemblages and habitat

Each habitat on the Queen Charlotte Islands has a characteristic assemblage of species. The occurrence and relative abundance of different taxa are associated with diverse factors such as shoreline cover, surface area, water depth, water colour, and productivity (Reimchen unpubl. data). For example, rainbow trout are common in clear water whereas cutthroat trout predominate in stained water. Flocks of avian piscivores are often abundant on dystrophic lakes but are rarely seen on oligotrophic lakes of comparable size. Large diving birds such as common loon did not occur on ponds less than 2 ha (Douglas and Reimchen 1988). Macroinvertebrates were common where cover such as submerged branches or vegetation was prevalent.

The major habitat types and the assemblage of species can be summarized as follows:

- (1) Dystrophic ponds (< 1 ha) all with intermittent drainage: macroinvertebrates common (including odonate naiads and beetle larvae), small avian piscivores occasionally present (horned grebe, hooded merganser, red-throated loon, oldsquaw duck, belted kingfisher), trout absent, Dolly Varden occasionally present;
- (2) large dystrophic lakes (1–200 ha) with intermittent drainage: small and large-bodied avian piscivores (common loon, red-throated loon, red-necked grebe, horned grebe, double-crested cormorant, common merganser, other diving ducks, belted kingfisher), macroinvertebrates present, predatory fish absent, otter occasional;
- (3) large dystrophic lakes (1–200 ha) with open drainage: small and large-

bodied avian piscivores common (common loon, red-throated loon, grebes, double-crested cormorant, mergansers, other diving ducks, belted kingfisher), predatory fish resident (cutthroat trout, Dolly Varden, sculpin), otter usually present, macroinvertebrates present;

- (4) Oligotrophic lakes (1–1800 ha) with open drainage: predatory fish common (rainbow trout, cutthroat trout, Dolly Varden, sculpin), avian piscivores present but probably less abundant than in dystrophic lakes (common loon, belted kingfisher, mergansers), otter present, macroinvertebrates present;
- (5) small forested creeks: predatory fish usually common (rainbow trout, cutthroat trout, Dolly Varden, salmon, sculpin), avian piscivores present (hooded merganser, belted kingfisher, great blue heron), macroinvertebrates common, otter usually present;
- (6) large unforested creeks and rivers: predatory fish common (cutthroat trout, rainbow trout, sculpin), avian piscivores present (double-crested cormorant, oldsquaw, common merganser, great blue heron, belted kingfisher), macroinvertebrates less evident, otter usually present.

Among these habitat types, which are part of a continuum, I recognize two basic predator assemblages: (A) invertebrate/bird (habitat categories 1, 2) and (B) fish/bird (habitat categories 3–6).

Given the taxonomic complexity of these predator regimes among each habitat type, it is not clear how predation intensity can be easily evaluated in a broad geographic survey. Stickleback in larger lakes appear to experience greater risks of predation because there is a greater diversity of predatory fish and birds in such lakes. However, these habitats also have a greater diversity of alternate prey (i.e. juvenile salmonids), a factor that could reduce the intensity of predation on a particular prey type. Stickleback in small dystrophic lakes would seem to experience low predation intensity because predators are seldom common, yet as demonstrated at one of these localities (Reimchen 1980), even a small number of avian piscivores combined with a paucity of alternate prey can produce substantial predation intensity. Ranking populations with respect to predation intensity, while a laudable goal, is in practice not possible without data on amount of predator-induced mortality in the survivorship curve for each population.

Lateral plates, predator assemblage, and lake area

Lateral plates have been the focus for many studies of stickleback. I extracted data on number of plates (on left side of the stickleback) from 58 lake populations (listed in Moodie and Reimchen 1976a; Reimchen 1983, 1988; Reimchen *et al.* 1985) and examined these in relation to predation regime. One of these populations was monomorphic for the complete morph ($\bar{X} = 33$ plates per side), while the remainder had only low morphs (grand

$\bar{X} = 4.1$, range 0–10.8). Partitioning for predator type yields a mean of 1.8 plates (range 0–4.6) for the bird/invertebrate assemblage ($N = 31$) and a mean of 6.6 (range 1.2–10.8, $N = 27$) for the fish/bird assemblage (F -ratio = 131; d.f. 1, 57; $P < 0.001$).

Lake area (ha) and lateral plate number are positively correlated in the bird/invertebrate, but not in the fish/bird assemblage (Fig. 9.2). Populations in small lakes (< 3 ha) average only a single lateral plate (Fig. 9.1(c)) whereas those in the largest lakes with the bird/invertebrate assemblage (200 ha) have three or four plates (Fig. 9.1(b)). None of the six populations with reduction in number of dorsal and pelvic spines occurs in habitats with the fish/bird assemblage.

Is any of this variation in lateral plate number adaptive? The average values near seven lateral plates in populations exposed to predatory fish and birds are consistent with those found in the small preliminary survey of this region (Moodie and Reimchen 1976a) and are similar to those found elsewhere in the geographical distribution of this stickleback (Hagen and Gilbertson 1972; Gross 1978). The seven lateral plates include the four structural plates that buttress the dorsal and pelvic spines and the three plates in the immediate postcranial and supracleithral region (Reimchen 1983). These anterior plates (Fig. 9.1(a)) also provide physical protection against a toothed predator (Reimchen 1992). That the populations with five

to seven plates had cutthroat trout as a dominant predator while those with more than seven lateral plates had rainbow trout as the dominant predator (Fig. 9.2) suggests fine-scale tuning of the population, perhaps owing to differences in pursuit or manipulation behaviour of these predators.

Populations in larger lakes without predatory fish but with a diversity of avian piscivores have an average of three or four lateral plates. The difference in number of lateral plates from those observed in localities with predatory fish involves loss of plates at the anterior three positions (Fig. 9.1(a),(b)) and does not affect the major structural plates that buttress the dorsal and pelvic spines. Unlike toothed predators which can puncture the epidermis of the prey, avian piscivores hold the fish by compression, and only superficial scarring results (Reimchen 1988). The anterior lateral plates found where toothed predators are prevalent may not provide any advantage when birds are the dominant predators. These could conceivably be a disadvantage during pursuit by predators if burst swimming performance is compromised. Freshwater stickleback of the low-plated morph have a higher body flexure and higher burst swimming speed than the complete morph in anadromous stickleback (Taylor and McPhail 1986). If such differences also occur among stickleback with and without the anterior three plates, loss of these plates could be favoured when pursuit escapes were a major component of the total foraging failures by the predators (see below). Even small differences in burst velocity might be important against diving birds such as loons or grebes which submerge for only brief periods.

It is unclear why populations in small ponds and lakes exhibit a reduction in the number and size of the structural plates, as this would weaken the effectiveness of the spines (Fig. 9.1(c),(d)). As well, reduction of these structural plates is associated with reduction in size of spines (Reimchen 1983, 1984) and loss of spines (Fig. 9.2). Nelson (1969) suggested that reduced spines might be useful during escape into dense vegetation. Although the bog ponds have few macrophytes, they often have soft organic substratum. If stickleback with reduced spines and lateral plates are able to avoid capture by gaining refuge in the ooze more quickly than spined individuals, this trait could be favoured. Giles and Huntingford (1984) considered but rejected this hypothesis in analyses of spine deficiencies from the Outer Hebrides because there were no detectable differences in escape behaviour among individuals from populations with normal and reduced spine expression. However, differences between phenotypes within populations were not addressed, and therefore Nelson's suggestion remains untested. Alternatively, reduction in spines and plates (Fig. 9.1(c)) in progressively smaller lakes could result from a gradual shift in the predation regime. As lake size decreases, species diversity of avian piscivores is reduced, and it is possible that macroinvertebrates account for a greater proportion of stickleback mortality. If so, this might produce the observed reduction in spines and plates, given the grappling manipulation behaviour of these

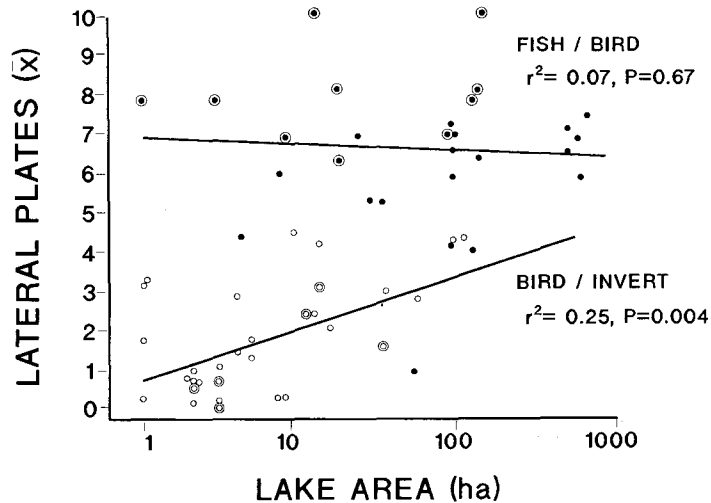


Fig. 9.2 Variation of mean number of lateral plates in relation to lake surface area and predator assemblage. Each point represents a separate population. Fish/bird communities are shown as solid points, and bird/invertebrate communities as open points. ● Cutthroat trout major fish predator; ○ rainbow trout major predator; ◐ populations with normal spine complement; ⊗ populations with spine deficiencies. All samples have $N > 50$.

predators (Reimchen 1980; Reist 1980*b*). However, in the Outer Hebrides, predatory fish are also present in populations with spine and lateral plate reduction; Giles (1983*a*) suggested that reduced calcium levels in the water could be the selective agent. An association between low calcium levels and loss of armour is also present in Alaska (Bell *et al.* 1985*a*, in press) and in the Queen Charlotte Islands (Reimchen unpubl. data), yet this is coupled with characteristic predation regimes. These competing hypotheses will not be satisfactorily resolved until causes of mortality and predator-foraging behaviour are evaluated in some of these populations.

Current deficiencies in data

Although considerable progress has been made towards determining the role of predators as selection agents in stickleback populations, more attention is required on specific predator-prey interactions in each locality. Previous efforts at estimating predation intensity, either by categorizing localities according to the presence or absence of predatory fish or by compiling lists of potential predators, are not sufficient to yield realistic estimates. Furthermore, these data may provide little, if any, useful information on selection intensities because selection will be dependent on foraging efficiencies of the predators.

PARTITIONING CAUSES OF MORTALITY: DRIZZLE LAKE

Despite the wealth of studies on predator-prey interactions in numerous taxa (see Vermeij 1987 for review), the causes and amount of age-specific mortality throughout the life history of the prey have not been determined for any population or species, including stickleback. This information is fundamental to evolutionary studies of predation. During ontogeny, spines on the stickleback are expressed shortly after hatching, but lateral plates which buttress the spines are not fully expressed until the stickleback reach about 25–40 mm SL (Hagen 1973; Bell 1981; unpubl. data). Predation attempts that occur prior to full development of lateral plates, such as are observed for macroinvertebrate predators (Reimchen 1980; Foster *et al.* 1988), would have profoundly different evolutionary consequences from attacks on adults. Seasonal differences in mortality could alter the nature of selection. For example, the relative advantage of lateral plate phenotypes of stickleback against predatory fish depends on whether the stickleback were acclimated to summer or winter temperatures (Moodie *et al.* 1973). Habitat of stickleback changes with season, with fish moving offshore during autumn and onshore during spring. This alteration can be expected to impose different predator regimes (Reimchen 1980; Werner *et al.* 1983). Habitat preferences of fish generally shift during ontogeny, and there is

evidence for corresponding changes in ecological interactions (Werner and Gilliam 1984). Yearly differences in predation regime could alter strength and direction of selection. The occasional extremes, rather than average conditions, may generate the important evolutionary effects on the population (Boag and Grant 1981). The relevance of each of these ontogenetic, spatial, or temporal factors could be compounded if there were multiple causes of mortality with distinctive selective effects on phenotype.

For this purpose, a 10 yr investigation of the interactions between stickleback and their predators was undertaken at Drizzle Lake on the Queen Charlotte Islands in western Canada. Several aspects of this study have been completed, including the analyses of seasonal and spatial patterns of avian piscivore activity (Reimchen and Douglas 1980, 1984*a*), examination of functional relationships between spines and lateral plates (Reimchen 1983), spatial and temporal variation in vertebral phenotypes within the lake (Reimchen and Nelson 1987), description of predator-induced injuries, their frequencies over time and among size classes (Reimchen 1988), and the analysis of yearly size-specific mortality caused by cutthroat trout (Reimchen 1990). Other aspects, such as evaluating predator foraging efficiencies, are continuing. Here I synthesize available data on the predator complex at Drizzle Lake and consider age-specific causes and levels of mortality through the life history of the stickleback.

Description of study area

Drizzle Lake is located on the north-eastern corner of the Queen Charlotte Islands, western Canada (Fig. 14.1), on a low-elevation plain (< 100 m) covered with *Sphagnum* bogs and coniferous forests. The lake (112 ha) is dystrophic with simple bathymetry, reaching a maximum depth of 30 m. Its water is deeply stained (transmission at 400 nm = 67 per cent; Reimchen 1989) and aquatic macrophytes are rare. The locality, apart from being representative of the broader region, was chosen for several reasons. Stickleback reach a large body size (110 mm), are highly melanic, and are endemic to the locality. Although exposed to trout predation, stickleback have fewer lateral plates than are observed in virtually all other equivalent populations (Moodie and Reimchen 1976*a*). Due to its remoteness, the lake has received negligible human-induced or other known ecological disturbance in recorded history. This is important for evaluating life history and phenotypic variability because the genetic and phenotypic structure of the population should be intact. The watershed has been given protected status as an ecological reserve and should remain undisturbed in the future.

Methods for estimating prey and predator abundance

Mark-recapture methods were employed to estimate population sizes of adult stickleback and cutthroat trout (Reimchen 1990). The size distribution and abundance of stickleback were determined from horizontal and vertical transects over the lake. These represented 96 sites in the lake which were generally sampled every two months from 1980 to 1983. Densities of littoral fish (salmonids and stickleback) were also surveyed using beach seines. Numbers and species of avian piscivores were determined daily throughout much of the year over a 5 yr period, and records were kept of foraging positions on the lake (Reimchen and Douglas 1984a).

Evaluating mortality

Causes of mortality in the life history of the stickleback were determined using a combination of techniques, including stomach-content analyses of gill-netted predatory fish (Reimchen 1990), shoreline surveys for regurgitated pellets from kingfishers and spraints from otters, and littoral collections of macroinvertebrates. Observations were made through spotting scopes on the foraging behaviour of avian piscivores and otters (Reimchen and Douglas 1980, 1984a). Prey were identified to the lowest taxon possible (species in most cases).

The size of stickleback consumed by predators was determined by several methods. Those in trout stomachs were measured directly if there was only limited digestion. For disarticulated stickleback in trout stomachs and in kingfisher pellets, I measured pelvic spine length, which is a good estimator of standard length ($r^2 = 0.92$, $N = 679$, $P < 0.001$). In otter spraints, dorsal and pelvic spines were fractured but the hypural plate was generally intact, and this was used to estimate stickleback size. Maximum width of this plate measured on radiographs of reference specimens provided a good predictor of stickleback body length ($r^2 = 0.93$, $N = 95$, $P < 0.001$). Odonates captured in the lake were placed in small aquaria and within 24 h generally produced intact faecal pellets which were preserved and later examined for fish bones.

For all of the avian piscivores that brought stickleback to the surface, I made rough estimates of stickleback size relative to bill length. A number of manipulation events were videotaped, allowing more detailed measurements (methods in Reimchen and Douglas 1984b; Reimchen 1988). Where stickleback were large relative to the bill, manipulation time by the bird was much greater than with smaller stickleback, as might be expected for gape-limited piscivores (Werner 1974). Accordingly, I was able to use relative manipulation time to recognize three general size classes (30–50, 50–70, 70–90 mm) in foraging events that were too distant to permit direct measurement. Several of the diving ducks, such as scaup and white-winged scoter, swallowed most of their prey beneath the surface. For these infre-

quent foragers, I estimated an average prey size based on combinations of bill size, dominant foraging habitat in the lake, and size availability of stickleback. Such data deficiencies are identified in the results.

The number of stickleback eaten yearly was estimated for each predator, based on daily caloric requirements, proportion of stickleback in the diet at monthly intervals, length distributions of stickleback in the diet, and average number of predator foraging days per month. The last was based on data over a 5 yr period. Daily caloric requirements (D_{cal}) for predatory fish were calculated as

$$D_{cal} = 15.116 * W^{0.767} * e^{0.138 * T} \quad (9.1)$$

(Elliott 1976), where W is weight of the predatory fish (g) and T is water temperature ($^{\circ}\text{C}$). This was converted to g assuming a caloric equivalence of 5.0 J kg^{-1} (Cummins and Wuycheck 1971). These calculations provide a close approximation to the actual daily consumption by trout (Reimchen 1990).

The daily weight of fish consumed (D_g) by avian piscivores was estimated as

$$\log_{10} D_g = -0.293 + 0.85 * \log_{10} W \quad (9.2)$$

(Nilsson and Nilsson 1976), where W is weight of bird (g). I was able to compare actual daily fish consumption with D_g for a common loon which brought the majority of the prey to the surface prior to swallowing. On two days, separated by two weeks, an individual bird was observed continuously from dawn to dusk and all prey captures were recorded. The loon ate 135 fish (estimated total weights 300–405 g) and 198 fish (estimated weight 380–495 g) on the two days. Predicted daily consumption (D_g) for a 3000 g loon is 460 g, which is comparable to the actual value. The average numbers of foraging days for avian piscivores are shown in Table 9.2.

Daily fish consumption by the river otter ranges from 10 to 23 per cent of its body weight (Erlinge 1968; Chanin 1985). I assume a value of 10 per cent and an average otter weight of 13 kg (Chanin 1985).

Piscivores: diet, abundance, and yearly occurrence

Piscivory was observed in 21 species over the 10 yr study period, and in all of these, stickleback were present in the diet. This assemblage of predators comprises birds (15 spp.), fish (4 spp.), mammals (1 sp.), and odonates (1 sp.) (Table 9.2). Fish and odonates were resident, while the remaining species were seasonal itinerants, occupying the lake for variable periods. Population estimates and number of foraging days varied considerably among species and among seasons (Reimchen and Douglas 1984a). All size classes of stickleback were eaten, ranging from 10 to 100 mm SL (Fig. 9.3).

Table 9.2 Species that preyed on stickleback observed at Drizzle Lake, Queen Charlotte Islands, between 1976 and 1985. Non-foraging species are excluded. Mean foraging days yr⁻¹ is the total number of individuals × number of foraging days. Stickleback in diet is proportion of predator's total diet.

Species	Years observed										Population estimate	Stickleback in diet (%)
	76	77	78	79	80	81	82	83	84	85		
Resident												
Cutthroat trout <i>Oncorhynchus clarki</i>	+	+	+	+	+	+	+	+	+	+	220	0.80 ^a
Dolly Varden <i>Salvelinus malma</i>	+	+	+	+	+	+	+	+	+	+	100	0.15 ^a
Coho salmon <i>Oncorhynchus kisutch</i>	+	+	+	+	+	+	+	+	+	+	4000	0.05 ^a
Stickleback <i>Gasterosteus aculeatus</i>	+	+	+	+	+	+	+	+	+	+	75 000 adults	0.015 ^a
Dragonfly <i>Aeshna palmata</i>	+	+	+	+	+	+	+	+	+	+	?	0.17? ^a
											Average foraging days yr ⁻¹	
Seasonal visitors												
Red-throated loon <i>Gavia stellata</i>	+	+	+	+	+	+	+	+	+	+	118	0.10 ^b
Pacific loon <i>Gavia pacifica</i>				+							4	1.00 ^c
Common loon <i>Gavia immer</i> , summer	+	+	+	+	+	+	+	+	+	+	710	0.50 ^b
winter	+			+	+	+		+	+		99	1.00 ^c
Pied-billed grebe <i>Podilymbus podiceps</i>					+						1	1.00 ^c
	76	77	78	79	80	81	82	83	84	85		
Horned grebe <i>Podiceps auritus</i>	+	+	+	+	+	+	+	+	+	+	24	1.00 ^c
Red-necked grebe <i>Podiceps grisegena</i>	+	+	+	+	+	+	+	+	+	+	196	1.00 ^c
Western grebe <i>Aechmophorus occidentalis</i>							+				<1	1.00 ^c
Double-nested cormorant <i>Phalacrocorax auritus</i>	+	+	+	+	+	+	+	+	+		42	1.00 ^b
Great blue heron <i>Ardea herodias</i>	+	+		+	+	+	+		+	+	<1	0.20 ^b
Scaup <i>Aythya</i> spp.	+	+	+	+	+	+	+	+	+	+	12	0.20 ^b
Oldsquaw <i>Clangula hyemalis</i>	+	+	+	+	+	+	+	+	+	+	51	1.00 ^b
White-winged scoter <i>Melanitta deglandi</i>	+	+	+	+	+	+	+	+	+	+	11	1.00 ^b
Bufflehead <i>Bucephala albeola</i>	+	+	+	+	+	+	+	+	+	+	253	0.05 ^c
Hooded merganser <i>Lopodytes cucullatus</i>	+		+	+	+	+	+	+	+	+	95	1.00 ^c
Common merganser <i>Merganser merganser</i>	+	+	+	+	+	+	+	+	+	+	53	1.00 ^c
Belted kingfisher <i>Ceryle alcyon</i>	+	+	+	+	+	+	+	+	+	+	258	0.91 ^a
River otter <i>Lutra canadensis</i>					+	+	+	+		+	15	0.95 ^a

^a Dietary data derived from stomach or pellet analysis.

^b Dietary data inferred from foraging habitat, prey availability, and gape.

^c Dietary data derived from surface manipulation behaviour.

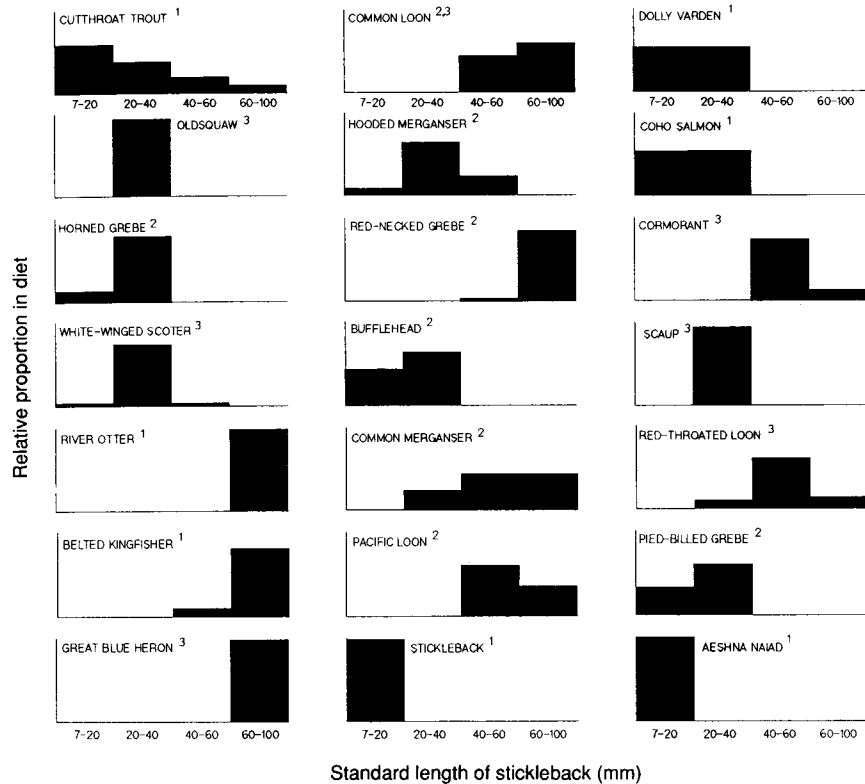


Fig. 9.3 Estimated size classes of stickleback eaten by predators. Data on size distributions are (1) derived from stomach or pellet analysis, (2) observation of surface manipulation behaviour, and (3) inferences from foraging habitat, prey availability, and gape.

Cutthroat trout

Stickleback constituted more than 80 per cent of the diet (Reimchen 1990). Of 1900 fish extracted from trout (range in SL 120–410 mm) over an 8 yr period, all but 8 were stickleback. There was a mean of 5.8 stickleback (range 0–55) per trout stomach, with the prey size ranging from 10 to 95 mm SL. Ratios of stickleback SL to trout SL were lowest in summer, increasing during autumn and winter and reaching a maximum in late spring. Mark-recapture methods provided population estimates of about 90 trout in winter and 250 in summer.

Dolly Varden

Benthos (primarily trichopteran larvae) was the dominant prey in 84 per cent of all stomachs ($N = 67$), while fish eggs were dominant in 16 per cent. Seven

of the stomachs contained masses of trout eggs, and three contained an entire stickleback nest including eggs, fry, vegetation, and adhering sand. Low levels of piscivory (16 per cent of all stomachs) were detected throughout the year, and in all cases, the prey were small stickleback (< 40 mm). The number of Dolly Varden that were large enough (120–250 mm SL) to consume stickleback was estimated at 150 during winter and 25 during summer. During winter, many anadromous Dolly Varden (250–500 mm SL) enter the lake, but stomach content analyses ($N = 160$) from November to April showed no evidence of foraging.

Coho salmon

Non-foraging adult coho salmon enter the lake in November en route to stream spawning gravels. Juveniles, which appear in the lake the following spring and remain for 1 yr prior to migration to the ocean, primarily eat insects and benthos throughout the year. In 109 coho collected during the peak of the stickleback breeding season (April–July), I found no evidence of predation on fry, and only one stomach contained stickleback eggs. However, of 151 stomachs from August to November, two coho had consumed juvenile stickleback (1.3 per cent). From seining, I estimated the coho population at about 4000 individuals (40–130 mm SL).

Stickleback

Stickleback primarily took plankton, and secondarily benthos. During summer months, all size classes of stickleback engaged in low levels of conspecific predation. Of 67 adults (> 70 mm SL) examined, 11 (16.4 per cent) contained eggs and 2 (3 per cent) had fry. Of 134 subadults (50–70 mm), 7 (5.2 per cent) contained eggs while 2 (1.5 per cent) had fry. Of 543 large juveniles (30–50 mm), none had eggs in the stomach but 7 (1.9 per cent) had fry. Of 509 small juveniles (15–30 mm), none had eggs and a single individual (0.2 per cent) had fry. There were an estimated 75 000 (range 30 000–120 000) adult stickleback in the lake. Based on recaptures, the adult cohort is composed of at least five year classes (3–8; Reimchen 1992a). From nest densities and the number of eggs per nest, yearly production of fry was estimated at 12 million (range 4 million to 24 million).

Macroinvertebrates

Over the 10 yr data-collection period, which included numerous visual observations, beach seining, and minnow trapping, I rarely encountered any macroinvertebrate piscivores. Odonate naiads were present but rare. Leeches (Hirudinea), which are egg predators (Moodie 1972a), were rarely seen.

Eight odonate naiads were collected from the littoral zone when stickleback fry were abundant. Only one of these contained the bony remains of a stickleback fry (about 12 mm). Naiads placed in aquaria quickly stalked,

attacked, and consumed fry, suggesting familiarity with this prey. The population of naiads was small and I did not estimate the size.

River otter

Analyses of spraints collected in 1979 ($N = 14$) and 1988 ($N = 8$) yielded the remains of 325 fish (323 stickleback and 2 salmonids). In both years, more than 90 per cent of the stickleback taken by otter were of adult size. Stickleback consumed were larger in 1988 than those in 1979 (83 mm v. 78 mm, $P < 0.01$, t -test). With a spotting scope, I observed 65 prey captures, all of which were adult stickleback.

Belted kingfisher

Three hundred and twelve prey were identified in 106 pellets of the belted kingfisher collected over 3 yr. These include stickleback ($N = 283$, 90.7 per cent), salmonids ($N = 16$, 5.1 per cent), and odonate naiads ($N = 10$, 3.2 per cent). The diet was similar between months and between years. The majority of stickleback captured were adults (75–85 mm SL).

Common loon

Loons that inhabited the lake in spring and autumn predominantly consumed stickleback (Reimchen and Douglas 1980). In autumn 1979 and spring 1981, I observed 674 prey brought to the surface and swallowed; all were stickleback. Most of the stickleback captured were 50–70 mm SL (range 40–90 mm).

During summer, large numbers of common loons (up to 89 individuals per day) foraged regularly, but they rarely brought prey to the surface (6 adult stickleback in approximately 2000 dives). The loons were taking either small stickleback or small salmonids, either of which can be swallowed underwater. Minnow traps set in limnetic regions where the loons foraged yielded exclusively stickleback. Large-mesh gill nets set for salmonids in this region were usually empty, but occasionally had coho salmon fry and rarely cutthroat trout. Traps set about 30 m from shore, which is generally as close to shore as common loons will forage, yielded predominantly stickleback (98 per cent) and rarely coho salmon fry and Dolly Varden. I searched the shoreline during periods of intensive loon foraging activity and frequently found injured fish with 'aviscars' (Reimchen 1988) at the drift line. Among 580 fish collected with injuries, there were 576 stickleback, 2 trout, 1 Dolly Varden and 1 coho fry. The evidence, although circumstantial, indicates that in summer common loons forage primarily on subadult stickleback (40–60 mm SL) and secondarily on larger size classes of fish (60–80 mm). For estimating total prey consumption, I will assume conservatively that stickleback represent 50 per cent of the diet during summer.

Red-throated loon

These loons foraged intermittently on the lake at dusk (Reimchen and Douglas 1980). During this period, I saw 23 fish captured by the loons, all of which were subadult stickleback (50–70 mm SL). On three instances, we observed pre-fledged loons capture stickleback in the nesting territory. During parental feeding of the young loons, all the prey brought to the young were marine fish and none were stickleback (Reimchen and Douglas 1984b).

Red-necked grebe

Grebes were regular seasonal residents on the lake, usually occurring in low numbers (1–5) between October and May. Stickleback were the only prey brought to the surface ($N = 63$). Based on number of stickleback consumed at hourly intervals over the day ($\bar{X} = 6.7$ fish h^{-1} , range 0–12), total daily consumption would exceed the estimated daily caloric requirements by 30 per cent. As a consequence, I assume that the grebe is not swallowing other species of prey such as salmonids beneath the surface. The average size of captured stickleback was estimated at 65 mm (range 50–90 mm SL).

Common merganser

Large flocks of mergansers regularly stayed overnight on the lake in spring and autumn (Reimchen and Douglas 1984a). In autumn, these flocks rarely foraged, but during April and May, I observed intensive surface foraging on stickleback at twilight. Stickleback are abundant at dusk just beneath the surface, and the mergansers captured the fish without underwater pursuit. Most of the captured stickleback appeared to be about 25–40 mm SL, which is the most abundant size class in the lake during spring.

Other predatory birds

Piscivores such as horned grebe and oldsquaw duck were seasonal residents (usually winter) and were uncommon, with rarely more than two individuals occurring on the lake at any time. Young-of-the-year stickleback (10–40 mm SL) appeared to be the predominant food item of these species. Double-crested cormorant, present during January and February, did not return prey to the surface. I sampled fish in the area of the lake where the cormorant foraged, and as I caught only stickleback I infer that this is the principal item in the diet. A single pair of hooded merganser nested adjacent to the lake in several years, and during the pre-fledging period, the adults and young were irregularly observed within 20 m of shore foraging on young-of-the-year stickleback. Other birds such as bufflehead were common winter residents that ate primarily trichopteran larvae and only rarely were observed capturing stickleback. Based on their foraging positions and

prey capture, I estimated that 5 per cent of the bufflehead diet was composed of stickleback.

Numbers of stickleback eaten yearly by predators

An estimated total of 562 000 stickleback are consumed per year by all predators combined. Cutthroat trout and common loon were the two major predators (> 100 000 fish yr⁻¹). The remaining species each consumed < 30 000 fish yr⁻¹ and can be considered minor predators (Fig. 9.4). I have been unable to make meaningful estimates of prey consumption by odonate naiads and stickleback. Conspecific predation could be very high, since juveniles, subadults, and adult stickleback ate fry.

Partitioning of total consumption between size classes of stickleback yields different rankings of predator importance. The estimated mortality of stickleback greater than 40 mm SL (i.e. > 12 months of age, full expression of lateral plates) was 228 000 individuals yr⁻¹. Avian piscivores accounted for 69 per cent of this total, while trout and otter consumed 30 per cent and 1 per cent respectively. Among adult stickleback (> 70 mm), 26 082 individuals were taken yearly. Common loon took 51.8 per cent, red-necked grebe 16.4 per cent, trout 11.9 per cent, and otter 10.8 per cent. Therefore, predators that were minor with respect to total mortality for all size classes combined (Fig. 9.4), and were uncommon on the lake,

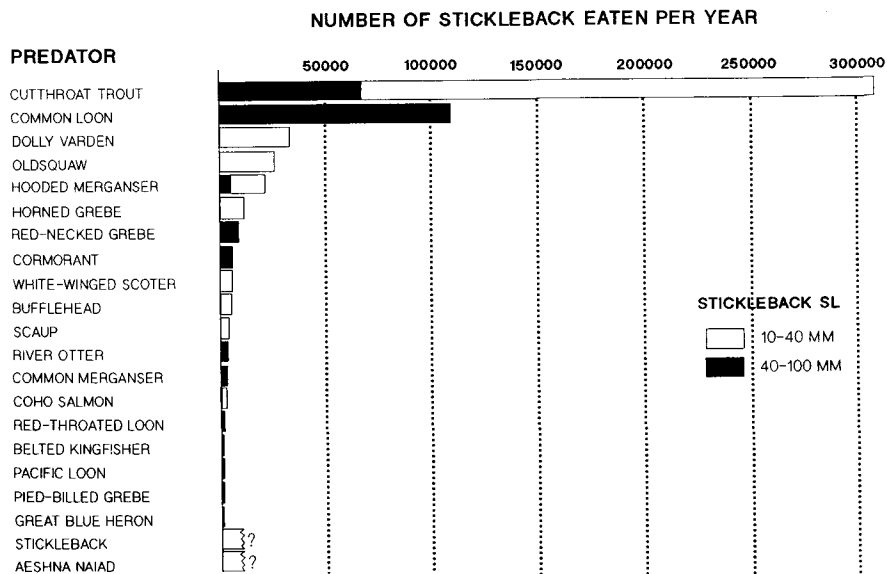


Fig. 9.4 Number of stickleback consumed annually for each predator at Drizzle Lake (averaged over five or more years). Rare species such as western grebe (one sighting in 10 yr) are not included.

become very important when considering mortality of subadult and adult size classes. Conversely, cutthroat trout, the most important predator overall, is only a minor predator on adult stickleback.

Seasonal differences in stickleback mortality

Total numbers of stickleback eaten by predators differed seasonally (Fig. 9.5(a)). The two major predators had their greatest yearly consumption during summer months. This was due to the very regular influx of large numbers of common loon onto the lake (Reimchen and Douglas 1980) and to the increased metabolic requirements of resident trout during the higher summer temperatures. Most minor predators were limited to a single season occupancy, but the cumulative effect produced a relatively uniform mortality level throughout the year. When only subadults and adults are included in this mortality (Fig. 9.5(b)), the seasonal trends are similar, although there is a more distinctive peak in late summer and autumn during the residency of hooded merganser and red-necked grebe.

Yearly differences in stickleback mortality

Considerable yearly heterogeneity occurs in predation by some of the foragers. Total yearly consumption by common loon ranged from 55 000 (1984) to 157 000 (1987). This species normally foraged during autumn and winter, yet none were present in the autumn of four of ten years. Red-necked grebe, which is one of the major sources of mortality in winter and spring, taking up to 9000 stickleback from January to May, were absent from the lake during this period in 1978, 1982, and 1985, although they were present

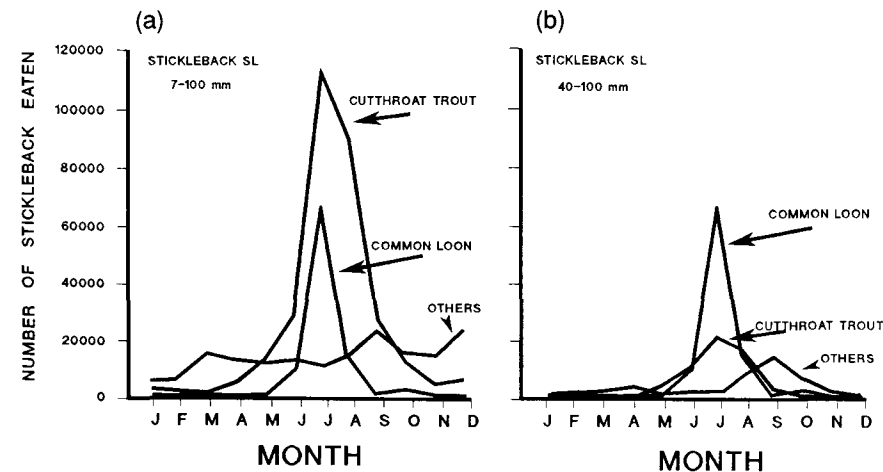


Fig. 9.5 Monthly consumption of stickleback for major and minor predators at Drizzle Lake: (a) total stickleback eaten, (b) subadult and adult stickleback eaten.

during the autumn of each year. Common merganser, which was abundant each year, rarely foraged on the lake (Reimchen and Douglas 1984a), yet in winter 1981, and early spring 1985, extensive foraging occurred, with some 11 000 stickleback taken during each period. River otter occurred in only five of ten years; in 1979, a single individual was resident for 3 wk and took about 10 000 adult stickleback. Oldsquaw duck, rare or absent during most years, was resident during the winters of 1980 and 1981, and consumed an estimated 15 000 stickleback each year. Hooded merganser, which takes up to 50 000 individuals yearly, took fewer than 1000 individuals during four years when the pair did not breed.

Lake foraging positions

There were consistent differences among species in the use of foraging localities on the lake, the major distinction being the relative proportion of littoral and limnetic activity (Fig. 9.6). Belted kingfisher only foraged in littoral regions within 10 m of shore. Some species such as hooded merganser, horned grebe, bufflehead, and river otter were largely within 100 m of shore. Others such as the common loon, red-necked grebe, oldsquaw duck, and common merganser exploited both littoral and limnetic habitats, although common loon rarely foraged in water less than 1 m deep. From fyke and gill netting throughout the year, cutthroat trout appeared to be most common in littoral regions during spring and autumn, and were often netted in water less than 1 m deep (Reimchen 1990). Individuals were not typically captured in open-water regions at any depth. Some limnetic predation may occur because I observed offshore movement of trout in July and August (Reimchen 1990; see also Andrusak and Northcote 1971).

The depths at which different piscivores foraged are poorly known. Avian piscivores would have been restricted to near the surface as the black waters of this lake are aphotic below 2–3 m depth. Horned grebe, common merganser, and otter pursued and often captured stickleback immediately beneath the surface, behaviour evident from the hydrodynamic wake on the surface during their dives. Among the predatory fish captured in gill nets which had been set at various depths and distances from shore (Reimchen 1990), trout and salmon were usually within 3 m of the surface, whereas Dolly Varden were benthic. Surface pursuit by trout was commonly observed in littoral but not in limnetic regions.

Predator foraging efficiencies

The development of defensive adaptations of prey to pursuit and manipulation by the predator should be associated not only with predation intensity, but also with the amount of unsuccessful predation (Vermeij 1982). If a predator is highly efficient, then few prey will escape and there is little

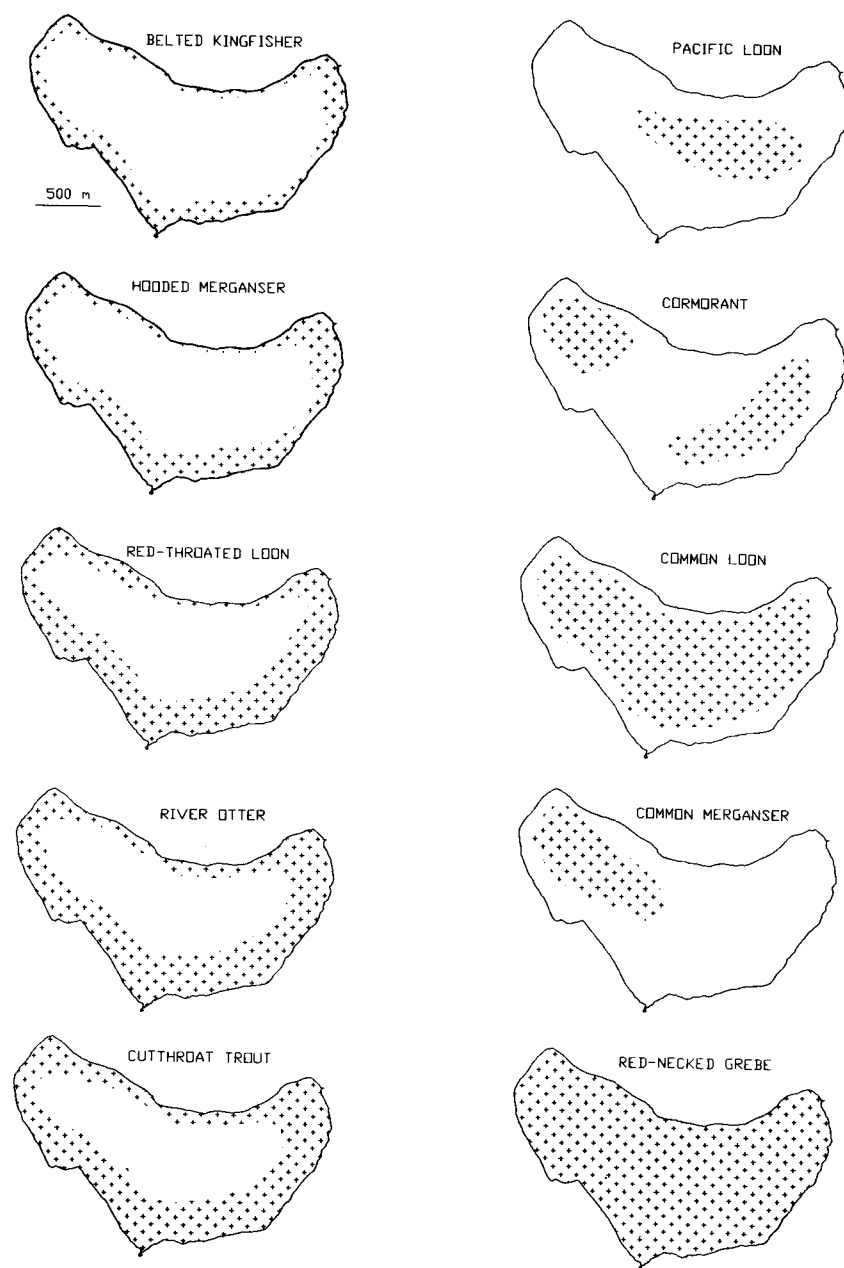


Fig. 9.6 Dominant foraging localities at Drizzle Lake for selected piscivores. Species are ranked from most littoral (*top left*); mainly littoral, some limnetic (*bottom left*); littoral and limnetic (*bottom right*); to most limnetic (*top right*).

opportunity for differential survival. In contrast, if the predator is inefficient, and consumes the same number of individuals as the efficient predator, then many more prey will escape and there is a far greater opportunity for selection. Thus, the substantive predator-induced mortality of stickleback observed at Drizzle Lake, which comes from a diversity of predator species and involves all size classes of stickleback, will be of no selective consequence unless there are foraging inefficiencies by one or more of these predators and body alignment (Reimchen 1991b).

The major stages to a foraging event are search, pursuit, and manipulation. Evaluating natural foraging efficiencies of these stages is difficult because such events are seldom observed with sufficient frequency to allow quantification. Substantial experimental data exist, and there is major variation between and within species dependent on attributes of the predator, such as experience, and on attributes of the prey, such as body size (Krebs 1978; see Vermeij 1982 for review).

Three fundamental questions must be addressed to evaluate the evolutionary importance of the assemblage of stickleback predators observed at Drizzle Lake. First, is there evidence to suggest predator inefficiency in one or more of the foraging phases? This will determine the potential for adaptation of the prey. Second, do predator species differ in their efficiencies? If so, this may result in some predators being much more important for the evolution of the prey population than would be predicted from their contribution to total mortality. Third, which of the variable traits of the prey maximize the probability of escape during each of the search, pursuit, and manipulation phases for each of the predators? This would provide insight into whether there are opposing selective forces among the three phases or among the different species of predator. Currently, I have an incomplete assessment of these questions but can provide data on efficiencies for several predator species.

Search and pursuit efficiencies

Among dives recorded in winter months ($N = 1025$), common loon returned fish to the surface on 679 instances ($\bar{X} = 65.3$ per cent over 41 different time blocks, 95 per cent confidence limits, 57–73 per cent). During similar periods of the day and in the same lake regions, and so where encounter rate should be comparable to that of the common loon, red-necked grebe captured 63 fish in 257 dives ($\bar{X} = 29.2$ per cent over 15 time blocks, 95 per cent confidence limits = 16–42 per cent). Efficiency was significantly different for these two species (F -ratio = 23.7, d.f. = 1,54, $P < 0.001$). As noted previously, it is unlikely that the grebe is swallowing additional fish underwater. Assuming that these efficiencies are realistic, it is possible to estimate number of pursuit failures. Common loon from autumn to spring consume a predicted 13 440 stickleback; since this represents about 65 per cent of the prey they initially dove for, 7195 search and pursuit failures should have

occurred. Red-necked grebe consume a predicted 8553 stickleback during the same period, which should result in 29 316 additional failures. Consequently, although the red-necked grebe accounts for only 39 per cent of the winter consumption by the two species, it accounts for 80.3 per cent of their failures. If there are any attributes of the stickleback associated with their ability to avoid detection or evade capture during pursuit (for example, behavioural responses, body size, swimming speed), the red-necked grebe could theoretically have much greater selective influence than the common loon. During summer, common loon swallowed most of their prey beneath the surface, and I am unable to estimate efficiency. If it is comparable to that in winter, then there would be a total of 55 774 search and pursuit failures yearly by this predator, about twice as much as the yearly failures by red-necked grebe. These represent minimum values for both species since there may be multiple pursuits during each dive.

Manipulation efficiencies

Following capture, stickleback are subject to varying amounts of manipulation prior to swallowing. Some of these manipulations are unsuccessful, the major evidence for this being the occurrence of predator-induced injuries on stickleback collected from the natural population. Analyses of 8718 stickleback (predominantly adults) sampled over a 3 yr period at Drizzle

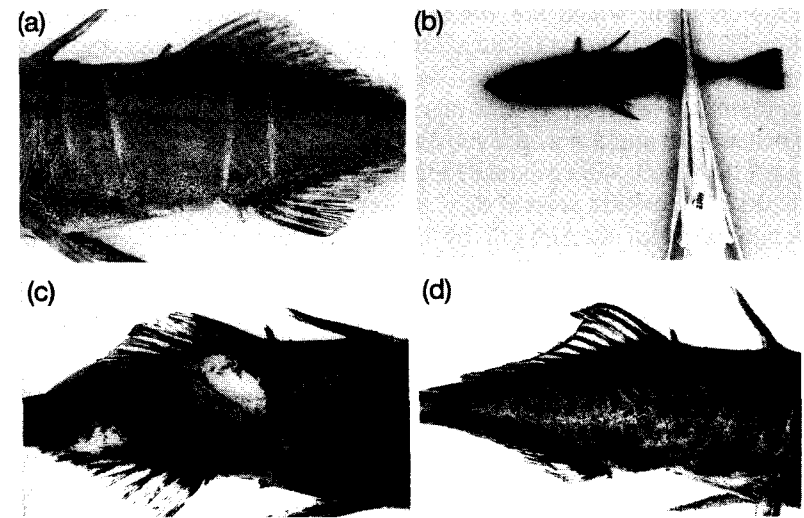


Fig. 9.7 Predator-induced injuries on stickleback at Drizzle Lake: (a) characteristic 'aviscar' on adult stickleback (SL 7.5 cm); (b) bill of red-necked grebe positioned on trunk for perspective; (c) skin laceration incurred from cutthroat trout attack; (d) tooth scars from cutthroat trout attack.

Lake (Reimchen 1988) showed that 13.4 per cent of the population have predator-induced injuries such as fractured dorsal and pelvic spines and skin lacerations. About one-third of the injured fish have 'aviscars', characteristic imprints of the bill profile from bird attacks (Fig. 9.7(a),(b)), about one-third of the fish have skin punctures and scratches from trout attacks (Fig. 9.7(c),(d)) (unpubl. data), while the remainder have fractured spines without skin injuries, probably from bird manipulation. Injuries were rare or absent on small stickleback (<50 mm) but became progressively more frequent on larger and older individuals, reaching up to 35 per cent in the largest fish (80–90 mm).

Manipulation efficiencies were evaluated for three piscivores. Of 679 stickleback captured and brought to the surface by the common loon, I observed only 5 escapes (0.74 per cent). Of 63 stickleback captured by red-necked grebe, 10 escaped (15.9 per cent). There may, of course, have been additional escapes underwater. The higher frequency of failures by the grebe is probably a consequence of their smaller body size (1000 g) than that of the common loon (3000 g). This disparity is also reflected in their prolonged manipulation periods for fish of similar size. Common loon took an average of 13.5 s (range 1–58 s) prior to swallowing the stickleback, while red-necked grebe required 129.9 s (range 27–900) (ANOVA, $P < 0.001$). Although stickleback size could not be estimated with any precision, the extended manipulation periods and escapes all occurred when stickleback were large (>70 mm).

Common loon, which ate 104 187 stickleback yearly, would therefore produce 777 manipulation failures. Of the 8553 stickleback consumed yearly by red-necked grebe, there will be an additional 1617 escapes during manipulation. However, even a marginal increase in failures by common loon beneath the surface would substantially increase manipulation failures. I suspect that this occurs because I regularly found injured adult stickleback at the drift line within several days of loon foraging bouts in summer.

Manipulation of stickleback by river otter was observed during their periodic occupancy of the lake. Upon surfacing with the stickleback, the otter chewed for a short period ($\bar{X} = 17$ s, range 11–37 s) before swallowing the prey. I saw no instances of escape in 65 separate captures.

It is possible roughly to evaluate the relative importance of some of the major predators at this stage. Overall, cutthroat trout consume the greatest number of stickleback (55 per cent of total), followed by common loon (18 per cent) and minor predators such as red-necked grebe (1.6 per cent) and river otter (0.6 per cent). Among all adult stickleback consumed, common loon take 52 per cent, red-necked grebe 16 per cent, trout 12 per cent, and otter 11 per cent. Examination of injuries in the natural population indicates that about one-half of the injuries are attributable to bird attack and one-third to trout attack (Reimchen 1988, unpubl. data). From direct observation of predator manipulation efficiencies on the lake surface, it is

possible to account for 908 manipulation failures involving adult stickleback, of which red-necked grebe contributes 89 per cent, common loon 11 per cent, and otter none. Two conclusions derived from this analysis are that the major predator in the life history of the stickleback (i.e. cutthroat trout) produces fewer manipulation failures than avian piscivores, and among the latter, a relatively minor predator, the red-necked grebe, may contribute as many or more manipulation failures as the common loon, which is a major predator.

Pursuit, manipulation, and body size

From observations on the foraging behaviour of some of the piscivores and data on frequencies of injured stickleback in the population (Reimchen 1988), it seemed likely that probability of escape was directly related to body size of stickleback. The large size of adult stickleback at Drizzle Lake (70–110 mm), combined with the robust dorsal and pelvic spines, which increase effective diameter by 130 per cent, could represent an adaptation to gape-limited piscivores. I have tested this hypothesis using trout (Reimchen 1991a).

Six cutthroat trout (range in SL 19–34 cm) were collected from Drizzle Lake and placed in 400 l aquaria or in netted circular enclosures (3.14 m²) in the lake. After their length was recorded, stickleback were dropped individually ($N=1581$) into the centre of the enclosure; they immediately accelerated towards the edge, during which time the trout gave chase.

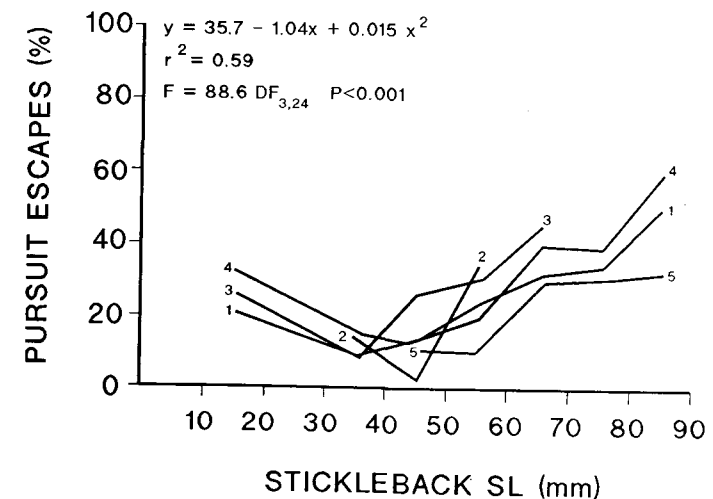


Fig. 9.8 Stickleback escape frequencies in relation to standard length (SL) during pursuit by cutthroat trout. Each line represents data from a different trout: 1, 19.0 cm SL; 2, 19.5; 3, 21.0; 4, 25.5; 5, 31.5 and 34.0 (data combined). Number of feedings per trout: 1, 464; 2, 97; 3, 357; 4, 514; 5, 149 (from Reimchen 1991a).

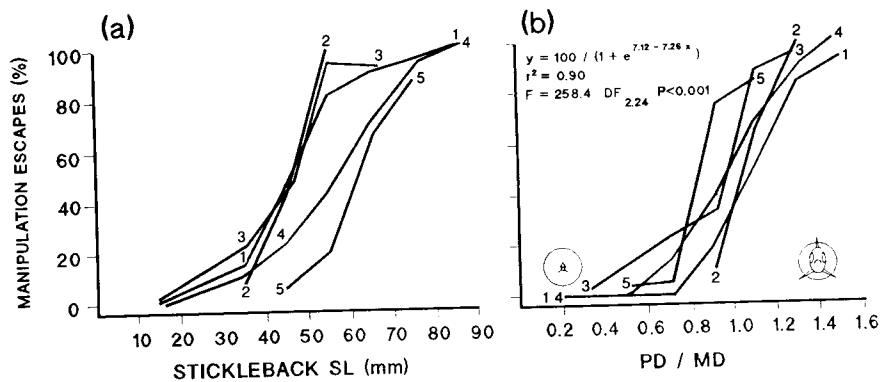


Fig. 9.9 Stickleback escape frequencies during manipulation by cutthroat trout versus (a) standard length (SL) of stickleback, and (b) relative body size (stickleback diameter with dorsal and pelvic spines erected divided by mouth diameter of trout, PD/MD). Insets show a schematic view of a stickleback in the mouth of trout when PD/MD is 0.2 and 1.4. Each line on the graphs represents data from a different-sized trout: 1, 19.0 cm SL; 2, 19.5; 3, 21.0; 4, 25.5; 5, 31.5 and 34.0 (data combined). Number of separate manipulation events per trout: 1, 316; 2, 71; 3, 267; 4, 389; 5, 96 (from Reimchen 1991a).

In the pursuit phase, there is a curvilinear relationship with escape frequency, small and large individuals having an increased probability of escape (Fig. 9.8). Stickleback between 30 and 50 mm SL were at the greatest risk to trout. A second-order polynomial described 60 per cent of the variance ($P < 0.001$).

In the manipulation phase, small stickleback (< 30 mm SL) rarely escaped after capture, but as stickleback size increased, there was a sharp increase in escape, reaching more than 90 per cent for the largest stickleback (> 70 mm SL) (Fig. 9.9(a)). Larger trout were more efficient manipulators of all stickleback.

Swallowing ability of a predatory fish is largely a function of its gape and the diameter of the prey (Werner 1974; Zaret 1980; Hoyle and Keast 1987). I measured the distance between the posterior edges of the upper jaw as an estimate of predator gape (MD) and the maximum diameter of stickleback with dorsal and pelvic spines erected (PD). Escape frequencies were re-examined in relation to PD/MD. These data (Fig. 9.9(b)) demonstrate that when PD/MD is less than 0.6, the prey very rarely escape. However, as PD/MD approaches unity, escape frequencies increase rapidly, reaching about 94 per cent when PD/MD = 1.4. A logistic curve describes 90 per cent of the variance. Therefore, large adult size of stickleback provides refuge during both pursuit and manipulation.

CONCLUSIONS

Is there any substantive ecological insight to be derived from this intensive study of a single population? The large number of predator species taking stickleback over a 10 yr period is much greater than that previously reported, and appears anomalously high in comparison with evolutionary studies of other taxa. However, within any short observation period such as a single season, the diversity and abundance of piscivores was usually low, and only with increased observational period did total diversity increase. Therefore, high diversity is the consequence of the extended time frame over which the observations were made, rather than a reflection of any elevated ecological complexity of the habitat. Because each of the predators has the potential to influence both demographic and selective processes in the life history, short-term investigations would have major conceptual limitations for evaluating life history evolution or functional morphology (see Greene 1986 for useful discussion).

What then are some evolutionary effects of this predator regime on variation in stickleback defences? A definitive assessment of this effect will not be available for a number of years because of the complexity and diversity of interactions in the Drizzle Lake population that have not yet been addressed. One interpretation of the available data is that the population is exposed to normalizing selection around a single optimal phenotype, a 'jack of all trades', representing an average response to salmonid, avian, and mammalian piscivores. Previous univariate assessment of variability in lateral plates (Moodie and Reimchen 1976a) indicates higher variance and higher asymmetry in adult stickleback from Drizzle Lake than in other populations where trout predators are abundant, a finding which is the inverse to that predicted on intense normalizing selection.

It seems more plausible that the population is subject to diversifying selection, as would be predicted in multiniche models (Van Valen 1965). Although direct evidence for this is rare in field studies (Schluter *et al.* 1985; Grant and Grant 1989a), there are many examples showing extensive variability of traits within populations associated with habitat complexity, for example, cladocerans (Kerfoot 1975), gastropods (Reimchen 1979), cichlids (Greenwood 1974), stickleback (McPhail page 422 this volume) and birds (Van Valen 1965), and the theory basic to the process of diversifying selection has been developed (see Endler 1986 and Wilson 1989 for reviews). In Drizzle Lake, there are numerous pursuit and manipulation methods among the predators, including plunging (kingfisher), wading (heron), diving (loon, grebe), surface feeding (merganser), laceration and puncture (salmonids), compression (birds), chewing (otter), and grappling (odonate naiads), as well as spatial differences in the distributions of the piscivores. Therefore, there may be multiple optima with different abundance of piscivores among habitats and among seasons, producing a shift

in the phenotypic distributions proportional to the number of pursuit and manipulation failures for each predator. Although a causal relationship has not been demonstrated with predators, phenotype frequencies differ from one part of the lake to the next (Reimchen and Nelson 1987) and from season to season (Reimchen unpubl. data) consistent with spatial and temporal differences in fitness of phenotypes. Analyses of these issues are continuing.

A major attribute of stickleback for evolutionary investigation is that much of the observed population differentiation is recently derived, probably since the last ice advance (Moodie and Reimchen 1976*b*; Bell 1984*a*, 1988; Bell and Foster page 16; McPhail page 401 this volume). Consequently the accumulation of historical factors that may confound analyses of form will be less important. Ecological evaluation of this variation has the potential, therefore, of generating fundamental insight into the processes of evolutionary change. From the investigations on Queen Charlotte Islands stickleback populations, it is possible to formulate some minimum criteria which would be required to realistically partition the causes of intra- or interpopulation variation in prey defences. These are:

- (1) causes and amount of age-specific mortality;
- (2) temporal and spatial patterns of habitat use by predators;
- (3) predator efficiencies during search, pursuit, and manipulation;
- (4) phenotype spatial distributions;
- (5) phenotype fitness against different predators.

Such criteria, which should in theory be basic to a study of prey defences, have not been determined for any population of any species, and consequently, their completeness cannot be assessed. This is not to imply that other selective forces, unrelated to predation, are not also operating on defence characters. Clearly, multiple factors such as drift, founder effect, linkage, ontogeny, and allometry can influence present population attributes. However, whether these are ever primary causes of variation in defensive characters can only be unambiguously determined if the role of predators can be empirically discounted.

These criteria offer considerable potential for addressing functional aspects of microevolutionary trends and may yield insight into larger-scale differences among related taxa. Gould (1984) has criticized evolutionary biologists for pursuing the causes of fine-scale differentiation among populations: 'It is time for the pendulum to swing back to a position at the pluralistic middle. I believe that both the great systematists of the 1930s and the great synthesists were correct—some geographic variation within a species is clearly adaptive, but much is a non-adaptive product of history.' (p. 236). I suspect that there is little relevant information in the primary literature to support or reject this belief. Continuing studies of Galapagos

finches (Grant and Grant 1989*b*), which may be the most thorough assessment of variability in trophic traits in any species, indicate major temporal and spatial components to fitness among phenotypes. As yet, there exists no consensus to assess the relative proportion of adaptive and non-adaptive components to this variation. Studies on population differentiation in stickleback are probably more extensive than for most species, and we are not even close to a stage where the relative amount of adaptive variation in traits can be evaluated with any confidence. We may be greatly underestimating the potential for endocyclic or diversifying selection within populations, and greatly under-estimating the selective differences among populations. Most studies, because of the constraints of time, have not been able to address the spatial and temporal complexities of life history interactions, and therefore full evaluation of variability remains impossible. Only when a rigorous assessment of fine-scale variability is obtained for different populations among representative taxa will it be possible to formulate significant generalizations on how much variation in prey defences in natural populations is a remnant of history, and how much is an adaptation to locality-specific selective pressures.

One of the major tenets of the last three decades of studies on stickleback is that predation intensity differs among populations and is associated with differences in morphological and behavioural traits. In virtually all populations, the occurrence of predatory fish is correlated with enhanced expression of spines and lateral plates, while the absence of predatory fish is associated with reduced expression of these traits. This relationship has been attributed to a relaxation of selection by predators (Hagen and Gilbertson 1972; Moodie and Reimchen 1976*a*; Gross 1978). From the investigations on the Queen Charlotte Islands populations, I suspect that categorizing localities according to the presence or absence of predatory fish or by compiling lists of potential predators, while providing useful insight into population differentiation, provides inaccurate information on relative predation and selection intensities. The reasons for this can be summarized as follows. (1) If multiple sources of prey are available, the presence of predatory fish in a locality does not in itself provide direct evidence that stickleback are subject to predation. It follows that locality differences in the abundance of predatory fish are not a meaningful description of relative predation intensity, since none or all may be consuming stickleback. (2) The absence of predatory fish does not indicate that predation levels on stickleback are low, because other piscivores, including avian and invertebrate taxa, which are present in most localities, may represent the major cause of mortality. (3) The presence of a single piscivore in a small stickleback population may produce the same predation level, relative to total population size, as that of multiple predators in a large population. An otter or a grebe need only briefly forage on a population, irregularly between years, to generate a substantial quantitative effect on that population.

(4) Extensive predation in a population does not provide evidence that selection is operating, because the strength of selection will be proportional, not to predation levels, but rather to the foraging inefficiency of the predators during search, pursuit, and manipulation (Vermeij 1982; Reimchen 1988). If all stickleback encountered by predators are consumed, there will be no selection on defensive traits, even if predation intensity is very high. Consequently, any evaluation of the importance of specific predators as selective agents requires a combination of data on foraging levels and failure rates during the life history of the prey. Estimates of the intensity of selection operating in the entire population become possible only if comparable data are collected for each piscivore in the locality.

In conclusion, there is mounting evidence that the morphology and behaviour of stickleback are associated with particular predator regimes. Lateral plate modes near seven are common among populations exposed to predatory fish and birds, stickleback with five lateral plates have higher survival than non-fives when individuals are exposed to garter snake predators in experimental tanks, modes of three or four occur where avian piscivores are prevalent, while lower modes, at least on the Queen Charlotte Islands, occur where macroinvertebrate piscivores are prevalent. I propose that it is the proportions of different predator species among habitats, rather than predation intensity, that constitute the driving selective force for population differentiation in lateral plates and spine morphology. Differences in search, pursuit, and manipulation efficiencies among the predators combined with amount of mortality will determine the selective pressures operating among populations.

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