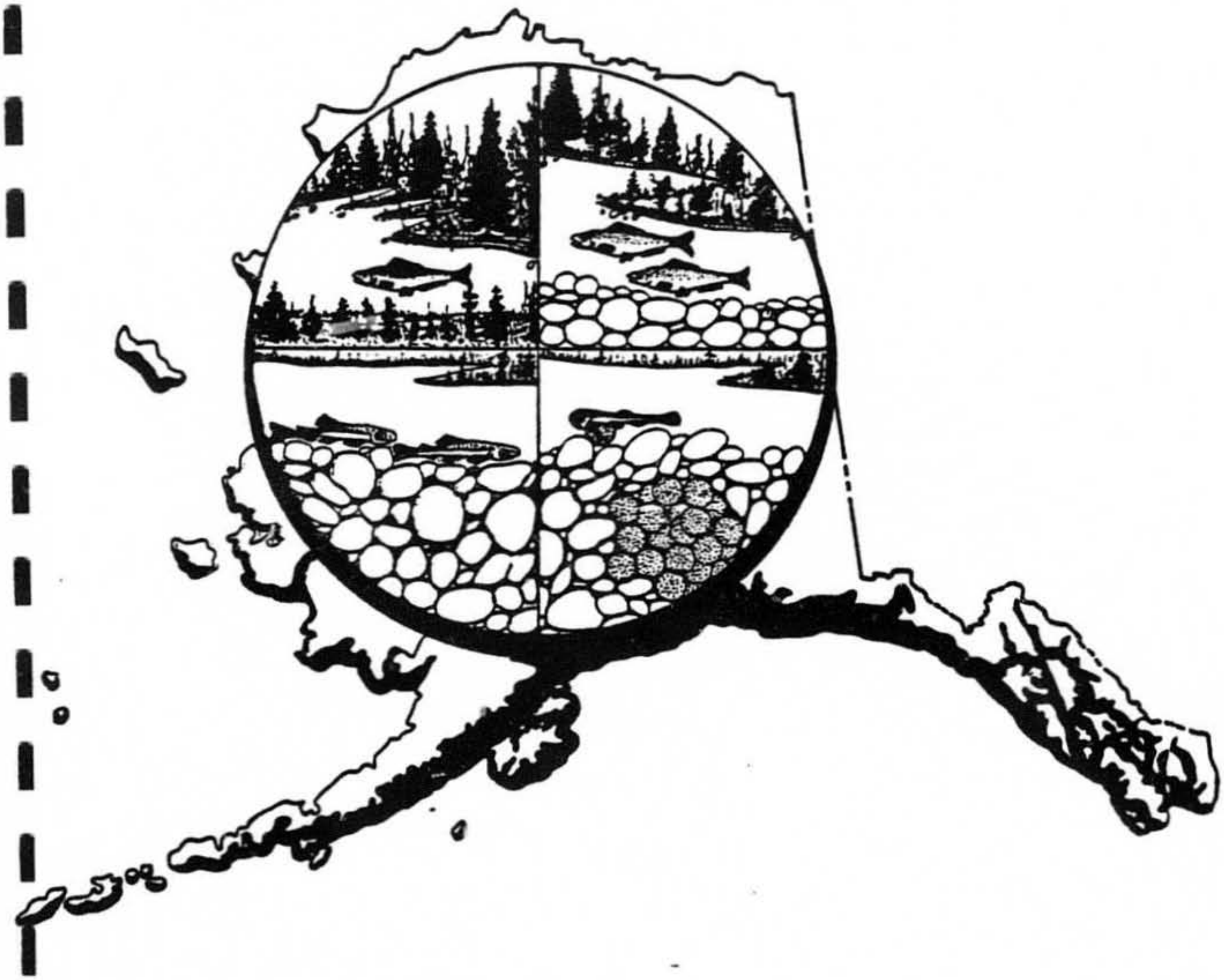
FRESHWATER HABITAT RELATIONSHIPS

THREESPINE STICKLEBACK - GASTEROSTEUS ACULEATUS



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FRESHWATER HABITAT RELATIONSHIPS
THREESPINE STICKLEBACK (<u>GASTEROSTEUS ACULEATUS</u>)

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I. INTRODUCTION

A. Purpose

This report compiles existing information on the freshwater habitat requirements, tolerances, and preferences of the threespine stickleback, Gasterosteus aculeatus (L.) and provides a data base for habitat evaluation procedures. The threespine stickleback is generally regarded as a hardy species, tolerant of a wide range of habitat conditions.

Information on physiological tolerances and requirements have been gathered from throughout the range of the species. However, observations on actual conditions observed in bodies of water where sticklebacks occur are generally restricted to Alaska. The threespine has been extensively used as a laboratory fish for behavioral and pollution studies. Much work has been done on the physiology of the species in Europe, but relatively little in North America. It is recognized that habitat requirements may differ for stocks from different geographic areas, but present data available from Alaska are insufficient to demonstrate this within the State.

Within the Gasterosteus aculeatus complex, three forms are generally recognized (McPhail and Lindsey, 1970). There is a partially plated freshwater form (called leiurus), a heavily plated marine form (called trachurus), and an intermediate form (semiarmatus). This report is restricted to the totally freshwater form (leiurus), even though the anadromous forms may use freshwater habitat during the breeding season.

This report emphasizes habitat requirements, primarily those of a physical and chemical nature. Certain biological factors affecting the well being of the population, such as feeding, predation, competition, parasites, and disease, are not comprehensively treated.

B. Distribution

The threespine stickleback is widely distributed in the northern hemisphere in North America, Europe, and Asia. Except for Europe, it is not found more than a few hundred kilometers from the coast. On the Atlantic coast of North America, it ranges from Baffin Island and the Hudson Bay area down to Chesapeake Bay. On the Pacific coast of North America, it occurs from Alaska to Baja California. On the eastern coast of Asia, it ranges from the Bering Strait south to Japan and Korea (Scott and Crossman, 1973; Wootton, 1976).

In Alaska, the threespine stickleback occurs in all coastal areas from Dixon Entrance to the Alaska Peninsula, the Aleutian Islands and Bristol Bay (Morrow, 1980). It also occurs in the western tip of the Seward Peninsula and on St. Lawrence Island; however, the freshwater leiurus form is not thought to be present in the latter areas (McPhail and Lindsey, 1970; Wootton, 1976). (See Figure I.)

The leiurus form occurs in both lakes and streams.

C. Life History Summary

An excellent synthesis of threespine stickleback life history has been presented by Wootton (1976). Behavioral aspects of threespine stickleback life history regarding reproduction (spawning and incubation of eggs) have been extensively documented and will not be dealt with in this report. Section II, Specific Habitat Requirements, will examine data on tolerances and preferences for physical and chemical parameters

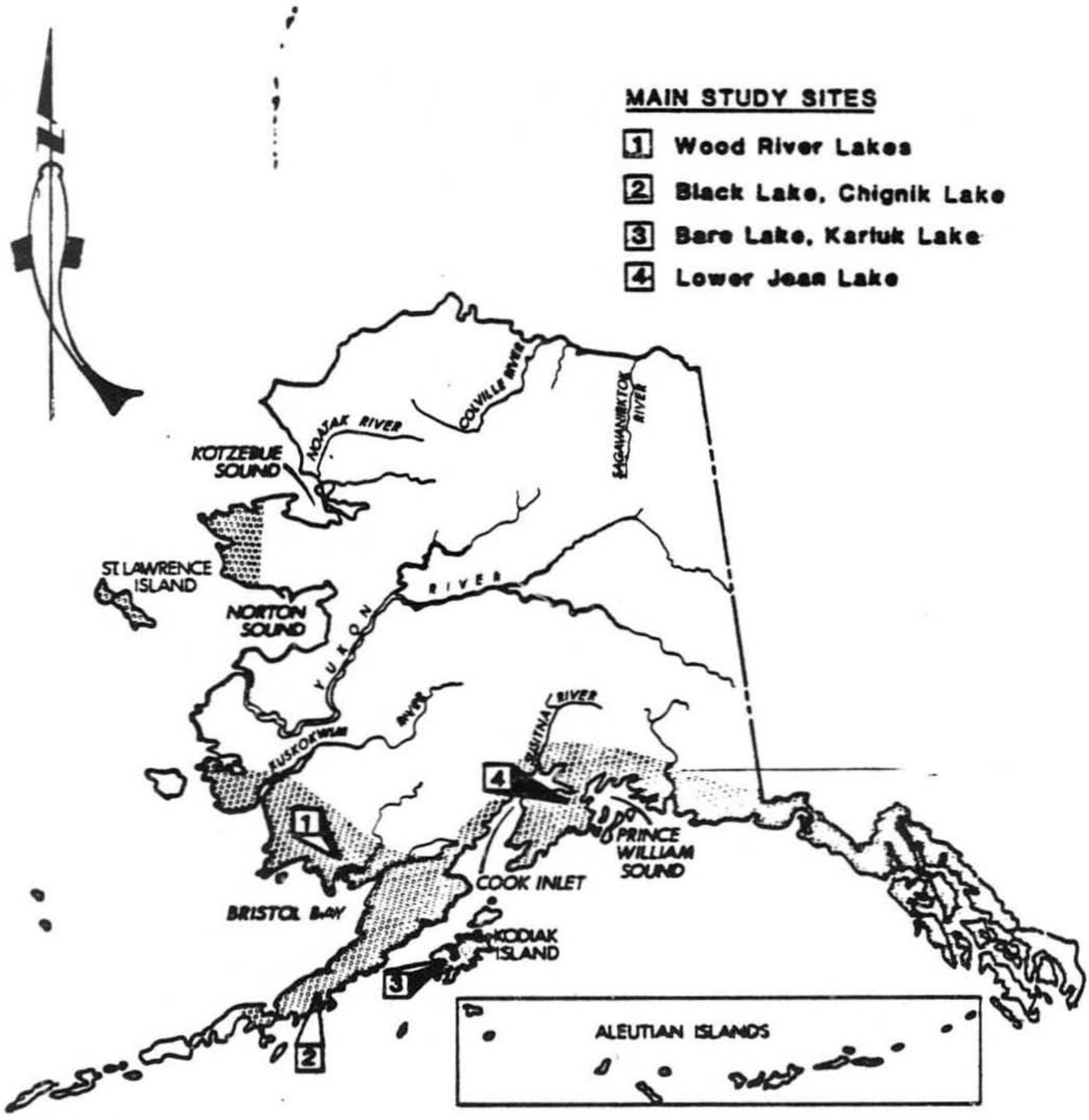

Figure 1. Distribution of Threespine stickleback in Alaska (Morrow, 1980) and main study sites.

history aspects other than reproductive behavior for juveniles and adults, emphasizing Alaskan studies. Much of this section has been provided by Cannon (1981), with permission of the author.

1. Size and Age

Cannon (1981) identified three discrete size classes of threespine sticklebacks in lower Jean Lake on the Kenai Peninsula. Standard lengths ranged from 22-71 mm. One size class ($\overline{SL}$ = 32-33 mm) was captured in surface tows in June and early July; weekly abundance for this size class in the catch decreased during this time. A smaller size class ($\overline{SL}$ = 28-29 mm) entered the catch in mid-June and rapidly dominated the catch by mid- July. During July and August, two size classes were distinguished in baited minnow traps fished on the lake bottom. Stickleback ($\overline{SL}$ = 38-40 mm) were taken in littoral areas; a larger size class ($\overline{SL}$ = 51-52 mm) was captured at depths of 19-20 m.

In Lake Nerka (Wood River lakes) Burgner (1958) observed a trimodality of size distributions which suggested the presence of three age groups in early summer. Stickleback fry did not appear in catches until August and were abundant in September. The maximum age was reached at three years or more and in adult fish, females were larger than males. The life history of populations inhabiting Karluk and Bare Lake on Kodiak Island was studied by Greenbank and Nelson (1959). Lifespan was determined to be 2+ years, some individuals probably lived past a third winter. Young of the year were first observed in collections made in early July; this size class was reported to be very abundant and soon dominated the catch. Mature females attained a somewhat larger size than did males. Narver (1968) described the general life history of threespine sticklebacks in the Chignik Lakes on the Alaska Peninsula. Determination of age was accomplished by examination of length-frequency. An interpretation of size distribution for a September sample placed Age 0 fishes within the 20-30 mm fork length (F.L.) size range, Age 1+ within 40-45 mm range and Age 2+ within 55-65 mm range. Fry first appeared in tow net catches in early August; their density increased rapidly. Engel (1971) also identified three size classes in beach seine and minnow trap catches in Johnson, Scout, and Bear Lakes on the Kenai Peninsula. Length of life was estimated to be 2+ years, mean lengths for ripe males and females in Bear Lake were 50.5 mm (F.L.) and 49.5 mm respectively. These lengths correspond to those found by Greenbank and Nelson for Age 2 fish. The abundance and size of threespine found in Lake Aleknagik (Wood River lakes) were examined by Rogers (1972). Age groups were assigned on the basis of length frequency. Age 0 fish were approximately 10-20 mm ($\overline{SL}$) by the first week of August and initially appeared in beach seine hauls in mid-July. Age 1 were 30-35 mm, Age 2 were 40-50 mm, and Age 3 were 55-65 mm.

The variations in age and size structure found in these studies undoubtedly reflects differences in genetic and environmental influences between the respective populations. Direct comparisons are confounded by differences in sampling gear and measurement methods used. Rogers (1972) demonstrated that in years of unfavorable growth, major stickleback age groups showed distinctive length frequencies; but in years of good growth, the older year classes overlapped.

2. Maturity and Reproduction

Initial sexual maturity in the Lower Jean Lake stickleback population probably occurs during the second summer of life (Cannon, 1981). Fishes thought to be Age 1 which were captured in tows and minnow pots were sexually mature; a smaller size class, Age 0, was not mature. Only one age class at sexual maturity was reported by Greenbank and Nelson (1959) and McPhail and Lindsey (1970). Rogers (1968), Burgner (1958), and Narver (1968) suggested that threespines mature at Age 2. Carl (1953) and Jones and Hynes (1950) stated that breeding occurred during the first year of life (Age 0). Variation in these estimates cannot be explained with available information; however, differences in length of season, food availability and genetic character were probably influencing factors.

A decrease in Age 1 stickleback catch per unit effort for surface tows in Lower Jean Lake during the course of the summer and the presence of a similar size class in shallow shoreline areas suggested that there was a migration from pelagic to littoral habitats (Cannon, 1981). Because Age 1 fish were sexually mature and were strongly suspected of spawning in littoral areas during this time, the movement appeared to be associated with reproductive activity. Tinbergen (1952) and Narver (1968) described a spawning migration of schools of threespine stickleback into shallows. Males then left schools to establish territories. Baerends (1957) stated that when reproductive instinct in threespine is activated, adult fish begin to migrate. These migrations appeared to correspond with a reproductive stimulus that is only satisfied when the fish reach shallow, warm waters with abundant vegetation.

Although characteristic behavior associated with breeding was not observed by Cannon (1981) in Lower Jean Lake, the majority of the lake population apparently spawned in the lake. Spawning emigrations from the lake were not observed during the summer, however, they may have occurred prior to mid-May. Sticklebacks were not found in high densities milling near the inlet and outlet creek weirs nor attempting to pass through them. Greenbank and Nelson (1959) reported that in Karluk Lake, threespine in breeding condition were observed in the lake, but nesting was not witnessed.

Various authors have noted a variety of materials used in construction of nests. Tinbergen (1952) described nests constructed of small twigs, grass and other debris; Greenbank and Nelson (1959) and Vrat (1949) discovered nests formed from cemented sand grains.

Male sticklebacks apparently require the sight of aquatic vegetation for the initiation of nest building (Pelkwijk and Tinbergen, 1937, cited by Aronson, 1957). Narver (1968) noted that the occurrence of stickleback in spawning condition was greatest in areas where submergent flora was plentiful. Hagen (1967) observed sticklebacks nesting in still and standing backwaters near dense stands of aquatic vegetation. Male sticklebacks exhibiting breeding colors and females with distended abdomens were observed in or near thick patches of <u>Chara sp</u>. in Lower Jean Lake (Cannon, 1981).

Egg production in European populations has been estimated to be 100-200 eggs per spawning (Assen, 1967; Wootton, 1973 b). McPhail and Lindsey, 1970) reported that in populations from the Pacific Northwest, gravid females will often spawn several times per season and lay 50 to 200 eggs at a time. The number of eggs per spawning and the number of spawnings per season have been shown to be positively correlated to the size of the female (Wootton, 1973 a). He suggested that population estimates which ignored the high potential of egg production and survival provided by the multi-seasonal spawning capacity of large females and the protective nesting behavior of males could grossly underestimate stickleback production and would incorrectly assess the importance of this species to the energetics of the freshwater community. Potapova et al. (1966) found that the quantity and viability of egg production is related to growth rate and lipid storage; large females exhibit higher fecundity.

The rigors of breeding evidently lead to increased mortality. This view is supported by detailed descriptions of the complex nature of stickleback reproductive behavior provided by Tinbergen (1952) and van Iersel (1953, cited by Wootton, 1976). High mortalities reported by Rogers in Lake Aleknagik may have resulted from a decreased resistance to high temperature due to the stress of spawning. Narver (1968) observed high death rates associated with spawning stress in the Chignik Lakes, Alaska. These high mortalities and the territorial spawning of sticklebacks were considered possible density-dependent population regulators. Hagen (1967) described post- reproductive mortality in the threespine population inhabiting the Little Campbell River, B.C. Many adults were found in extremely poor condition; fungus and other parasitic eruptions were noted. Sticklebacks in Karluk and Bare Lakes on Kodiak Island apparently incurred a high mortality after spawning and appeared nutritionally deprived (Greenbank and Nelson, 1959). Engel (1971) reported post-spawning mortality in study lakes on the Kenai Peninsula, Alaska.

3. Feeding and Competition

Feeding investigations of sticklebacks in North America have determined that their diet is composed mainly of zooplankton and insects. The fish are opportunistic and food sources are related to seasonal and regional availability. Carl (1953) found cladocera and copepods in the majority of stickleback stomachs collected in Cowichan Lake, B.C.; insects, ostracods, anphipods and algae were also observed. Greenbank and Nelson (1959) discussed the importance of chironomid larvae and pupae, copepods and cladocera in the feeding of sticklebacks in Karluk and Bare Lakes. Other items encountered occasionally were pea clams, ostracods, rotifers, snails, leaches, planarians, fish eggs and water mites. The importance of chironomids decreased over the summer. Most larger sticklebacks fed on ostracods and fish eggs; fewer of them fed on cladocera. Chironomid larvae and entomostraca were found to be primary food types in threespine sticklebacks in littoral areas of Lake Aleknagik with Entomostraca being their major prey in limnetic areas (Rogers, 1968). Sticklebacks inhabiting Black Lake, a shallow lake, fed predominately on insect larvae; threespines in Chignik Lake, which has only a small littoral zone, fed totally on zooplankton (Parr, 1972).

In Lower Jean Lake, feeding habits of threespines reflected differences in their distribution (Cannon, 1981) and seasonal availability. Fish utilizing bottom waters preyed on food species which were not caught in plankton hauls because most of these species live on or near the bottom. Threespines foraging in the limnetic surface zone preyed largely on planktonic invertebrates. Age 1 sticklebacks ($\overline{SL}$, 30-32 mm) fed predominately on copepods in mid-June; but for Age 0 sticklebacks ($\overline{SL}$, 28-30 mm) rotifers were dominate prey during July. The availability of prey species in surface waters may have fluctuated during the summer, due to variations in their abundance or distribution. Surface and bottom feeding threespine sticklebacks in Lower Jean Lake were ecologically separated (Cannon, 1981). Distributional differences were considered a mechanism by which stickleback age classes minimized competitive stress and maximized the utilization of lake resources. The ability of threespines to utilize limnetic waters as well as bottom environments demonstrated their adaptability to use a wide range of conditions thus allowing exploitation of diverse aquatic niches. Separation of age classes between limnetic and bottom habitats were believed to be associated with spawning migrations. Exposure to a wide variety of habitat types was facilitated by these movements. Anatomical and physiological differences between age groups may have enforced separation.

Because spawning and early rearing occur in shallows, stickleback life history is closely associated with littoral habitats. The quantity of suitable littoral area potentially serves as an important stickleback population regulating factor (Narver, 1968). Ecological expansion would depend on the physical condition and the magnitude of co-actions (competition and predation) found in adjacent environs. For these reasons, the variety of potential niches accessible to sticklebacks and consequently their distributional patterns can be expected to vary seasonally and between systems.

Spatial differences exhibited between Age 0 and Age 2 sticklebacks and rearing sockeye salmon in Lower Jean Lake provided a mechanism to reduce interspecific competition (Cannon, 1981). Rearing sockeye were not caught in surface tows after mid-July; this decline occurred in conjunction with a large recruitment of Age 0 sticklebacks.

Feeding similarities between sticklebacks and rearing sockeye have been reported by Burgner (1958) in the Wood River Lakes, Alaska, Narver (1968) in the Chignik Lakes, Alaska, and Krokhin (1957) in the Kamchatka Lakes, USSR. Common prey preferences have suggested potential competition for food. In nature, many similar species appear to coexist while seemingly in competition; however, detailed observations have revealed differences in habitat and behavior that permit coexistence.

Rogers (1968) compared the food of sockeye salmon fry and threespine sticklebacks in the Wood River Lakes. In littoral areas, the benthos was used more by sticklebacks than sockeye fry; surface insects were utilized more by sockeye. In limnetic areas, winged insects were an important prey for sockeye, but were rarely ingested by sticklebacks. Parr (1972), who studied the feeding of juvenile sockeye and resident fish species including threespine in the Chignik Lakes, indicated that a dissimilarity existed between stickleback and sockeye feeding. Sockeye more frequently fed on winged and pupal insects. In Lower Jean Lake, a comparison of feeding between these species (although limited to only a five week period) found similar differences (Cannon, 1981). Sticklebacks and sockeye inhabiting surface waters during this period utilized similar prey, but sockeye appeared to prefer winged insect species more than sticklebacks.

Partitioning rations among sticklebacks and rearing sockeye in Lower Jean Lake appeared to be accomplished through differences in spatial distribution (Cannon, 1981). Age 2 threespine utilized bottom habitats. Age 1 sticklebacks and juvenile sockeye exhibited similar distribution patterns and feeding; however, spatial overlap and prey similarity are only prerequisites to potential competition. A significant decrease in Age 1 threespines was observed during the summer in Lower Jean Lake. This reduction was believed to be associated with reproductive migrations which brought adult fish bottom environments. The rapid recruitment of Age 0 sticklebacks into the near surface waters during July may have influenced the apparent shift in vertical distribution of juvenile sockeye into deeper water stratums and restricted the return of Age 1 sticklebacks into limnetic areas. The high preference of Age 0 sticklebacks for rotifers was not shared with sockeye or adult threespine, a small mouth size possibly was responsible for the apparent differences in feeding preference, although Age 1 threespine of approximately the same size fed predominately on copepods in June when rotifers were abundant in the net plankton. Temporal variations in the vertical distributions of prey species may have been involved. Rogers (1968) suggested that temporal as well as spatial differences in stickleback-sockeye feeding relationships could exist.

Narver (1968) developed a conceptual model of sockeye-stickleback co-actions for populations in the Chignik Lakes. He concluded that threespine sticklebacks which were ecologically a littoral species would be displaced from limnetic areas by rearing sockeye if the young salmon remained abundant. Parr (1972) determined that the abundance of Age 0 sockeye in the Chignik Lakes had an adverse effect on resident fish populations including threespine sticklebacks. Burgner (1958), Kerns (1965), and Rogers (1972) have suggested a similar population regulation of stickleback abundance by large Age 0 sockeye salmon recruitments in the Wood River Lakes. Reduced spawning escapement due to overharvest or environmental factors have resulted in periods of reduced sockeye fry abundance in the Wood River and Chignik Lakes. During these years, sticklebacks were able to rapidly occupy vacant niches (Burgner, 1958; Narver, 1968).

The threespine stickleback is the dominant fish species inhabiting Lower Jean Lake (Cannon, 1981). Its dominance is favored by a prolonged spawning time, a substantial littoral spawning habitat with abundant submergent vegetation, an ability to utilize deep and shallow bottom habitats as well as pelagic areas for feeding, reduced intraspecific competition between age classes via differences in their spatial behavior and diurnal migrations, and an apparently low level of interspecific competition from rearing sockeye salmon in limnetic areas.

4. Distribution and Behavior

An apparent diel migration of threespines in surface waters of Lower Jean Lake was observed by Cannon (1981) during the summer. The abundance of sticklebacks in surface tow net samples collected in the Wood River Lakes by Burgner (1958) remained high throughout the day and night. Diel zooplankton migrations probably influenced stickleback distribution in Lower Jean Lake. Stomach analysis of threespine from different periods showed no significant decrease in numbers of whole undigested zooplankton. If feeding continued throughout the day and night, sticklebacks conceivably would concentrate at depths where prey density was high. Vertical migrations of limnetic zooplanktens commonly occurring in Alaska lakes have been observed (Rogers, 1974).

A reduction in interspecific competition between sticklebacks and sockeyes could result from seasonal variations in vertical distribution. Because threespine are more resistant to high temperature and illumination and because they are equipped with a self-contained defense mechanism, near-surface water residence would be less ecologically intolerable for stickleback than for sockeye.

Outside of breeding season, stickleback feed in schools (Tinbergen 1952). Generally, schooling fish are the same size because fish of similar size swim at the same speed. Size in sticklebacks varys between sexes and schools comprised of all males or all females have been observed (Narver, 1968). Possible benefits attributed to schooling behavior have included increased feeding efficiency, predator detection and defense, increased ability to locate a mate, enhanced learning ability, and efficiency of movement (Eggers, 1975). Schooling was observed in sticklebacks in surface waters (juveniles) and in shallow littoral areas (adults) of lower Jean Lake (Cannon, 1981).

MacMahon (1946) described the threespine stickleback as the fiercest freshwater fish in Britain for its size. Its highly flexible fin motions are well suited to feeding in the dense vegetation and submerged debris of the littoral environment. Hagen (1967), who conducted dispersion studies of threespine, reported that sticklebacks (leiurus) were a sedentary fish. Recaptures of marked fish were never made beyond 200 m from the point of release. Sticklebacks in Lower Jean Lake generally exhibited a lethargic swimming activity (Cannon, 1981). Adult sticklebacks observed in schools feeding in algae beds and solitary fish which were probably spawning moved slowly through the water. Even pelagically feeding schools of Age 0 threespine swam sluggishly near the surface. Rapid swimming motions occurred during territorial defense and occasionally in pursuit of prey, but only for short distances.

D. Ecological and Economic Importance

The threespine stickleback is often abundant where it is found and plays a significant role as a predator, competitor, and prey species in many lake ecosystems. There has been concern regarding the stickleback as a potential competitor with sockeye salmon (Oncorhynchus nerka) fry but recent studies (Cannon, 1981; Manzer, 1976; Rogers, 1972; Wootton, 1976) have indicated that competition to the detriment of the sockeye fry does not often occur. (See also discussion in Section I.C., Life History Summary.) In artificial situations, such as the reclamation and re-stocking of lakes with rainbow trout (Salmo gairdneri), the presence of threespine sticklebacks may be detrimental to the trout population (Engel, 1971). In many areas, sticklebacks are an important prey species for predaceous fish such as trout, salmon, and northern pike (McPhail and Lindsey, 1970; Wootton 1976) and for fish-eating birds (Scott and Crossman, 1973).

The threespine stickleback has been harvested only to a minor extent. They have been used for oil, meal, fertilizer, and animal food, including sled dog food (Wootton, 1976).

Because the threespine stickleback is hardy, easy to keep, and widely distributed, it has proven to be an important laboratory fish. It has been extensively used for behavioral studies and for studies on the effect of water pollution (Wootton, 1976).

II. SPECIFIC HABITAT REQUIREMENTS

A. Spawning

1. Temperature

The surface water temperature during the breeding season in Lower Jean Lake ranged from about 12 to 18°C (Cannon, 1981). In a stream of southern British Columbia, the average temperature during the breeding season was 16°C (Hagen, 1967) and a stream in England during the spawning season had temperatures ranging from 16 to 19°C (Lindsey, 1962).

Greenbank and Nelson (1959) stated that the water temperature in two lakes on Kodiak Island may influence the time of spawning. Threespine sticklebacks spawned earlier in Bare Lake (surface water temperatures from mid-May to end of July were 4.4-22.8°C) than in the deeper Karluk Lake (3.3-13.9°C). Baggerman (1957, cited by Wootton, 1976) found that increased temperatures (about 20°C), given a sufficiently long daylength, accelerate the maturation process.

2. Water Depth

Male threespine sticklebacks build their nests in streams or in shallow areas of lake shores. Hagen (1967) found that the average depth of nests in Little Campbell River, B.C., was 24 cm; some nests were built in water as shallow as 4 cm.

3. Substrate

The nests are constructed of small twigs, plant material, and sand. Some nests may be constructed mostly of sand grains (Greenbank and Nelson, 1959; McPhail and Lindsey, 1970).

Nests in the River Wear, England, were built on a "muddy" bottom (Wootton, 1976). The same substrate was used by the leiurus form in Little Campbell River, B.C. (Hagen, 1967). Hagen gave male sticklebacks a choice between "sand" and "mud" substrates in the laboratory and found that they demonstrated a strong preference to build their nests on the mud. The leiurus form in Mayer Lake, B.C. also occurred on a soft mud bottom (Moodie, 1972). Scott and Crossman (1973) state that threespines prefer sandy areas for nest building (form not mentioned).

4. Aquatic Vegetation

Stickleback nests are usually found in or near aquatic vegetation.

Hagen (1967) observed stickleback (leiurus) nests in the Little Campbell River, B. C. near dense stands of aquatic vegetation such as Oenanthe, Potomogeton, Nuphar, Carex, Myosotis, Glyceria, Typha, Lemma, and green algae. The fish always nested among broadleaved vegetation.

In the laboratory, Hagen (1967) presented males of the leiurus form with a choice between Oenanthe (a plant found in the headwaters) and Elodea (a lower river plant) and found a strong preference for the former. In a survey of streams on Vancouver Island, during breeding season, Hagen found leiurus plentiful only in areas with dense aquatic vegetation. The *leiurus* form in Mayer Lake, B. C., occurs only among the thick vegetation of inlet stream margins and stream mouths and apparently does not occur in open water (Moodie, 1972). The littoral zone of Mayer Lake is densely covered with *Sphagnum* and emergent grasses.

Narver (1966) reported that spawning sticklebacks in the Chignik Lakes were most abundant where aquatic vegetation was plentiful. However, Karluk and Bare lakes on Kodiak Island, which have good populations of sticklebacks, have only sparse aquatic vegetation (Greenbank and Nelson, 1959).

5. Light

Gonad maturation of threespine sticklebacks in the spring is dependent on both an adequate light intensity and on an adequate daylength (Baggerman, 1957, cited by McInerney and Evans, 1970). Baggerman found that high temperature (20°C) by itself is not effective in inducing sexual maturation, long photoperiods are also required. Baggerman also showed that sticklebacks exposed to 269-323 lux (25-30 ft-candles) matured slightly more rapidly than those exposed to 161 lux (15 ft-candles). McInerney and Evans (1970) reported that sticklebacks (presumably the *trachurus* form) exposed to an energy level of 370 ergs/cm^2-sec in the laboratory had maturation rates comparable to those of wild fish. This energy level is equivalent to illuminance levels ranging from 230 lux (at the green wavelength) to 5 lux (at the purple wavelength). McInerney and Evans also tested the effect of light quality (wavelength) by exposing fish to four segments of the visible spectrum ranging from 388-653 millimicrons (long ultraviolet to short red). They found no major differences among the four in affecting the rate of gonad maturation.

6. Size of Territory

Wootton (1976) states that the maximum density of threespine stickleback nests is 4-5/m^2 and that the minimum distance between nests is 30-50 cm. The average distance between nests in the River Wear, England, ranged from 143-237 cm (Wootton, 1976).

B. Incubation of Embryos

1. Temperature

The time to hatching is directly dependent on temperature. Wooton (1976) plotted the data of several investigators and found that the time to hatching varies from about 5 days at 25°C to about 15-43 days at 8°C. At 18-19°C, hatching occurs in about 8 days and the yolk sac is absorbed in another 4 days. Studies in Alaska have reported hatching times of 14 days at a water temperature ranging from 9-16°C (Kodiak Island; Greenbank and Nelson, 1959) and 5 days at a water temperature varying from 21.1-22.8°C (Kenai Peninsula; Engel, 1971). Neither of these studies was in situ.

Heuts (1947), in laboratory studies in Belgium, found that the best survival of eggs incubated in freshwater occurred at water temperatures of 16-26°C. Heuts showed that the eggs are adapted to a narrow range of temperatures. Lindsey (1962) reared the freshwater form in the laboratory at temperatures ranging from 10-28°C. No eggs were successfully reared in freshwater at 10°, 12°,14°, or 28°C, and survival at 16° and 18°C was less than optimum. However, there may have been factors present other than temperature which lowered the survival rate. Lindsey also found that fish reared at higher temperatures (22°C and greater) had a higher proportion of females than fish reared at 20°C and below. Lindsey further showed that eggs from females with few lateral plates have a higher optimum development temperature than eggs from females with more plates. The approximate optima were: 26°C (2 maternal plates), 20-27°C (4 or 5 maternal plates), 20- 22°C (6 maternal plates), and 16°C (7 maternal plates).

Wootton (1976), citing the work of Swarup (1958, 1959), stated that abnormal development occurs when newly fertilized eggs are exposed to very low (0°C) or very high (33°C) temperatures for a duration as short as 1.5-3.0 hours. One of the abnormalities was the production of fish with a triploid number of chromosones. These fish developed and grew at the same rate as normal (diploid) fish, but were misshapen.

Hagen (1967) measured water temperatures ranging from 16 to 23°C during the nesting of sticklebacks in Little Campbell River, B.C. Some approximate surface water temperatures for various lakes in Alaska measured at the approximate time incubation occurs are: Bare Lake, 6? - 23°C, and Karluk Lake, 4? - 15°C (Greenbank and Nelson, 1959); Lower Jean Lake, 13 - 18°C (Cannon, 1981); Johnson and Scout Lakes on the western Kenai Peninsula, 12 - 18°C, and Bear Lake in the Kenai Mountains, 7 - 15°C (Engel, 1971); Wood River Lakes, 10 - 14°C (Rogers, 1968); Lake Nerka, 9 - 18°C (Burgner, 1958); Black Lake, 12 - 15°C, and Chignik Lake, 9 - 13°C (Parr, 1972).

2. Dissolved Oxygen

Given the fact that sticklebacks nest in shallow areas with adequate light penetration and aquatic vegetation, dissolved oxygen levels in the water near the nests are probably rarely a limiting factor. However, the eggs are placed inside covered nests, often on muddy bottoms containing much dead organic matter, and often in areas of little or no current, so circulation of water through the nest to replace the oxygen used by the embryos is necessary and is accomplished by the fanning of the male. In the absence of fanning, van Iersel (1953, cited by Wooton, 1976) noted that eggs became moldy and died. The rate of fanning reaches a peak shortly before hatching; presumably, this is when the oxygen requirement of the embryos is highest. When van Iersel ran water low in dissolved oxygen and high in carbon dioxide through a nest in the laboratory, the amount of fanning by the male increased.

C. Juvenile Rearing

After leaving their nests, young sticklebacks form schools, which may be an adaptation for cover, and eventually join the adults. There is little information to suggest that young of the year have habitat tolerances, preferences, or requirements different from those of adults.

D. Adult Life

1. Temperature

The adult threespine stickleback is usually regarded as a eurythermal fish (Wootton, 1976). Jordan and Garside (1972) studied the upper lethal temperature of threespine sticklebacks (probably the *trachurus* form) from the harbor of Halifax, Nova Scotia (where the salinity ranges from 20-30 ppt) which had been acclimated to various combinations of temperature and salinity. The highest upper lethal temperature (28.8°C) was noted for fish acclimated to 20°C and 30 ppt salinity, tested at 12 ppt, and the lowest upper lethal temperature (21.6°C) was shown by fish acclimated to 10°C and a salinity of 0 ppt, tested at 30 ppt. Fish which had been acclimated to freshwater at 20°C, and tested in freshwater, had an upper lethal temperature of 27.2°C. There were no significant differences in survival among the different sized fish (total lengths ranged from 30-80 mm) tested. Coad and Power (1973), citing Bertin (1955) state that the threespine can tolerate temperatures around 25°C and is also tolerant of temperature changes. Heuts (1947) found with the leiurus form collected at 0°C and placed into water at 25 - 28°C that fish with fewer lateral plates survived longer than fish with more lateral plates. Mean survival time was around 40 hours. Heuts also stated that the freshwater form will not tolerate 'low' temperatures.

The threespine stickleback is found in Alaskan lakes with late spring to early fall temperature ranges of anywhere from 0° to 23°C (Burgner, 1958; Cannon, 1981; Engel, 1971; Greenbank and Nelson, 1959; Parr, 1972; Rogers, 1968 and 1972). The stickleback may not be found at the extremes of this range if they have a choice of more moderate temperatures. Little information is available on temperature preferences or on temperature distribution during late fall, winter, and early spring. In the summer, sticklebacks move into warmer, shallower, water but this is probably more a function of reproductive and feeding requirements than a demonstration of temperature preferences.

Temperature influences the rate of growth. Wootton (1976), citing the work of Cole, reported that the mean growth efficiency increases from 5.9% at 7.0°C to 11.3% at 20.0°C. Beukema (1968, cited by Wootton, 1976) found that the feeding rate also depends on temperature, the rate of stomach evacuation ranging from about 16 hours at 11-12°C to "one night" at 18-20°C.

2. Water Depth

The depth distribution of threespine sticklebacks in lakes results from temperature preferences, feeding migrations, reproduction requirements, predation and competition. They are generally a shallow water fish, particularly in the summer when they move into the shoals along the shore. During the summer they range from the surface to the bottom in lower Jean Lake (21.3m) (Cannon, 1981) and Johnson (4.0 m), Scout (6.1 m), and Bear (18.3 m) lakes (Engel, 1971) on the Kenai Peninsula. In Karluk Lake on Kodiak Island, they have been caught from the surface down to 24.4 m, but none were caught in attempts at 38.4 m or at 61.0 m (Greenbank and Nelson, 1959). Very few fish were caught below surface waters in Lake Nerka during the summer; the deepest stickleback was caught at 7.3 m (Burgner, 1958).

3. Current Velocity

Although threespine sticklebacks commonly occur in streams, they prefer areas with little or no current (Hagen, 1967). Hagen conducted a thorough study in Little Campbell River, B.C., and determined that swift waters are an unfavorable habitat. The average current velocity in a section of the stream where the leiurus form was plentiful was 3 cm/sec (gradient about 1.5 m/km). A section with an average velocity of 23 cm/sec had only a few sticklebacks of the *leiurus* form and a riffle section with an average velocity of 74 cm/sec had none. When Hagen transplanted the fish from the low current area into an area of fast current, they migrated into areas of slower current. When Hagen gave males a choice between standing water and moving water in an aquarium, they demonstrated a strong preference for nesting in the standing water. Hagen also reported that some fish successfully passed through a 70 m long culvert with a current velocity of 92 cm/sec, although this was not a common occurrence.

4. Dissolved Oxygen

Krokhin (1957) calculated that the oxygen consumption of threespine sticklebacks in Kamchatka lakes where the temperature ranges from 2.0 to 14.3°C would range from 0.127 - 0.365 mg O_2/hr-g live weight. He found that fish in the laboratory at a temperature range of 0.5 - 19.5°C used oxygen at a rate ranging from 0.12 - 0.55 mg O_2/hr-g live weight. Threespine sticklebacks from some English streams had an oxygen consumption rate ranging from 1.0 microliters O_2/hr-mg dry weight (1 microliter = 1.43 micrograms) for 500 mg dry weight fish to about 2.5 microliters/hr-mg dry weight for 70 mg dry weight fish (temperature not given; Lewis et al., 1972).

Jones (1948 and 1952, cited by Wootton, 1976) stated that the minimum dissolved oxygen (DO) level at which threespine sticklebacks can exist is about 0.25 - 0.50 mg/l. Jones found that the avoidance response of sticklebacks is triggered when the fish are exposed to water with a DO level of 0.3 mg/l at low temperatures. At 20°C, the response occurs at 2.0 mg/l, indicating the fish have a lower tolerance for low DO conditions at higher temperatures. In a survey of some English streams, Lewis et al. (1972) found that threespine sticklebacks were most abundant in waters with 8 - 12 mg O_2/l, less abundant in waters with 6 - 8 mg O_2/l, and absent from waters with 2 - 5 mg O_2/l.

In Lower Jean Lake, sticklebacks were caught near the lake bottom during the summer where DO levels ranged from 3.0 - 6.5 mg/l (Cannon, 1981). These levels apparently had no effect on feeding activity. Dissolved oxygen levels above the thermocline ranged from 10.1 - 14.0 mg/l. Greenbank and Nelson (1959) reported that the stickleback population in Karluk and Bare Lakes are in waters where there is an "abundance" of dissolved oxygen at all depths during the summer. They also stated that the threespine stickleback "is known to survive over winter in shallow lakes in northern temperate and subarctic zones, where.... dissolved oxygen sinks to a trace....".

5. Chemical Parameters

Threespine sticklebacks have been reported to occur in waters with a pH range of: 7.0 - 8.7 in Karluk and Bare Lakes (Greenbank and Nelson, 1959); 6.3 - 7.0 in three Kenai Peninsula lakes (Engel, 1971); and 6.8 in Little Campbell River, B.C. (Hagen, 1967). Jones (1948, cited by Wootton, 1976) tested the tolerance of the fish to a wide pH range and reported that they avoided a pH of less than 5.6 or greater than 11.4.

A survey of some English streams conducted by Lewis et al. (1972) showed that the threespine did not occur in waters which smelled of hydrogen sulfide and rotting vegetation.

6. Feeding

Krokhin (1957) calculated that threespine sticklebacks in some Kamchatka lakes, where the annual temperature range is 2.0 -14.3°C, consume daily between 0.08 g/fish in winter and 0.23 g/fish in August. This represents 1.8 - 5.1% of body weight. The monthly food consumption ranged from 2.70 - 6.77 g/fish, for an annual total of 42.49 g, which is equivalent to 8 or 9 times the average weight of an adult (4.5 g). In Lake Dal'neye, Krokhin (1970) calculated that the monthly food consumption ranged from 0.80[2] g/g live weight in January to 2.185 g/g live weight in August.

Manzer (1976) reported that the daily ration of threespine stickleback in Great Central Lake on Vancouver Island, B.C., was 6.6% of the body weight in July and 7.8% in October. Wootton (1976) states that, to support a population of threespine sticklebacks, an area must produce suitable food on the order of 10 - 100 g/m^2-yr.

III. CONCEPTUAL SUITABILITY INDEX CURVES

Conceptual suitability index curves are presented for water temperature, current velocity, water depth, dissolved oxygen concentration, and pH in Figures 2 through 4. Data to support the curves is included in Tables I, II, and III. These curves should not be construed as a graphical presentation of actual data. Rather, they are intended to be hypothetical models of the relationship between threespine sticklebacks and certain environmental parameters. As with any hypothesis, they must be tested and verified before being applied to any particular situation.

The curves are based on published and unpublished data and on conversations with fishery biologists who have worked with threespine sticklebacks. Both experimental laboratory data and field measurements and observations were used. The suitability index for each environmental parameter ranges from zero to one. An index of one indicates an optimum or preferred level of that particular parameter and an index of zero indicates a completely unsuitable level.

Data from laboratory physiological studies in European populations of threespine sticklebacks indicates that the optimum temperature during incubation of embryos is 8 or 9°C higher than the average surface water temperature during the presumed incubation period in several Alaskan lakes (Figure 2). Until the temperature tolerance of Alaskan sticklebacks has been studied in physiological laboratory studies, it must be assumed that the optimum temperature for European sticklebacks (about 22°C) does not apply in Alaskan waters which rarely reach 22°C. A problem encountered in constructing the curves is that much of the data in the literature concerning environmental parameters of threespine stickleback habitat does not relate various levels of the parameters to some measure of habitat suitability. Often, ranges of the parameter are given based on measurements taken throughout the area occupied by threespines but there is no indication that one point on the range is any better or worse than any other point in terms of habitat suitability.

The curves are drawn using data from throughout the natural range of the threespine stickleback. Although there probably are differences in habitat preferences and tolerances for different geographical areas or even in different streams of the same geographical area, there is not enough data to support drawing separate curves at this time. However, one must be aware that any point on the curve, especially toward either extreme, may be unsuitable for a particular stock. How far the stock deviates from the curve must be determined by field measurements and experimentation with that particular stock.

A second precaution regarding the curves concerns the interaction of various parameters. A given level of one parameter can have a different effect on the fish as the level of another parameter varies. For example, a dissolved oxygen concentration of 3 mg/l may be suitable at a water temperature of 5°C, but unsuitable at a temperature of 20°C. Ideally, given enough data, a separate dissolved oxygen curve should be drawn for each of several different temperatures. The overall suitability of any particular habitat is a summation of the interacting effects of many parameters.

A third precaution to consider is that the effect of less than optimum levels of any parameter on the fish depends strongly on the duration of exposure. Stickleback embryos exposed to a water temperature of 33°C for 1.5 - 3.0 hours experience an abnormal development (Swarup, 1958 and 1959, cited by Wotton, 1976), but survive. Embryos exposed to 33°C for a longer period of time would die.

Also, different ages within a life stage probably have different habitat requirements. For example, the oxygen requirement of embryos is highest just prior to hatching. However, because of insufficient data, it is not possible to draw separate curves for different ages.

Overall, the suitability index curves presented in this report provide an indication of conditions which make a desirable threespine habitat and conditions which make a less desirable habitat. Also, although the curves are general, they can show differences in habitat needs among threespines and other species. Further, the process of constructing these curves is beneficial in defining areas where more data is needed. Lastly, these curves can aid in the design of experiments and sampling programs. As more data becomes available, these hypothetical curves can be further refined.

Table I. THREESPINE STICKLEBACK

Adult - Spawning

Parameter	Observed Values	Remarks	Location	Reference
Temperature, °C	ca. 12 - 18	surface water temperature during breeding season	Lower Jean Lake	Cannon (1981)
	5.6 - 22.8 3.3 - 13.9	surface water temperatures during June and July	Bare Lake Karluk Lake	Greenbank and Nelson (1959)
	16	average during breeding season	Little Campbell River, B.C.	Hagen (1967)
	16 - 19	during spawning season	Hobson's Brook, England	Lindsey (1962)
Water depth, cm	4	shallowest nest	Little Campbell River, B.C.	Hagen (1967)
	24	average depth for nests		

Table II. THREESPINE STICKLEBACK

Incubation of Embryos

Parameter	Observed Values	Remarks	Location	Reference
Temperature, °C	16 - 26	best survival rate	Belgium (laboratory)	Heuts (1947)
	10 - 14	no eggs successfully reared	England (laboratory)	Lindsey (1962)
	16 - 18	survival less than optimum		
	20 - 26	best survival		
	28	no eggs successfully reared		
	> 22	lower male:female ratio than fish reared at ≤20°C		
	16 - 26	optimum development temperatures; the fish with fewer maternal plates having higher optimum temperatures		
	0, 33	exposure to these temperatures for 1.5 - 3.0 hours causes abnormal development	England ? (laboratory)	Swarup (1958 and 1959, cited by Wootton, 1976)
	8	time to hatching is 15 - 43 days	various	Wootton (1976)
	5	time to hatching is 5 days		
	25	time to hatching is 5 days		
	13 - 18	approximate surface water temp. during incubation period	Lower Jean Lake	Cannon (1981)
	12 - 18	approximate surface water temp. during incubation period	Johnson Lake	Engel (1971)

Table II. Cont'd THREESPINE STICKLEBACK

Incubation of Embryos

Parameter	Observed Values	Remarks	Location	Reference
Temperature °C	12 - 18	approximate surface water temp. during incubation period	Scout Lake	
	7 - 15	approximate surface water temp. during incubation period	Bear Lake	
	6? - 23	approximate surface water temp. during incubation period	Bare Lake	Greenbank and Nelson (1959)
	4? - 15	approximate surface water temp. during incubation period	Karluk Lake	
	10 - 14	approximate surface water temp. during incubation period	Wood River lakes	Rogers (1968)
	9 - 18	approximate surface water temp. during incubation period	Lake Nerka	Burgner (1958)
	12 - 15	approximate surface water temp. during incubation period	Black Lake	Parr (1972)
	9 - 13	approximate surface water temp. during incubation period	Chignik Lake	

Table III. THREESPINE STICKLEBACKS

Adults

Parameter	Observed Values	Remarks	Location	Reference
Temperature, °C	27.2	Upper lethal temperature for the *trachurus* (?) form acclimated to 20°C in freshwater	Halifax, Nova Scotia (laboratory)	Jordan and Garside (1972)
	25	tolerable	general	Bertin (1925, cited by Coad and Power, 1973)
	25 - 28	The *leiurus* form collected at 0° and placed into water with these temperatures died after an average of 40 hours; fish with fewer lateral plates survived longer than fish with more plates	Belgium (laboratory)	Heuts (1947)
	7.0	mean growth efficiency of 5.9%	?	Cole (unpublished, cited by Wootton, 1976)
	20.0	mean growth efficiency of 11.3%		
	11 - 12	rate of stomach evacuation was 16 hours	?	Beukema (1968, cited by Wootton, 1976)
	18 - 20	rate of stomach evacuation was "one night"		

Table III. Cont'd THREESPINE STICKLEBACKS

Adults

Parameter	Observed Values	Remarks	Location	Reference
Temperature, °C	6.9 - 17.7	early June-mid-July; observed water temp. fish present	Lower Jean Lake	Cannon (1981)
	3.9 - 15.0	Jun 1 - Sep.15; observed water temp. fish present	Johnson and Scout lakes	Engel (1971)
	8.9 - 18.3	Jun 1 - Sep.15; observed water temp. fish present	Bear Lake	
	4.4 - 22.8	mid May - mid Sept.; observed water temp. fish present	Bare Lake	Greenbank and Nelson (1959)
	3.3 - 15.0	mid May - mid Sep.; observed water temp. fish present	Karluk Lake	
	6.7 - 14.2	Aug., observed water temp. fish present	Wood River lakes	Rogers (1968)
	0.0 - 20.0	Jun - Sep; 6 yrs; observed water temp. fish present	Lake Nerka	Burgner (1958)
	11.5 - 15.0	early Jul - early Sep.; observed water temp fish present	Black Lake	Parr (1972)
	9.0 - 13.0	late Jun - early Sep.; observed water temp fish present	Chignik Lake	

Table III. Cont'd THREESPINE STICKLEBACKS

Adults

Parameter	Observed Values	Remarks	Location	Reference
Water Depth, m	0 - 21.3 (bottom)	summer	Lower Jean Lake	Cannon (1981)
	0 - 4.0 (bottom)	summer	Johnson Lake	Engel (1971)
	0 - 6.1 (bottom)	summer	Scout Lake	
	0 - 18.3 (bottom)	summer	Bear Lake	
	0 - 24.4	summer	Karluk Lake	Greenbank and Nelson (1959)
	38.4, 61.0	none caught; summer		
	7.3	greatest depth at which fish were caught; summer	Lake Nerka	Burgner (1958)
	0 - 10	Jun - Sept.	Kamchatka Lakes, USSR	Krokhin (1957)
	50 - 60	Dec., Jan., Feb.		
Current Velocity, cm/sec (stream population)	3	average in leiurus habitat	Little Campbell River, B.C.	Hagen (1967)
	23	marginal habitat		
	74	poor habitat		
	92	fish were able to negotiate a 70 m culvert with this velocity		

Table III. Cont'd THREESPINE STICKLEBACKS

Adults

Parameter	Observed Values	Remarks	Location	Reference
Dissolved Oxygen mg/l	0.25 - 0.50	minimum level tolerable	Great Britain	Jones (1948 and
	0.3	level at which avoidance response is triggered at low temps.	(laboratory)	1952, cited by Wootton, 1976)
	2.0	level at which avoidance response is triggered at 20°C		
	8 - 12	fish most abundant in reaches with this level	England	Lewis et al., (1972)
	6 - 8	fish less abundant in reaches with this level		
	2 - 5	fish absent from reaches with this level		
	3.0 - 6.5	healthy fish caught near lake bottom at this level; summer	Lower Jean Lake	Cannon (1981)
	10.1 - 14.0	level above thermocline, summer		
pH	< 5.6 or > 11.4	avoided by fish	Great Britain (laboratory)	Jones (1948, cited by Wootton, 1976)
	6.8	measured value	Little Campbell River, B.C.	Hagen (1967)
	6.3 - 7.0	measured value	Kenai Peninsula lakes	Engel (1971)
	7.0 - 8.7	measured value	Karluk and Bare lakes	Greenbank and Nelson (1959)

THREESPINE
STICKLEBACK

INCUBATION

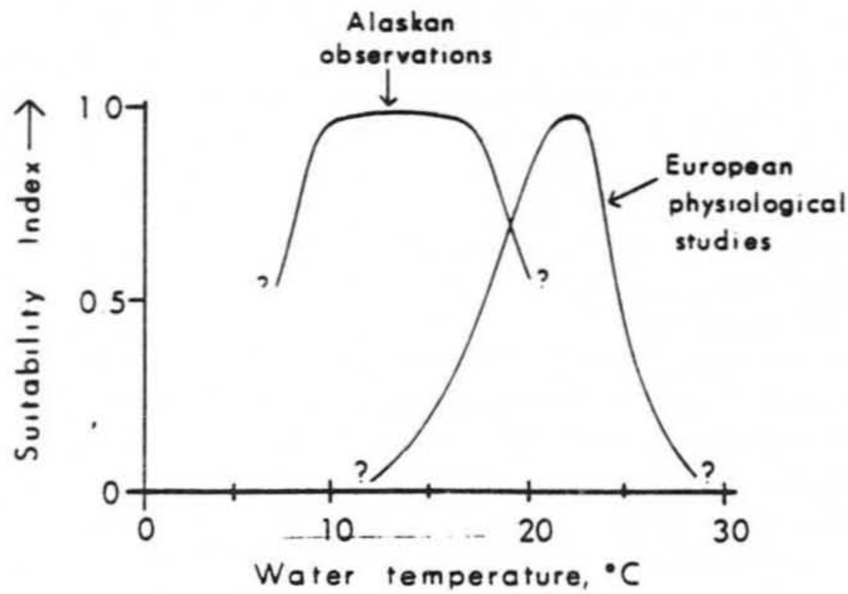

Figure 2. Conceptual model of relationship between Threespine stickleback embryos and temperature.

See text for qualifications for use of this curve
(NOT RECOMMENDED FOR APPLICATION TO SPECIFIC WATERSHEDS WITHOUT FIELD VERIFICATION)

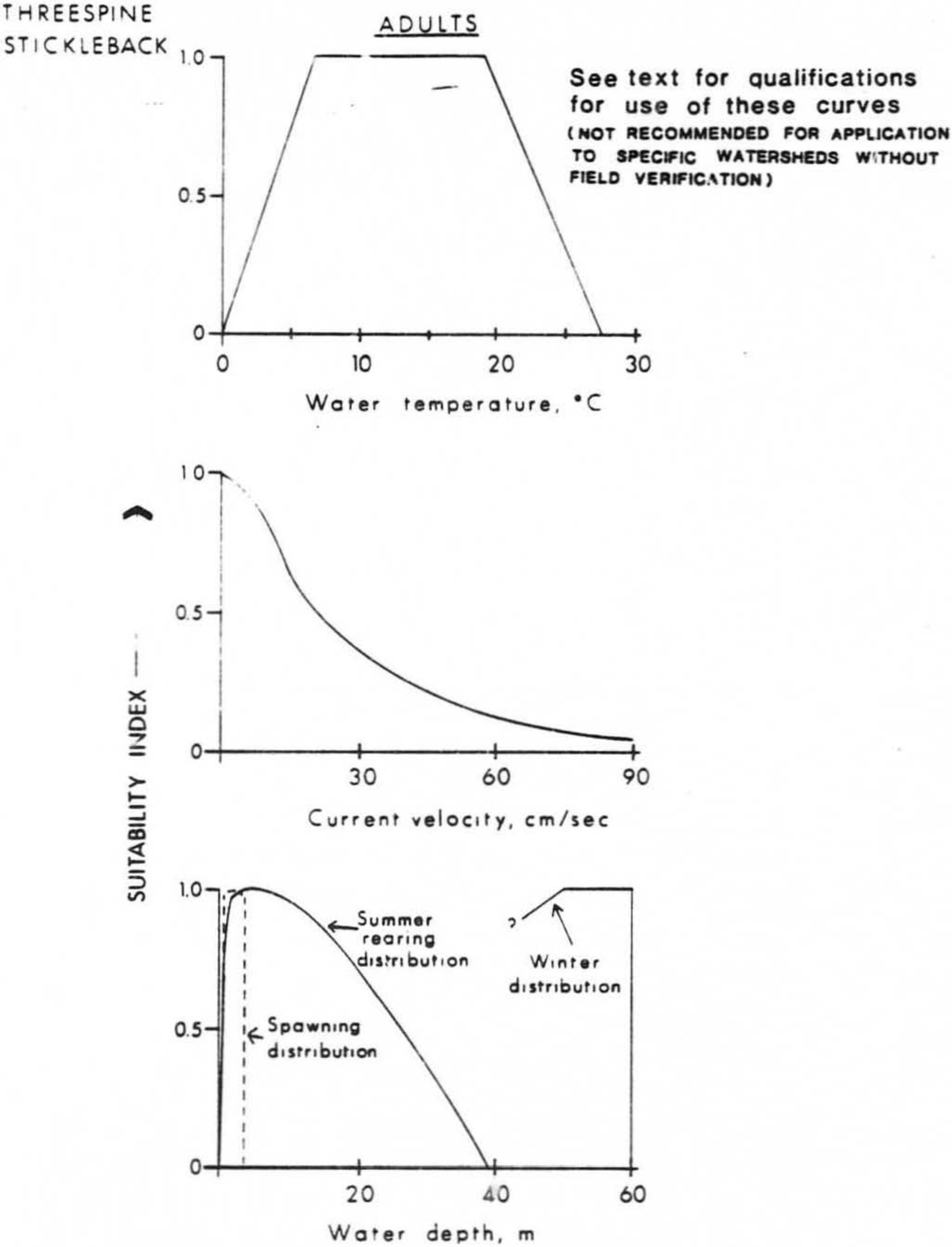

Figure 3. Conceptual model of relationship between Threespine stickleback adults and water temperature, current velocity (stream populations only), and water depth.

THREESPINE
STICKLEBACK

See text for qualifications for use of these curves
(NOT RECOMMENDED FOR APPLICATION TO SPECIFIC WATERSHEDS WITHOUT FIELD VERIFICATION)

ADULTS

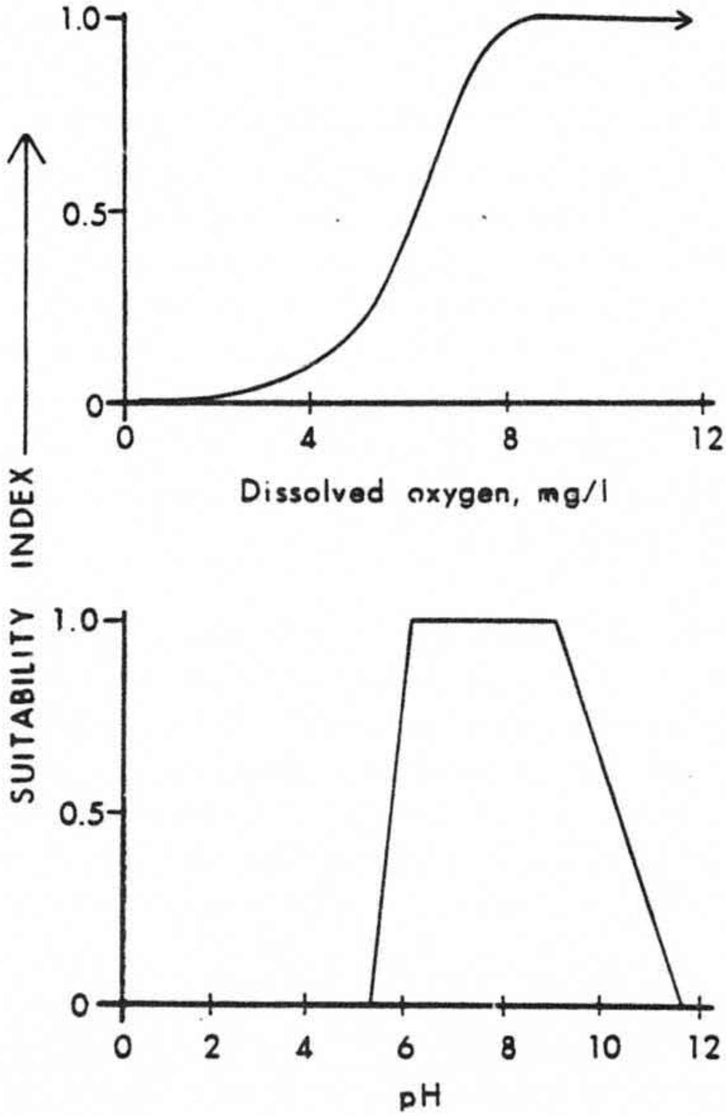

Figure 4. Conceptual model of relationship between Threespine stickleback adults and dissolved oxygen concentration and pH.

IV. DEFICIENCIES IN DATA BASE AND RECOMMENDATIONS

Although extensively used in behavioral and pollution studies elsewhere, the interest in the threespine stickleback in Alaska has centered mainly on its supposed role as a competitor with rearing sockeye salmon and rainbow trout. These Alaskan studies, therefore, have naturally concentrated on the distribution and feeding of sticklebacks.

Physiological studies on Alaskan populations are needed to define the tolerances to environmental parameters such as temperature and dissolved oxygen concentration. This need is dramatically shown by the difference between European physiological studies of temperature tolerance and the known temperature regime existing in Alaskan lakes where the sticklebacks are present (Fig. 2).

Information is needed on stream populations of threespine sticklebacks within the State. To date, Statewide investigations have concentrated on lake populations.

More data from Southeast Alaska is needed to describe regional differences within the State. The Southeast populations may be more similar to the populations described in British Columbia than they are to the Bristol Bay populations. Additionally, there is some indication that sticklebacks in the Kenai Peninsula area are exposed to and adapted to higher temperature regimes than sticklebacks in the Bristol Bay area.

A study in Alaska of differences in habitat requirements among the three forms of *Gasterosteus aculeatus* (*leiurus*, *trachurus*, and *semiarmatus*) would be beneficial as strong differences have been demonstrated elsewhere; for example, Hagen's (1967) work in British Columbia. Virtually nothing is known of the populations on the Seward Peninsula and Saint Lawrence Island (presumably *trachurus*). Because these populations are on the edge of the species range, studies of these fish may provide interesting information about the environmental limits of the species.

Very little information is available on the habitat needs of the threespine stickleback during the stage immediately after hatching but prior to leaving the nests. During this period, they are still under the parental care of the male. There are also many questions about their life history between leaving the nest until they first begin to show up in minnow traps and fyke nets as young of the year. In Alaska, few observations have ever been made of actual nests.

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