

Drizzle Lake

Ref. No.:

154

ECOLOGICAL RESERVES COLLECTION
GOVERNMENT OF BRITISH COLUMBIA
VICTORIA, B.C.
V8V 1X4

DRIZZLE LAKE ECOLOGICAL RESERVE

INTERIM RESEARCH REPORT

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May 23, 1977

208

CONTENTS

1. General
2. Faunal Inventory
3. Floral Inventory
4. Observations on the nesting habits of the red-throated loon
5. Aspects of the species and sex differences in colour among some aquatic birds
6. Studies on Gasterosteus
 - (a) Drizzle
 - (b) Boulton
7. Proposed research for the 1977-78 year

1. GENERAL

In continuation of the work begun in 1975, the research at the Ecological Reserve at Drizzle Lake has included basically a faunal and floral inventory, systematic sampling for fish species, and natural history observations on certain divers. A proportion of the grant was used for float plane rental, owned by Robert Dalgleish, in order to sample lakes on the west coast of Moresby and Graham Islands.

A population of Gasterosteus in Boulton Lake, 20 km south of Drizzle Lake, was extensively surveyed and sampled. To the present, much of the following discussions on pigmentation patterns in relation to predator-prey interactions, will be based on the analysis of samples from Boulton Lake. The comparative samples from Drizzle Lake have not yet been examined.

There have been two major pieces of equipment purchased from the grant including a \$250 balloon trawl, and a \$130 spotting scope. Both of these have provided considerable assistance in the research.

2. FAUNAL INVENTORY

Species	Numbers
<u>Ursus americanus</u>	3
<u>Odocoileus hemionus</u>	28
<u>Procyon lotor</u>	1
<u>Peromyscus maniculatus</u>	many
<u>Sorex</u> sp	1
<u>Myotis lucifugus</u>	6

Aves

Resident	
<u>Gavia immer</u> (2 pairs nesting)	13
<u>Gavia stellata</u> (2 pairs nesting)	10
<u>Podiceps grisegena</u>	4
<u>Phalacrocorax auritus</u> (juvenile)	1 (Nov.-Mar.)
<u>Branta canadensis</u> (4 pairs nesting)	app. 25 (night only)
<u>Anas platyrhynchos</u>	7
<u>Bucephala albeola</u>	4
<u>Dendragapus obscurus</u>	3
<u>Grus canadensis</u> (prob. nesting)	4
<u>Megaceryle alcyon</u>	5
<u>Sphyrapicus varius</u>	app. 20
<u>Corvus corax</u>	app. 15
<u>Parus atricapillus</u>	common
<u>Parus rufescens</u>	common

<u>Troglodytes troglodytes</u>	2
<u>Turdus migratorius</u>	8
<u>Regulus satrapa</u>	1
<u>Spinus pinus</u>	common
<u>Junco oreganus</u>	common

Occasional visitors

<u>Podiceps auritus</u>	2
<u>Anas acuta</u>	4
<u>Mareca americana</u>	2
<u>Anas carolinensis</u>	1
<u>Aythya marila</u>	4
<u>Bucephala clangula</u>	2
<u>Bucephala albeola</u>	15
<u>Melanitta deglandi</u>	2
<u>Mergus merganser</u>	6
<u>Accipiter gentilis</u>	1
<u>Buteo jamaicensis</u>	1
<u>Haliaeetus leucocephalus</u>	8
<u>Larus argentatus</u>	12
<u>Colaptes cafer</u>	4

Pisces

<u>Gasterosteus aculeatus</u>
<u>Oncorhynchus kisutch</u>

Salvelinus malma

Salmox clarki

Herbs

Bufo boreas

3. Floral Species Observed in 1976

S	Species	Abundance
	<u>Kalmia polifolia</u>	xxx
	<u>Ledum groenlandicum</u>	xxx
	<u>Gaultheria shallon</u>	xxx
	<u>Andromeda polifolia</u>	xxx
	<u>Calypso bulbosa</u>	x
	<u>Dodecatheon jeffreyi</u>	x
	<u>Nuphar</u> sp.	xx
	<u>Menziesia ferruginea</u>	xx
	<u>Vaccinium oxyococcus</u>	xxx
	<u>Vaccinium parvifolium</u>	xx
	<u>Vaccinium uliginosum</u>	xxx
	<u>Empetrum nigrum</u>	xxxx
	<u>Cornus unalaschensis</u>	xxx
	<u>Rubus chamaemorus</u>	xx

4. OBSERVATIONS ON THE NESTING HABITS OF THE RED-THROATED LOON

Bristol - I am sorry but I came to write this up from my diary, I found that on June 30, 1976 I started a new book and I only have this one with me, the other being at Drizzle. It is important as it has all the dates when the eggs first appeared and subsequently lost and some of the interactions at various times during the incubation. So I will have to wait until I get back to the Charlottes to write this one.

Sorry about this.

5. ASPECTS OF THE PLUMAGE COLOURATION IN SOME AQUATIC BIRDS

The wide diversity of colour patterns in aquatic birds has not received much attention in respect to the adaptive significance of such characters. Two prevailing explanations in the literature involve camouflage and species or sex recognition. The former is probably best exemplified by the well countershaded common murre, with its characteristic dark back and white breast, and the females of numerous species of ducks which appear well camouflaged during their nesting period. The remaining species in which the colour bears no obvious relationship to the background have been most conveniently explained as an adaptation for conspecific or sexual recognition. Some obvious examples of these would be the conspicuous colour patterns of the male buffleheads, mallards, goldeneyes, canvas backs, etc. The recognition hypothesis is popular as it allows an explanation for all variations in colour pattern and tone. Yet another concept, not dissimilar from the recognition hypothesis, is one involving a thermoregulatory function in which the prevalence of white and dark colours in these birds is interpreted as an adaptation to absorb or reflect heat from the sun. Again, this explanation is popular among physiologists and can account for any colour pattern.

During the course of the research at Drizzle Lake, it has been possible to observe some species of birds in a wide range of lighting conditions, and in interactions with some of their predators. The species include the red-throated loon (Gavia stellata), the common loon (Gavia immer), the red-necked grebe (Podiceps grisegena), the

bufflehead (Bucephala albeola), and the kingfisher (Megaceryle alcyon). As a result of some of these observations, there are some suggestions that the differences in colouration between the two species of loons, the throat colouration of the grebe, and the sexual dimorphism the bufflehead and kingfisher may have an additional adaptive function besides the species or sex recognition hypotheses which have become tacitly assumed.

Loons and Grebes

For a piscivorous bird such as an alcid, or diver, the advantage of countershading is well established. Selection has favoured colour patterns which serve to maximize the probability of successful prey capture by allowing a close approach to the prey. These demands for prey capture in the alcids must have a greater value than any selection for a sexual dimorphism in colour such as is observed in the ducks. In fact the majority of piscivorous birds show no obvious sexual dimorphism in colour. This broad assemblage includes the orders Gaviiformes, Podicipediformes, Procellariiformes, Pelecaniformes, Ciconiiformes, and the families Laridae (in respect to terns), Rynchopidae, and Alcidae. The only exceptions appear to be the subfamily Merginae, and the family Alcedinidae, the mergansers and the kingfishers. The selective pressures have generally favoured a common pattern for the two sexes. If one can assume therefore that the demands of a piscivorous existence are indeed strong, is it reasonable to suppose that the differences between species such as the common loon and red-throated loon, the western grebe and red-necked grebe can be satisfactorily explained as species recognition. Superficially, there

would appear to be some merit in this explanation as the differences between the species occur only in summer or during breeding when such differences might indeed be required if there is overlap in the breeding distributions. When these species leave the fresh-water habitats in fall and return to a marine habitat, there is a major convergence in colouration to that approaching the winter plumage of most alcids, that is, a simple countershading with a dark dorsal surface and a white ventral surface.

Considering the changes in colour of the red-throated loon from winter through to summer, it appears peculiar that this species should alter its throat colouration to what would appear to be a more conspicuous form at a time when its energy demands must equal, if not exceed, those in winter. This species does fish extensively in fresh-water systems not only for its own requirements but also for the young. At Loulton and Grizzle Lake, the incidence of dives is much more frequent when young are present than for an equivalent time period during winter when the birds are found on the ocean. This change in throat colouration may relate to changes in the prevailing wavelength distribution of the light between the marine and fresh-water habitats as the following discussion suggests.

Muskeg Lakes, the most common habitat for the red-throat in summer, are typically tea-coloured from the effects of the muskeg run-off. If one snorkels in this water, it is immediately apparent that the dominant hues are of a reddish nature. This has been documented by others in inland lakes, and work with spectrophotometers show a strong absorption of the shorter wavelengths such as the blues and a greater transparency to the longer wavelengths, resulting in a shift to the red

end of the spectrum. Mountain Lakes and the oceans show the opposite trend with a strong absorption of the reds and a transmission of the blues giving the typical bluish or clear colouration. The red hue in the muskeg lakes appears more pronounced in water less than 1 meter in depth, or at least in those conditions where the bottom is visible, as there is a greater reflection and scattering of the light off the bottom. In waters of greater depth, the light is almost entirely absorbed in the upper 1.5 m resulting in a very dark appearance to the water beneath this depth.

Another factor influencing the water colouration in these lakes is the roughness of the surface waters. In an attempt to gain some comprehension of the fishes visual world some shallow water diving was carried out in a very sheltered bay at Drizzle Lake and one in which the surface waters were rippled from the effects of wind. In the sheltered bay, again in shallow water where the bottom was visible, when one looks upward at the surface at an angle less than 45 degrees above the horizontal, what is visible is not the background above the surface, but rather the mirror reflection of the bottom, in this case sand with a reddish hue. Only in a narrow angle around a vertical view was it possible to see light directly entering the water, this light being predominantly white with only a light reddish hue. This reflection of the bottom was present only when the surface waters were glass calm. All of the incident light which strikes a mirror surface at an angle less than 30 degrees is reflected back. If one is then to predict the optimal colouration that a fish eating bird should exhibit in these set of conditions, it should show a colouration on

its ventral surface (at least towards its anterior end), that most resembles its background, that is, one with a reddish hue. This red background is even more pronounced at dawn and dusk when the incident light through the atmosphere displays a shift to the longer wavelengths.

The visual background from the more exposed bay in which the surface waters were rippled, was quite different from the sheltered bay. Although a horizontal view showed a reddish hue, when looking towards the surface there was no reflection off the bottom but rather the background from above the water surface was seen. In addition there appeared to be an increase in the total amount of light entering the water presumably owing to the rippled surface which allowed a greater capture of the light, with less reflection off the surface. At dawn and dusk, when the sun was near the horizon, most of the incident light which struck the sheltered bay was reflected off the surface, while in the rippled bay much of this light was captured. When one moves to slightly deeper waters, whether in calm or rippled conditions, there is no reflection off the bottom when looking towards the surface, but rather an appearance of that approaching the incident light. For example, if there was cloud cover, the surface appeared a dull white, while if the sky was blue, the surface appeared principally white with a slight bluish-green tinge and also a faint tinge of red.

These observations provide some explanation for differences between the two species of loon and the ventral colouration of the grebe. From a partial inventory on some of the Charlotte Lakes, one broad generalization emerges from the breeding distribution of the

common and red-throated loons. The latter is found mainly in small muskeg lakes usually less than $\frac{1}{4}$ square kilometer and often surrounded by stands of sitka spruce. Examples of these included Loon Lake, Boulton Lake, Stellata Lake, and Lac la Rouge. They are also found occasionally in the larger muskeg or stained lakes such as Lower Victoria. The common loons have not been seen in these small lakes but only on the larger lakes both stained and bluewater. Example: include Drizzle, Mayer, Lower and Upper Victoria. These larger lakes are usually seen with rippled surfaces and only on rare occasions glass calm, as is usually the case in the small sheltered lakes. Broadly speaking therefore, the red-throated loon is found in those habitats which from the shallow, stained, and calm nature of the waters should favour a ventral colouration including a large component of red. The common loon on the other hand is found in the larger lakes which are more often rippled, and thus having few conditions where the bottom is reflected and the red background most expressed. They are also more likely to be found in the bluewater lakes where the optimal strategy for countershading is typically that of white ventral surface. The red-necked grebe is found in close association to the red-throat but also in larger lakes with the common loon.

More specifically, what visual interactions would likely occur between a prey item such as a stickleback and a fish eating bird in a lake like Drizzle. The loon, when diving, swims in a horizontal plane close to the surface and from observations with a spotting scope shows only slight tendencies for turning. There would appear to be a

limited field directly in front of the loon in which the stickleback would be at risk. Those directly below or on the side of the loon's visual field should be less likely to be captured. A fish in direct line of a loon's hunting foray would be confronted principally with head on view of the loon in which the bill, neck, and anterior parts of the breast would be visible. It seems possible that since the most prevalent hue to the background is reddish, the throat colouration serves to break up the outline of the loon's body. It would be of interest to determine whether the neck feathers are flared during the dive judging from the type of propulsion that they utilize.

While the loon makes long, semi-unidirectional dives, the red-necked grebe often makes dives of equivalent time span but surfaces often near the place where the dive was begun. Therefore, the grebe must be multi-directional in its dives using more a three-dimensional foray including all components to not only the horizontal field but also the vertical one. It would seem that a stickleback directly below a grebe has a higher probability of capture than in a similar position with a loon. The extensive red colouration on the neck in comparison to the loon may pertain to this manoeuvrability component. The horned and eared grebe, which are considerably smaller than the red-necked and may be expected to show yet greater manoeuvrability, and have an even more pronounced redness on the ventral surface. The western grebe, on the other hand, is much larger than the red-necked and shows a colouration similar to the common loon. From observing this species in the ocean, they usually make very long distance dives and may lack the manoeuvrability of the smaller grebes. In contracts, however, the

smallest grebes, the pied-billed and the least, show no red colouration on their ventral sides and presumably feed on small fish as the larger grebes. The bill shape of the pied-bill may, however, reflect less of a piscivorous nature and more of a crustacean feeder where the colour strategy would be of a defensive nature rather than for an aggressive camouflage. At least on the red-necked grebe where observations have been made, it seems eminently feasible that the red colouration is an adaptation for minimizing the approach distance to their prey in a habitat which predominates in reddish hues. Observations on the spatial hunting positions of the red-neck show it to be in the shallows of both Drizzle, Doulton, and Mayer Lake in waters less than 2 m in depth. It is also most likely to be found in sheltered bays. In each of those situations, the former where light is reflected off the bottom, and in the latter where the surface is calm and a mirror image exists of the bottom, the red hues predominate.

There are differences in the hunting areas of the red-throat and the common loon at Drizzle Lake. Throughout the summer, the majority of dives observed of the red-throat were within 50 m of the shoreline. The common was seldom seen in these situations except when returning to its nest site. It was more often found near the center of the lake which varies from 10-30 m in depth. It would seem contradictory at first sight that the common loon with its white ventral surface should be as well as adapted to a fish-eating existence as a red-throat in waters which show a strong red component. This is not the case for the center of lakes usually contain waves which provide an increased intensity of incident light: the water when viewed from beneath the surface is usually similar in hue to the sky conditions. The absence

of a reflected bottom also reduces the effect of the longer wavelengths. There may be other factors which allow the common loon an alternate strategy for prey capture.

Throughout the summer, the common loons from Drizzle Lake were observed to leave the lake and fly westward presumably to Masset Inlet. Usually within 2 hours they returned to the lake. These short flights may suggest that the species is hunting some of the time in a marine habitat. This was also observed for the red-throated loon at Stellata Lake where an adult left this small sheltered waters for 30 minutes and returned with a 5" flatfish which it proceeded to feed to its mate. The two young were observed to pull at the fish but were not capable of swallowing any portions. It is definite therefore that some hunting does occur by the red-throat in a marine habitat. It will be necessary to determine the incidence of these flights in the two species of loons. If in fact a large proportion of the hunting by one of the parents of red-throats occurs in a marine habitat, some of the suggested colour adaptations will be wrong.

Buffleheads

While the fish-eating birds often show an aggressive camouflage, that is, a colour pattern which allows a minimum approach distance to their prey without detection, most ducks, at least in the females show defensive camouflage, a colour pattern for avoiding detection from predators such as canids, felids, and raptors. The bufflehead Bucephala albeola is one representative of a number of different species of ducks in which the female is typically dark and drab on its dorsal surface with a small white patch on the site of the head, while the male shows a more conspicuous plumage owing to the increased amount of white on

the head and the body.

In many situations where the male and female are encountered together, it is usually the male which is initially observed with the white head standing in contrast to the background. Watching the males in a sheltered bay of a lake or in an estuary, it would seem that the colouration of the male must indeed relate to sexual selection and species recognition as the females so easily merge into the background. It is difficult however to assess the significance of these colour patterns unless some understanding has been gained of the predator-prey interactions, or in other words to view these birds on a background which would be most commonly seen by their predator, a situation not necessarily the same as that seen from a human standpoint.

In the last summer, six encounters have been observed between the bald eagle the small groups of buffleheads, four of these on Drizzle Lake and two on Masset Inlet. Each of these cases involved a high pass over the lake by the eagle terminating when the eagle landed on a snag or trees no closer than 100 m from the birds, and often at much greater distances. The eagles were seen to leave the perch, swoop low over the water and begin a series of very rapid wing beats and increase in speed travelling in the direction of the buffleheads usually within 2 m of the surface. When the small group of birds was approached, the eagle increased its height to about 10 m. At this time the buffleheads either all dove or took to the air. In the former case, the eagle hovered or flew in a tight circle until an individual appeared at the surface. The eagle then dropped down on to the bird, which by this time had dove again. In the other cases where the buffleheads had taken to the air, the eagle singled out an individual and began a rapid

pursuit. Usually within two minutes the exhausted bufflehead plunged back into the water and dove. The eagle hovered again until the bird appeared and again plunged down at the bird into the water. In one situation the eagle performed three plunges before abandoning the attempt. In none of the six cases were any attacks successful.

One method to emulate in part the visual background that an eagle perceives is from a small float plane. During sampling trips to the west coast with float plane, it was possible to assess some of the backgrounds, and what, from shore, appeared to be a rather uniform background, contained a number of different and often discrete components in colour. These different backgrounds were influenced by the smoothness of the surface waters, height above the water, proximity to shore line, direction of movement towards or away from the shore line, and the sky conditions. The amount of staining of the waters does not greatly affect the changes in background colour. What is interesting about these observations is that the females are camouflaged in only some of the backgrounds and quite conspicuous in others, while the males appearing quite conspicuous from the shoreline, are often very well camouflaged from the air.

(a) Approaching the calm waters near the shore line from the central parts of the lake, one is exposed to a very dark-green background from the reflection of the trees. The extent of this reflection is a function of the height above the water, the greater the height, the less the reflection. When one is very near the water surface the entire waters show a dark reflection when looking towards shore. Were a predator to approach from this direction, the most optimal camouflage

pattern of a prey species would be a dark brown-green to black body with a slight mottling as the reflections are seldom a uniform dark colour. When this same approach is carried out, but with rippled waters near the shore line, the background is not dark as no reflection of the shoreline is present. There is instead a reflection of the sky conditions thus exhibiting either a blue or white background depending upon the cloud cover. In this situation, a darkly coloured bird stands out in contrast to the background, while a bird with considerable whiteness blends in.

(b) When the center of the lake is approached from the shoreline, the background is again influenced by the height above the water, the smoothness of the surface, and the condition of the sky. When the lake is calm, and a low pass is made, one observes the reflection of the opposite shore. A slightly higher approach shows a background very similar to the sky conditions. When the lake surface is rough, irrespective of the height, the background is of a very light nature, often blue, with silvery flashes of the sun. In these conditions a more "gaudily" coloured bird is relatively well camouflaged.

These differences observed from the plane were well exemplified in one situation at Drizzle Lake when 10 buffleheads were present in a relatively tight group. From the shoreline, the buffleheads were initially seen very near to shore at the opposite side of a small bay. The five males were immediately apparent and it was not until the spotting scope was used that the five extremely well camouflaged females were seen against the reflected image of the shoreline. It was in fact the slight ripples on the water from the forward movement of the birds which initially brought attention to them. Owing to my

presence the birds moved along the opposite shore in the direction of the bay opening. At this stage, it was still only the males which were visible with the unaided eye. However, as they left the bay, the mirror surface and shore reflection were lost owing a rippling of the now more exposed waters. It appeared startling when the birds crossed into this rippled area for the five females appeared as dark silhouettes against the silvery white background and the five males were no longer visible with the unaided eye. For up to 15 minutes, the birds drifted slowly back and forth between these two very distinct backgrounds with the two sexes totally replacing each other as the most camouflaged.

These lighting conditions were not exceptional and were subsequently seen in most bodies of water including the marine habitat. These observations combined with the hunting forays of the eagle would suggest that more than one strategy for plumage colour is available. It is possible that the males tend on average to prefer slightly more open waters, while the female preferring the sheltered and calm bays or rivers. Observations of this sort will be continued to determine whether any subtle differences occur in the general background colouration of the two sexes. This camouflage hypothesis is not exclusive of the traditional display and recognition explanations for the colours of the males with their white bobbing head would indeed exhibit the most contrasting colours possible. The advantage of this potential double adaptive function is quite apparent for it allows an expression of epigamic characters without the reduced fitness incurred by conspicuous colour patterns. It seems possible that this strategy may occur in other species of ducks, many of which show a dimorphism in

colour similar to the buffleheads. Thayer in 1908, and totally neglected, has indeed proposed that the male mallards, the wood ducks as well as the male peacock are well camouflaged in their restricted habitat.

Boulton Lake

- i. General life history parameters from Boulton Lake stickleback
- ii. Stability of morph frequencies between age classes and years
- iii. Stomach analysis in relation to vertical zonation
- iv. Differential parasitism by Schistocephalus solidus and parasite frequencies of Cyathocephalus and Dunodera in relation to the intensity of bird predation
- v. Predation by dragonfly larva (Aeschna sp.)
- vi. Pigmentation patterns of the stickleback in relation to spine morphology, vertical zonation, and type of predation
- vii. Examination of meristic and morphometric traits of specimens stained and cleared with the trypsin and alizarin technique.

i. Life history parameters

The general life history of the Gasterosteus in this lake is similar to that observed elsewhere for this species. It shows a two year life-span and breeds usually in its second year though some individuals can successfully breed at the end of their first. Breeding season begins in May and lasts through until August, the first young appearing in July. Each female lays approximately 50 - 150 eggs depending upon her adult size. The males construct nests in the shallows around emergent vegetation and beside sunken twigs and logs. As in many of the other Charlotte Lakes only a small proportion of the

males develop a brilliant red throat so characteristic of this species in other parts of the world.

The principal food includes cladocerans (Bosmina), copepods (Cyclops), caddis flies, chironomids, damsel fly larva, small coleopterans, and gamerids. The abundance of each of these items is dependent upon the specific locality of the lake and the time of year. Different age classes consume different instars of the various invertebrate.

The principal cause for the survivorship curve appears to be due to predators including primarily the dragonfly larvae (2 species of Aeschna), and the fish eating birds such as the red-throated loon, red-necked grebe, and belted kingfisher. Other potential predators that have been observed to occasionally take the stickleback are the dytiscus water beetle and leeches. The relative importance of each of these predators has yet to be quantitatively established.

Genetically, this population is completely isolated from other populations except for a potential mixing with the marine form of the species, which could in years of very high water ascend the outlet stream to the lake for breeding purposes. Since 1969, however, no individuals of the marine form have been captured in the lake proper or the outlet stream. The maximum age for this population must lie in the vicinity of 7000 years during the hypsotherm at which time the sea level would have submerged the lake.

The population has a number of unique morphological traits for the species including an absence of the pelvic girdle in about 80% of the individuals, an absence of the second dorsal spine in 70% of the

individuals, and an infrequent disappearance of the 3rd dorsal and anal spines. The population is unusual also in lacking all other types of fish competitors or fish predators.

ii. Morph Frequency Stability

The different spined phenotypes show about the same frequency in 1977 as they did when the population was initially sampled in 1969. It can be inferred therefrom, that we are dealing with a relatively stable polymorphism or at least one which is changing very slowly. In the samples from 1970, a change in the frequency from young through to adult was noted in the dorsal spine morphs, with the three spined phenotype showing a reduction in frequency relative to the two spined individuals. The examination of samples from the last two years shows that this trend is consistent yet with no overall reduction in the fully spined morph from year to year. This would appear to be a reliable case of endocyclic selection which would provide some mechanism for the stability of frequencies.

Females tend to be associated with the presence of a full spined compliment compared to the males. They also show a relative increased incidence of the full pelvic girdle and its spines. They are in effect more similar to the typical form of the Gasterosteus from the mainland and from some of the other lakes on the Charlottes which contain fish predators.

There are ontogenetic changes in the development of the spines. The fry or young of the year up to approximately 15 mm show no phenotypic expression of either the dorsal or pelvic spines. The spines in

fact are well developed but lay underneath a fold of skin. In comparison, young of the year from Mayer Lake even at 10 mm have well exposed spines. This lake contains extensive fish predation on the juveniles.

iii. Stomach Analysis

Attempts have been made to identify each of the common food species and estimate their relative proportions. This is ultimately to determine whether there are consistent differences between the feeding habits of the spined morphs and also to determine the changes with the different age classes.

In 1970 samples the fully spined individuals were observed to feed more extensively on pelagic food items in comparison to the "spinless" morphs which were more often benthic in their food preferences. This trend is not as apparent in the 1976, 1977 samples though a slight tendency does exist. Continuation of the sampling over the year will provide a better means for comparison.

There are expected differences in the food preferences of the juveniles and adults and between males and females at least in the adult stage. The problems encountered to the present result from the sampling techniques which have basically been by trap or seine. Very few individuals from the central parts of the lake have been captured. The purchase of the balloon trawl will alleviate this difficulty and it should be possible to gain a much broader understanding of benthic versus pelagic forms.

Although the cladocerans are more pelagic than the chironomids, this is complicated by the fact that there are diurnal migrations towards and

away from the surface. It is therefore difficult to correlate the vertical feeding positions of the stickleback simply in relation to the stomach contents unless the time of feeding is known. Sampling will be carried out in the following year at various times of the day and night in an attempt to estimate the more general feeding positions of the different spine morphs.

iv. Parasitism

The most common coelomic parasite of the Boulton Lake stickleback is the tapeworm Schistocephalus solidus. The frequency of infection of this parasite indirectly provides an estimate of the intensity of predation by aquatic birds. Its life cycle passes from an agg through to a cyclopoid, then in some cases to a gammerid, through to the fish, and then to its definitive host, a bird, where it reproduces, lays eggs which pass out into the water for the completion of the lifecycle. At present the incidence of parasitism is approximately 15% though in the juveniles it is much lower and in the very large post-reproductive adults, much higher, often reaching 80%. The association observed in the early 1970's showing a statistically greater frequency of S. solidus infection in the fully spined individuals is still present. As the rate of infection reflects the amount of bird predation it seems apparent that the fully spined individuals do indeed undergo a greater amount of this predation in comparison to the more spineless individuals. This bit of information has been the most crucial in the understanding of the multiple predator-prey interactions which exist in this lake. The relative low incidence of parasitism in the juveniles may indicate one of two factors. Either there are developmental limitations in the

growth of the parasite such that there is an insufficient time available for maturation of the parasite or that the lower incidence of infection is an adaptive strategy of the parasite to maximize its probability of being consumed by a bird predator rather than some other predator. A few observations made with the spotting scope on the loons suggest that it is the adult stickleback which are being consumed. If this is the case then a parasite which completes its development in a juvenile will unlikely complete its life cycle. It is possible however that the small stickleback are swallowed both by the grebe, loon, and kingfisher before the birds surface.

A rather trivial observation on stickleback kept in the aquarium would suggest that the juveniles are not subject to at least kingfisher predation. When the hand is passed over the aquarium and the fingers brought in and out from a fist position, a poor attempt to resemble a hovering kingfisher, the young in the tank show no avoidance response whatsoever but the adults become highly agitated attempting to leap from the aquarium or dig into the bottom. This response is a very consistent one, the adults seldom showing any habituation to repeated movements of the hand. It would seem reasonable that this behavioural response reflects some interaction with a predator that hunts from above. The energetics would also suggest that the adults would be more prone to bird predators as the energy expenditure of a single dive, especially with a kingfisher, would not be replaced with a 16 mm juvenile stickleback.

There are two intestinal parasites, Bunoderina, and Cyathocephalus, the latter unreported in Gasterosteus according to a colleague in Edmonton. They show no differential infection with spine morphs though a slight negative correlation with the presence of Schistocephalus. These two species of parasite do not require a bird as a final host but complete their lifecycle in the fish.

v. Predation by Dragonfly Larvae

The wide occurrence of this larvae in Boulton Lake and repeated examples of predation in the aquarium and in minnow traps suggest that this is an important predator of the stickleback. Individuals in the aquarium consume an average of one juvenile stickleback per day. Adult fish are often attacked and killed though only partially eaten. From observations in the aquarium on the hunting strategy of the larvae, it became apparent that spined and spineless fish would not be equally susceptible to this predator. The spines on the fish allow the larvae a means for grasping the fish and would seem to be a distinct disadvantage for the stickleback. Spineless individuals, although often successfully attacked would in theory be more prone to escape as most of the body surface is smooth allowing little opportunity for the grappling larvae to hold the fish.

Experiments were planned for this last year involving young of the year fish. Unfortunately only a few of these fish were captured and the experiments lack the replicates required for analysis. The balloon trawl should provide large numbers in the coming year.

The experiments which were completed showed that the larvae, varying in length from 35-45 mm, had a marked preference for the smallest stickleback in the tank. Fish from 20-30 mm were readily captured and consumed. Adult fish were left in the tank for up to two months and not attacked or captured by larvae which were being fed juveniles. When the juveniles were no longer supplied some of the adults were attacked and partially consumed. A group of ten larvae were held in an aquarium at Drizzle Lake from November through until April with one adult stickleback. The fish showed no sign of external injury, yet the first juvenile which was added was immediately captured and eaten.

In the experiments where both spined and spineless juveniles were supplied there was a trend though not significant for the spined individuals to be more heavily predated when the water level was less than 30 mm in depth. When the water level was at least one-third of a meter the spineless were more heavily consumed. These differences appear to be owing to a difference in the vertical zonation of the morphs with the spineless individuals being found near the bottom, the same place in which the larvae are found. The larvae are therefore feeding on that which is available. More experiments with young of the year should a more reliable statistical measure of the relative fitness of the two morphs in respect to this predator.

Another factor which would suggest the advantage of a reduced spine compliment is the delayed expression of the spined in the juveniles. A great deal of elimination has already occurred by the time the population of juveniles reaches 15 mm in size. Were the spines to be advantageous,

at this early stage, selection would have favoured their phenotypic expression as the spines are fully developed but retained with a fold of skin. It would seem rather that the spines are a disadvantage at the early length classes perhaps owing to the predation of Aeschna larvae, themselves of the early instars rather than the 40 mm individuals which are most commonly seen in the traps.

Returning to the incidence of parasitism, the reduced frequency in the spineless individuals, at least of the Schistocephalus, would appear an adaptive strategy for the parasite if this morph does incur greater elimination by the larvae. This would result in the death of the parasite as the larvae would consume it would the fish.