INTERTIDAL CHIRONOMIDAE OF THE BRITISH COLUMBIA COAST

by

RICHARD LORNE MORLEY

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INTERTIDAL CHIRONOMIDAE
(DIPTERA) OF BRITISH COLUMBIA

R.L. Morley

Supervisor: Assistant Professor Richard A. Ring

ABSTRACT

Intertidal Chironomidae (Diptera) are represented on the coast of British Columbia by *Paraclunio alaskensis* Coquillett and *Saunderia pacificus, S. marinus* and *S. clavicornis* Saunders. The larvae of these species can now be easily separated using the labium as a major taxonomic character.

These species inhabit a variety of rocky shore types, being found on exposed as well as protected shores. Their range includes the Queen Charlotte Islands, although *P. alaskensis* was collected only on the most southerly end of these Islands. *S. clavicornis* is the most common of the four species.

Within their habitat larval distribution is contagious and is well described by the negative binomial distribution. It is probable that the "clumped" larval distribution is due to environmental factors rather than active aggregation.

Adult emergences occur throughout the year but are most extensive in the fall and smallest in the spring. Generally, the larval population fluctuations follow the adult emergence trends. It is hypothesized that the fluctuations in larval populations are caused by a combination of overlapping multiple generations occurring in the field and differential larval growth rates at fluctuating temperatures.

Larvae of these species feed upon green algae (*Enteromorpha linza, E. intestinalis, Ulva* sp., etc.) as well as diatoms (*Navicula* sp., *Melosira* sp., etc.), but it has been shown that diatoms are their main food source.

Among the predators of these insects are mites, intertidal sculpins and young salmon. It has been suggested that salmon feed extensively on intertidal Chironomidae during the summer months and as demonstrated in this study the chironomid populations are largest at this time of the year.

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Finally, without my wife's support this work would never have been completed.

INTRODUCTION

An intertidal insect can be defined as any insect which spends at least part of its life cycle in the littoral zone (Newell, 1970) and is periodically covered by tidal seawater. Generally, entomologists and marine biologists have neglected these animals and although they are only a small part of the insect fauna they are of world-wide distribution. In addition, the group provides good material for studies of the phenomenon of lunar periodicity which has been demonstrated in some intertidal chironomids (Oka and Hashimoto, 1959; Hauenschild, 1960; Neumann, 1967), and of the changes that have occurred as a result of their adaptation to the sea.

The intertidal insects in this study are members of the Chironomidae (=Tendipedidae), (Diptera), a large family of nematocerous Diptera. Adult chironomids have reduced mouthparts and do not feed. Their life span is ephemeral, virtually the only activities being dispersal, copulation and egg-laying. The larvae are aquatic and are most abundant in the shallow waters of lakes, ponds, and streams. They are important as food for fish and may be the exclusive food of adult bass, trout and whitefish (Usinger, 1956).

In general taxonomists agree that the North American chironomid fauna is not well known, especially the subfamilies Diamesinae and Orthocladiinae (Beck and Beck, 1968; Saether, 1969) and a number of major revisions of this taxonomy have been made. (Johannsen, 1937; Townes, 1945; Pagast, 1947; Wirth, 1949; Brundin, 1956, 1967; Hamilton, et al., 1969; Saether, 1969).

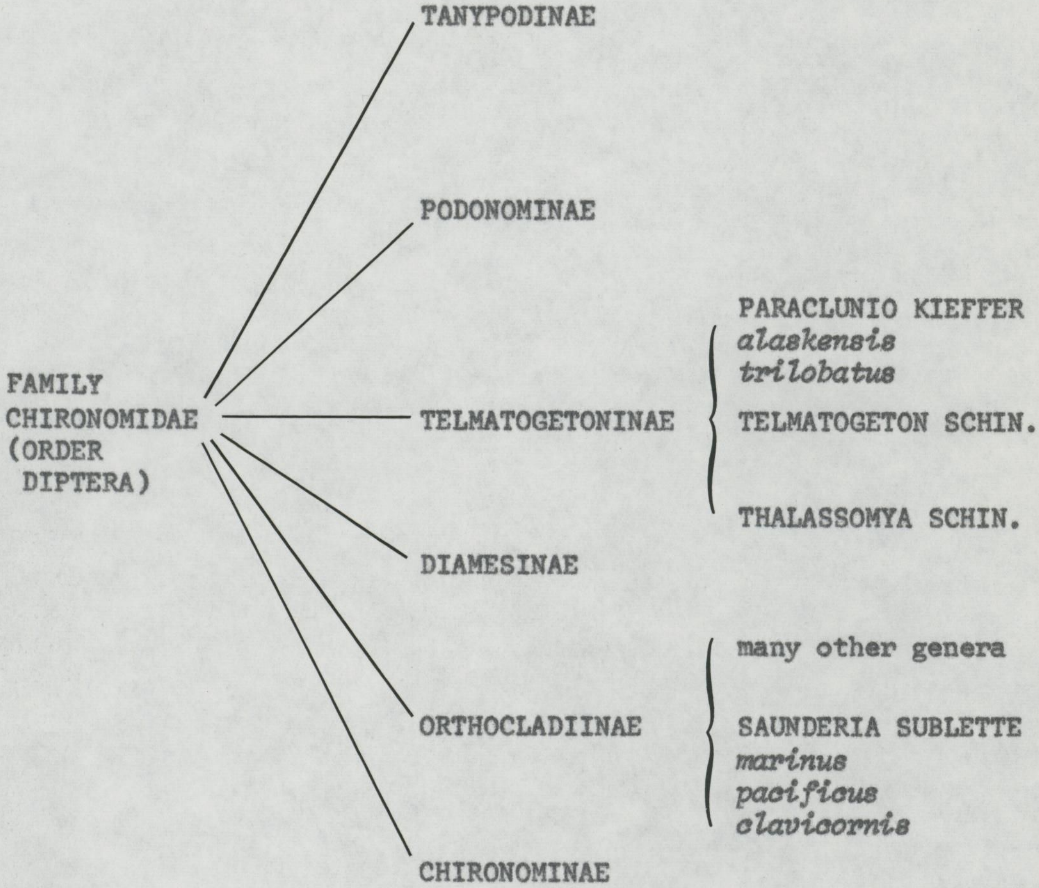
There have been two predominant schools of thought, the German which emphasized the importance of immature stages and the British and American, which emphasized the adult features. Although Brundin has attempted to reconcile these two systems the taxonomy remains problematical. The system proposed by Hamilton, Saether and Oliver (1969) for nearctic Chironomidae has been followed in this study. Fig. 1 presents a synopsis of this system as it relates to the species being studied.

Of all marine insects the Chironomidae show the most complete series of adaptations to the marine environment. Hashimoto (1969) presents the hypothesis that marine chironomids are divided into three ecological types each showing a greater degree of adaptation to the marine habitat. There is the Flying Type, in which the legs are used only for support and which swarm during mating (eg. *Tanytarsus* spp., *Chironomus* spp., etc.), the Walking Type, with legs modified for movement over the intertidal zone and which mate on the substrate (eg. some *Saunderia* spp., *Paraclunio* spp.), and the Gliding Type, in which the male's legs are modified for gliding on the water surface; the female is vermiform, and mating again taking place on the substrate (eg. *Clunio* spp., *Pontomyia* spp.).

Two genera are reported in this study: *Paraclunio* (Kieffer), which has one local species, *P. alaskensis* Coquillett, and *Saunderia* (Sublette), which has three species, *S. pacificus, S. marinus* and *S. clavicornis*, Saunders. *Saunderia marinus* and *S. pacificus* are the least modified for marine life and fall into Hashimoto's "Flying Type". *S. clavicornis* and *P. alaskensis* are of the "Walking Type".

Paraclunio alaskensis was first described from Yakutat, Alaska in 1900 and named *Telmatogeton alaskensis* by Coquillett but there was no description of its early stages nor of its intertidal habitat. In 1928

Fig. 1 - A synopsis of the proposed system of classification by Hamilton, Saether and Oliver (1969) for nearctic Chironomidae as it relates to *Saunderia pacificus, marinus, clavicornis* and *Paraclunio alaskensis*.


TANYPODINAE
PODONOMINAE
FAMILY CHIRONOMIDAE (ORDER DIPTERA)
TELMATOGETONINAE
PARACLUNIO KIEFFER
alaskensis
trilobatus
TELMATOGETON SCHIN.
THALASSOMYA SCHIN.
DIAMESINAE
many other genera
ORTHOCLADIINAE
SAUNDERIA SUBLETTE
marinus
pacificus
clavicornis
CHIRONOMINAE

Saunders published a revised description of *P. alaskensis*; and described three new intertidal species, *Saunderia* (*Camptocladius*) *pacificus*, *S. marinus* and *S. clavicornis*. In the latter paper some ecological information was presented but was primarily observational and unsupported by quantitative data. The objectives of this study were, therefore, to identify and associate the eggs, larvae and pupae with the adults of the four species; to study the distribution of these Chironomidae in terms of their shore habitats and range; to obtain some measure of their abundance (primarily in the larval stage) both temporally and spatially and to investigate the larval diet.

When slide preparations were required for adult identification they were prepared as described in Appendix B.

B. DISTRIBUTION

The southern shore of Vancouver Island from Saanish Inlet to Otter Point was collected extensively throughout the summer and winter of 1969-70 (Fig. 2). At chosen sites a 100-yards of beach was surveyed at 2 ft. or lower tides. A physical description of the area, noting exposure, and the dominant flora and fauna was recorded. The algal zones were examined for larvae and subjective estimates of adult emergence noted. Algal and diatom samples were preserved for later study.

Two collecting trips were made to Northern Vancouver Island and the Queen Charlotte Islands in October 1969 and May 1970. The stations sampled are shown in Fig. 3.

C. ABUNDANCE

Preliminary observations suggested that measurement of spatial and temporal abundance of larvae would require a sampling program designed to deal with the following considerations:

1. The larvae were not randomly distributed, the areas of high population density corresponding with green algal or diatom cover.
2. The green algal bands were often not continuous, either spatially or temporally.
3. Chironomid larvae inhabited a variety of rocky shore types and consequently accurate sampling was difficult.

Fig 2 - Map of Southern Vancouver Island showing:

▼ - occasional collecting sites

(▼) - major collecting sites

Approximate scale: 1 inch = 4 miles

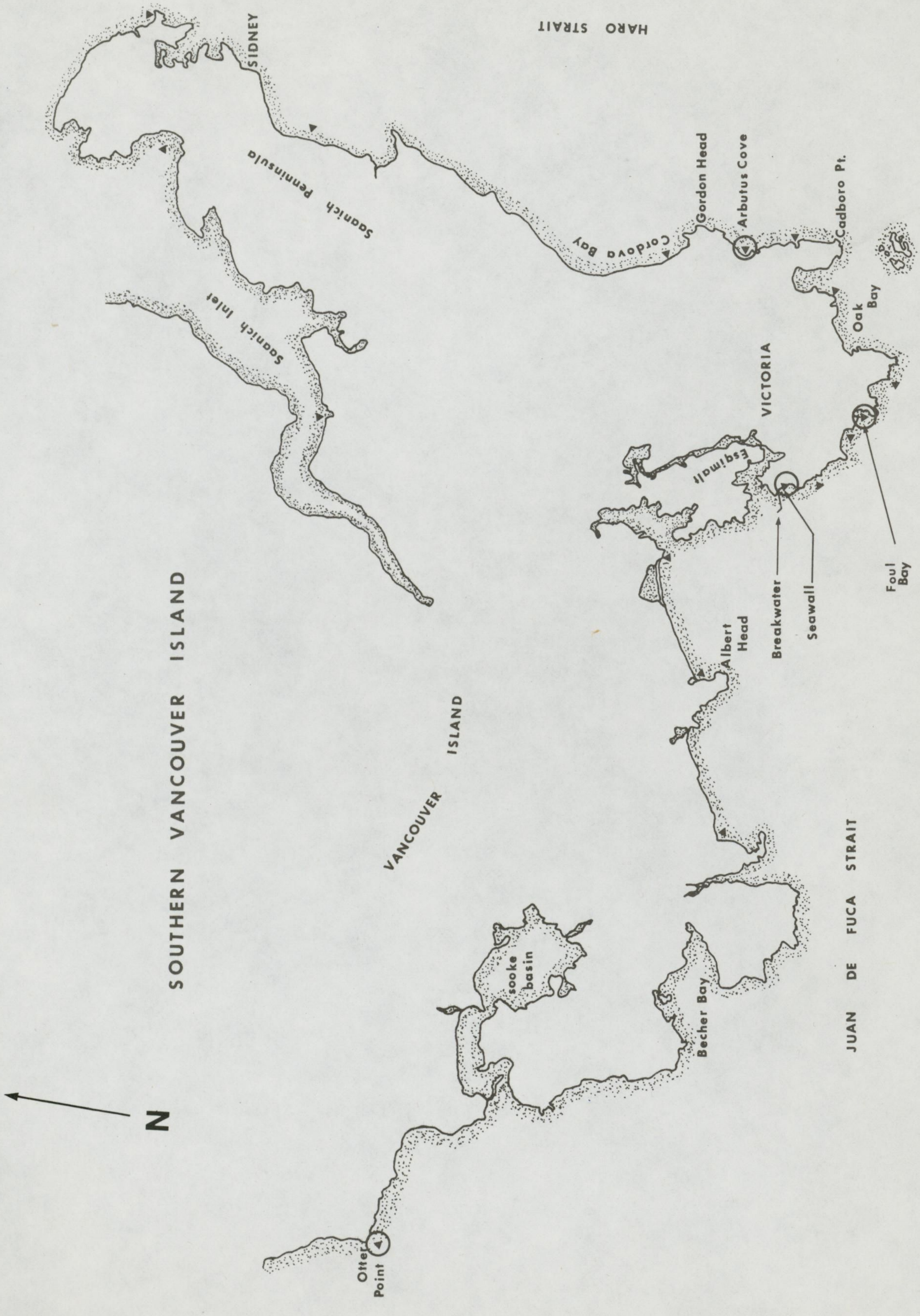
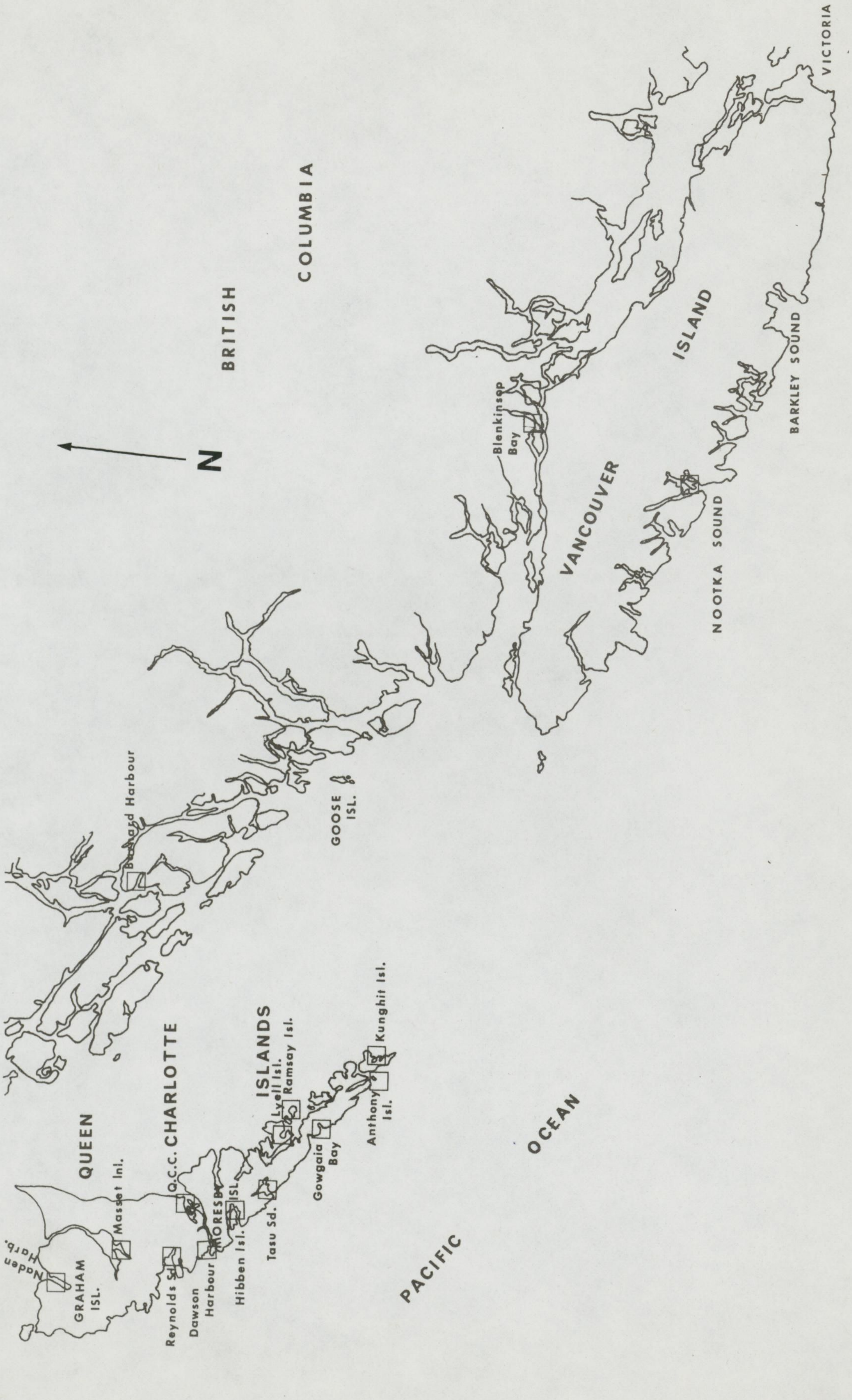

SOUTHERN VANCOUVER ISLAND
N
SIDNEY
HARO STRAIT
Saanich Peninsula
Saanich Inlet
Cordova Bay
Gordon Head
Arbutus Cove
Cadboro Pt.
Oak Bay
VICTORIA
Esquimalt
Breakwater
Seawall
Foul Bay
Albert Head
VANCOUVER ISLAND
JUAN DE FUCA STRAIT
sooke basin
Becher Bay
Otter Point

Fig. 3 - Map of the British Columbia coast from Southern Vancouver Island to the northern end of the Queen Charlotte Islands.
Collection sites are enclosed in boxes.
Q.C.C. = Queen Charlotte City.

Approximate scale: 1 inch = 60 miles

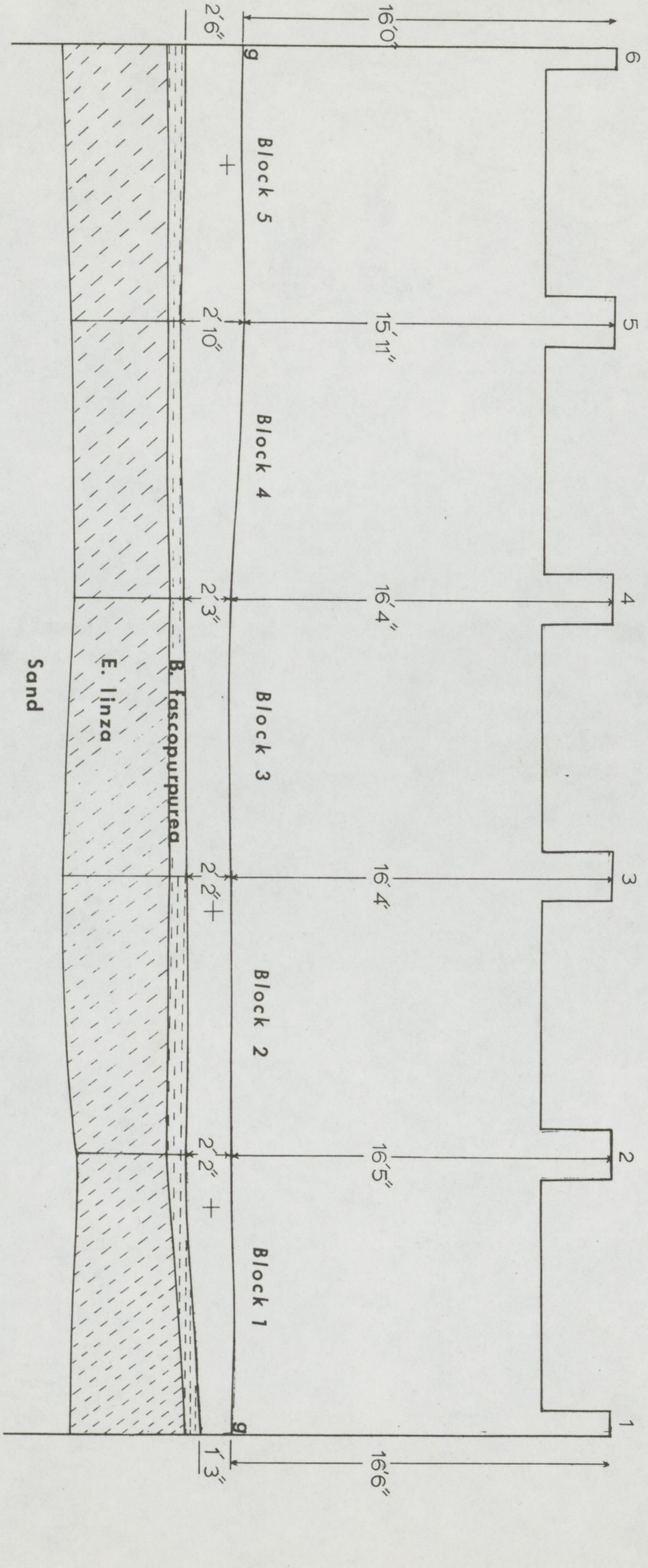

N
BRITISH COLUMBIA
QUEEN CHARLOTTE ISLANDS
GRAHAM ISL.
Naden Harb.
Masset Inl.
Q.C.C.
MORESBY ISL.
Reynolds Sd.
Dawson Harbour
Hibben Isl.
Tasu Sd.
Gowgaia Bay
Lyell Isl.
Ramsay Isl.
Anthony Isl.
Kunghit Isl.
Barnard Harbour
GOOSE ISL.
PACIFIC OCEAN
VANCOUVER ISLAND
Blenkinsop Bay
NOOTKA SOUND
BARKLEY SOUND
VICTORIA

A solution to the major sampling problems was accomplished by selecting a concrete and granite block seawall (Fig. 2) with a relatively stable algal banding pattern. The remaining difficulties were taken into account in the sampling design.

The site chosen was a sixty ft. section of seawall (Fig. 4) which was divided vertically into five 12ft. wide sections using nails inserted at the boundary between the granite blocks and the overlying concrete (Fig. 5). The height of each block varied from 6' 8" to 8' 8" depending upon the amount of sand deposition which was continually shifted about by waves and currents at the base of the wall. Prior to each sampling day the current extent and position of the algal bands were carefully mapped. A 6" square grid placed over the map enabled the algal areas to be individually identified. Sample points were then drawn randomly. Translation of the sample map coordinates to the wall was accomplished by means of a telescopic aluminum pole (y-axis) and sliding cord (x-axis) both marked in 6" intervals. Once located the sample area was isolated with a plastic jig leaving a 1" x 1 1/4" area exposed in the center. All of the living material and other debris was carefully removed from this area into a plastic bag. The 1 1/4" x 1" area was selected as having acceptable variance estimates, higher larval density measurements and a shorter analysis time than larger areas tested early in the field program. A total of thirty 1" x 1 1/4" samples (6 per 12ft. section and 3 per algal band were taken per month, usually on the day of the lowest predicted tide.

D. FOOD CONSUMPTION

Two aspects of larval feeding were examined. The first was an attempt


16'0"
2'6"
6
g
Block 5
5
15'11"
2'10"
Block 4
4
16'4"
2'3"
Block 3
3
16'4"
2'2"
Block 2
2
16'5"
2'2"
Block 1
1
g
16'6"
1'3"
Sand
E. linza
B. fascopurpurea

to establish a maintenance diet for larvae under culture conditions, and the second, a gut analysis of larvae collected under natural conditions. For gut analyses approximately 18 larvae were collected from each of two habitats along with a sample of the algal and diatom growth. The gut contents of 10 larvae from each site were analysed within two hours of collection using a method modified after Armitage (1968). The living larva was put onto a glass slide and the cuticle behind the head severed. The scalpel was then moved anteriorly while the caudal end of the larva was held under a thick cover slip. This movement usually removed the head capsule to which the alimentary tract remained attached by means of the oesophagus. The gut contents were then examined under the microscope and the abundance of material classified as follows:

RARE - less than approximately 10% of the gut contents.

COMMON - approximately 50% of the gut contents.

DOMINANT - the species in question making up the majority of the gut contents.

The habitat sample was examined at the same time as the gut contents and the relative abundance of each species was expressed in a similar way, i.e. as percentage of the total flora sample.

RESULTS

A. SPECIES IDENTIFICATION

(i) Life Stages

The eggs of *Saunderia* spp. are light yellow and are laid in masses of 95 to 135. They are surrounded by a transparent gelatinous covering (Fig. 6). The egg size was not determined. The eggs of *P. alaskensis* are deposited singly and are light yellow when first laid. Within five days, if fertile, they turn brown to greenish in colour (Fig. 7) and their size is approximately 0.4 x 0.2 mm. (Saunders, 1928).

The larval stages except those of *S. pacificus* were identified from cultured material and a larval key to the four species is given in Appendix C. *P. alaskensis* has a relatively robust larva whose head has a noticeably 'square-cut' appearance dorsally (Appendix A). Around the mouthparts and occiput it is usually a dark brown to black. Members of *Saunderia* spp. lacks the 'square-cut' head capsule of *P. alaskensis* and the head is distinctly smaller in relation to the first thoracic segment.

The labium was found to be an especially useful taxonomic character. *P. alaskensis* can immediately be identified by the 'flaired' medial tooth and the dark, almost black, mouthparts (Fig. 8). *S. marinus* can be identified by the rounded medial tooth and the four flanking teeth which have their axes sloping toward the medial tooth. *S. clavicornis* is the most distinctive as its medial tooth is 'square-cut' and has sloping sides, the tip being flat. The four flanking teeth, unlike those of *S. marinus* do not slope toward the center of the labium and are more widely separated from each other than those of *S. marinus*.

Pupal identification was not difficult. The key used is presented in Appendix D (modified from Saunders, 1928), specimens being positively identified from their culture records. The pupa of *P. alaskensis* was distinctive since not only was it larger than the pupa of *Saunderia* spp. but also had an unusual obliquely truncated terminal abdominal segment (Fig. 9). The adult males were readily identified using the available keys. *P. alaskensis* (males) was recognized by its much larger size which, incidentally, varied from winter to summer, but even in its smallest form was over 3 mm in length as compared to just over 2 mm in *S. marinus* and *S. pacificus*.

S. clavicornis was the next most easily recognized as it is much smaller than the other species of *Saunderia*, being 1.5 to 1.9 mm in length compared to 2.2 mm for *S. pacificus* and 2.0 to 2.3 mm in *S. marinus* (Saunders, 1928). Its most reliable characteristic was its much reduced antennae (9 segments) in the male. Finally, *S. marinus* and *S. pacificus* were readily separated by the presence in *S. pacificus* of stout chitinous pegs located on the tips of the male claspers, structures absent from *S. marinus* (Fig. 10). Appendix E presents a key to the four species.

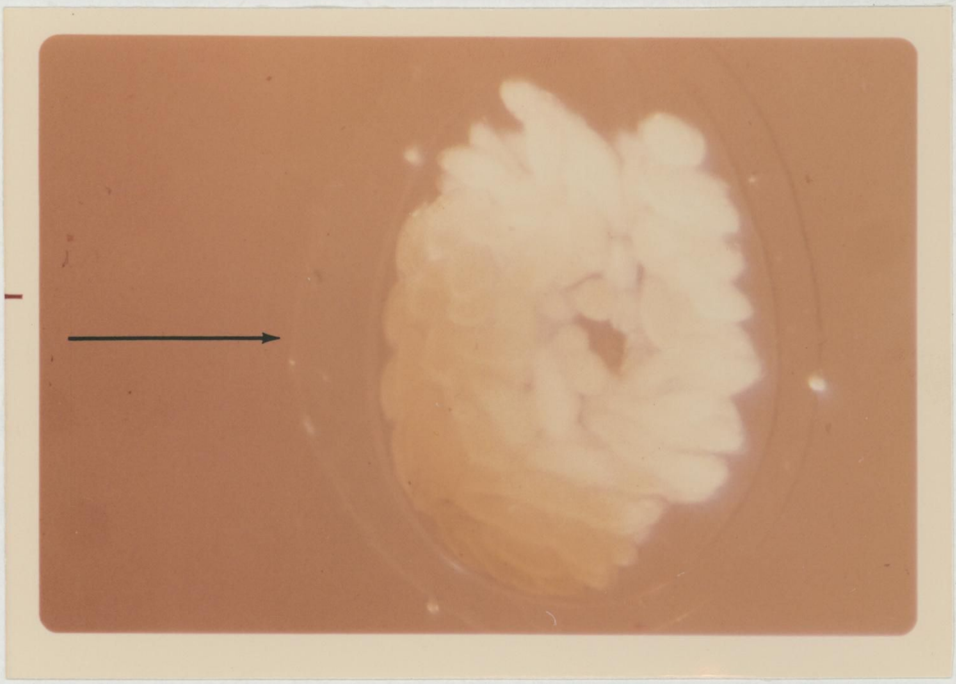
(ii) Culturing

In *S. marinus* and *S. clavicornis* small red eyespots appeared at the apical end of the egg about 3 days before hatching. Developmental time within the egg was approximately 2 weeks and upon emergence the larvae remained within the gelatinous case for a few days (Fig. 11). In *P. alaskensis* the yolk occupied approximately half the volume of the egg and 3 days before hatching small red eyespots became visible at the apical end. Generally, at 19 days after oviposition the entire larva could be seen within the chorion and the head capsule had its dorsal surface pressed against the chorion. Within a few days the larva would hatch and was

Fig. 4 - **Victoria Seawall off Dallas Road looking North. Sampling area enclosed by arrows. Steps from the road above can be seen on the extreme right of the photo.**

Approximate scale: 1" = 25'

Fig. 6 - Egg mass of *Saunderia* spp. showing the gelatinous covering (indicated by the arrow). (x 25)



<u>Fig. 7</u> - Eggs of *Paraclunio alaskensis* deposited on *Ulva* sp. All have turned the characteristic green-brown color.

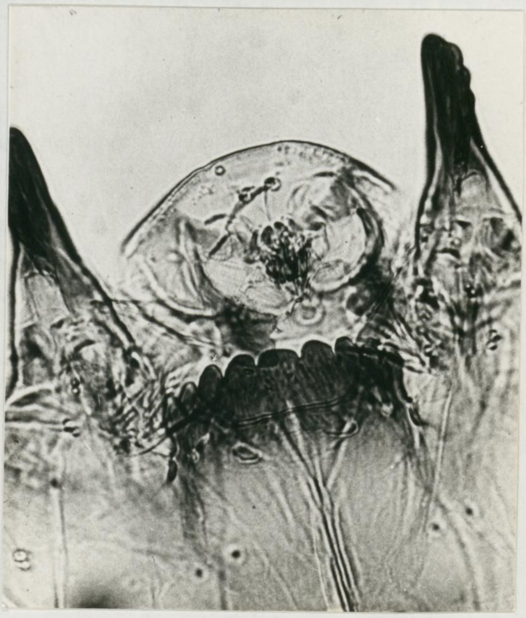
(x 12)

__Fig. 8__ - Ventral view of the mouthparts of:
A. *P. alaskensis* (x 100)
B. *S. marinus* (x 200)
C. *S. clavicornis* (x 200)
D. *S. pacificus* (x 200)
c = labium
m = mandible

A

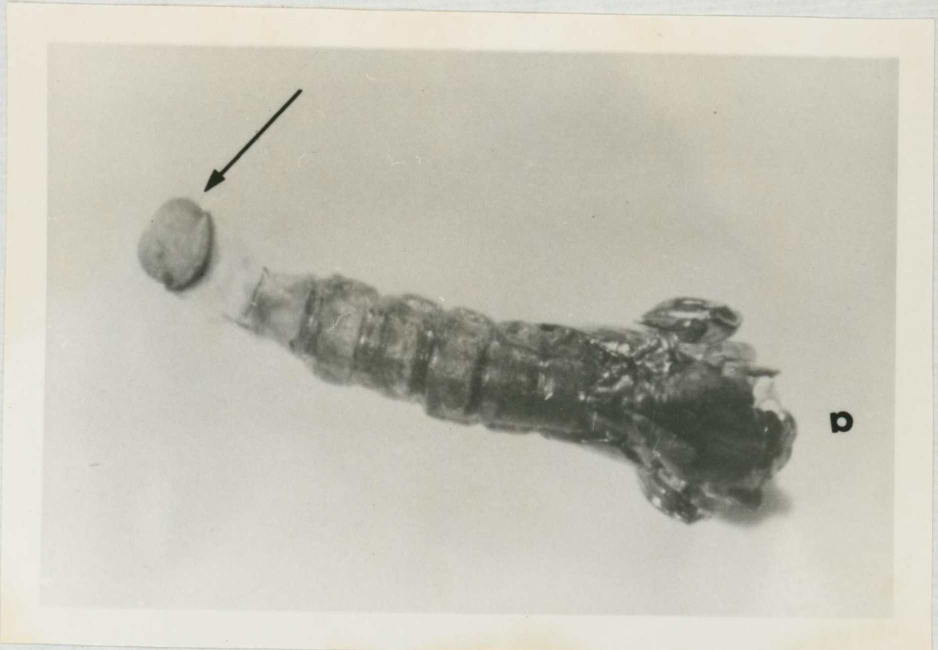
B

C



D

Fig. 9 - P. *alaskensis* pupae showing the truncated terminal abdominal segment (indicated by the arrows). (x 12)
a = anterior
d = dorsal.


a

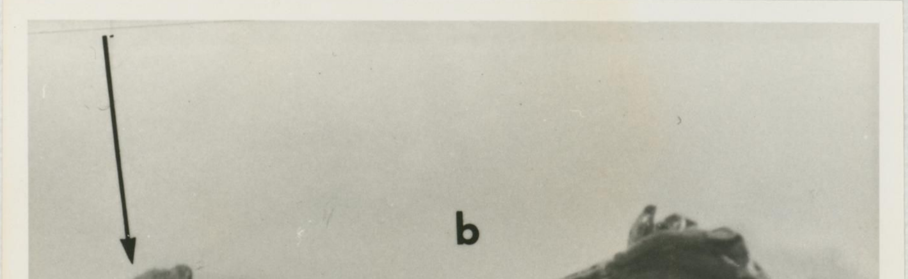
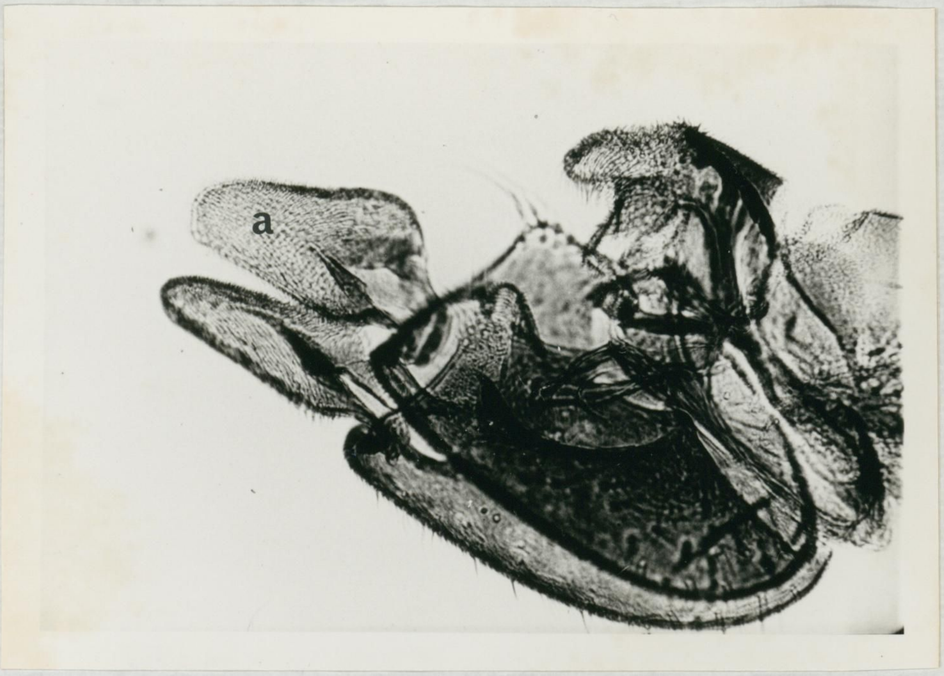

b
a

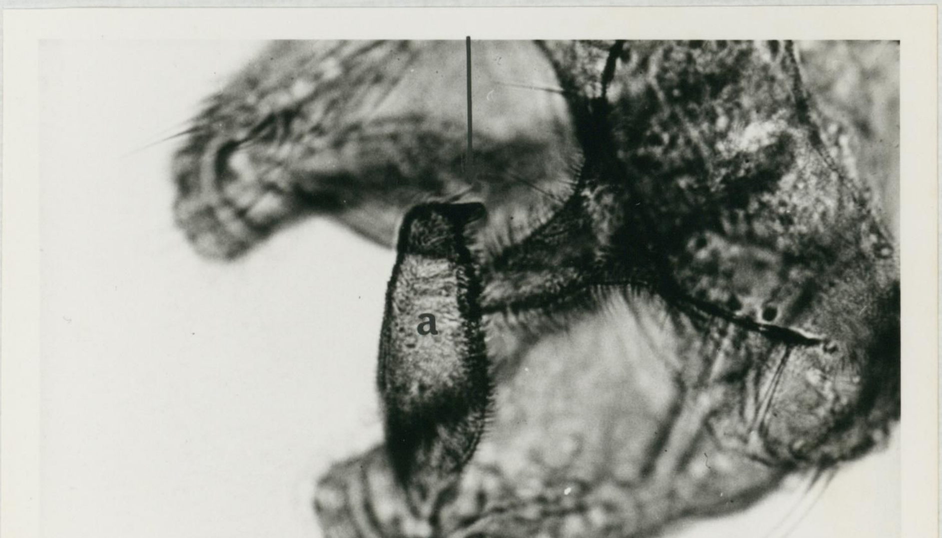
Fig. 10 - Genitalia of:
A. *S. marinus;* lateral view (x 200)
B. *S. pacificus;* dorsal view (x 200)

a = claspers

Arrow indicates the chitinous peg on the claspers of *S. pacificus*.



A



B

Fig. 11 - Egg mass of *Saunderia* spp. in a late stage of development.

(x 25)

very active. It emerged from the egg by means of a longitudinal slit starting from the apical end (Figs. 12 and 13). Egg developmental records are presented in Appendix A.

Saunderia spp. were found to have four larval instars and at 10°C the developmental period from egg laying to adult emergence was approximately 150 days for *S. marinus* and 110 days for *S. clavicornis*. *P. alaskensis* was found to have four larval instars also and a developmental time of approximately 204 days at 10°C. Additional observations were taken on miscellaneous larval activities such as feeding, case-building, movement, etc. and are presented in Appendix F.

In *Saunderia* spp. pupal emergence was relatively successful, and many adults emerged that were able to fly about the culture dishes. Emergence was observed, in detail, for a female of *Saunderia* sp. The sequence of events was as follows:-

1. The larval case was partially opened to reveal a pupa. Two days later the pupa rose to the surface with air visible beneath its cuticle.
2. After two days the pupa was observed to be active while floating on the water surface. The movements consisted of a slow telescoping of the abdominal segments.
3. Shortly thereafter a slit appeared in the middle of the pro- and mesonotum.
4. There followed a more rapid telescoping of the abdominal segments combined with rotation of the adult abdomen within the pupal exuviae.
5. The movements pushed the adult anteriorly within the exuviae until the point of the adult pronotum appeared through the pupal thoracic slit. The adult pronotum emerged first with the head

Fig. 12 - Empty *P. alaskensis* egg from which a larva has recently emerged. The narrower end is apical.

(x 100)

Fig. 13 - Emerging *P. alaskensis* larva. White eggs are not fertile and have not changed color.

(x 50)

tucked under the "over-hanging" pronotum.

6. The whole adult body was withdrawn through this slit.

Approximate time for complete emergence was half an hour.

Emergence in *P. alaskensis* cultures was less successful than for *Saunderia*. Approximately 60% of the pupae died and the remaining 40%, although the adults emerged, either died with an appendage(s) stuck to the pupal exuviae, or were trapped by the surface tension of the water.

Few adults emerged in culture (Appendix G). The majority of those that did emerge were preserved immediately to ensure undamaged specimens for taxonomic work since they provided the most reliable source of identification at the species level. A few observations indicated that under culture conditions *Saunderia* spp. may live up to 3 days after emergence, exactly the same life span as adults collected in the field. Adults emerging from culture have never been observed to lay eggs.

B. DISTRIBUTION

(i) Shore Habitats

Of the many beaches visited four were studied intensively (Fig. 2). Tables I and IIpresent a physical description of each along with a profile of the fauna and flora. Some observations from each site are presented in Table III.

At Arbutus Cove the larvae were not confined to the clumps of green algae but could be found amongst the diatom layer that covered most of the intertidal area. The swarms of adult *S. marinus* were thick in the fall and early winter and when night collecting necessitated lamps they had a strong positive phototropism. Their swarms continued through the winter but tended to fall off in the spring. No *S. pacificus* were

TABLE I

LOCAL COLLECTION SITES

Name of Beach	Slope	Direction Shore Faces	Exposure	General Beach Type	Type of Rock	Size of Rock	General Description of the Shore
Arbutus Cove	Moderate	East	Protected	Boulder	Igneous Granite	2" - 8" also larger boulders	Sand and gravel overlain with boulders of varying size.
Foul Bay	Gentle	South	Moderate protection	Rocky	Glaciated igneous granite	varying	sand slopes down to rock tables with occassional boulders.
Seawall and Beach (see also "Methods" section)	Moderate	South West	Moderate protection	Rocky	Glaciated igneous	varying	sand slopes down to rock outcroppings with tide pools.
Otter Point	Steep	South	Exposed	Rock Cliffs	Igneous	Cliffs and large boulders	Rock cliffs followed by large boulders on large gravel.

TABLE II

FLORA FAUNA PROFILES OF COLLECTION SITES

Arbutus Cove	Foul Bay	Seawall Shore	Otter Point
Verrucaria sp. (especially on the cliffs)	Bare sand and gravel.	*Verrucaria* sp.	*Verrucaria* sp. (on the rock cliffs).
Brownish diatom film.	*Balanus* sp. with diatom film in places.	*Bangia fascopurpurea.*	Limpets, Littorinids, Isopods.
Littorinids and Limpets.	*Fucus* sp. with patches of green algae (*Enteromorpha* spp., *Ulva* spp., etc.)	*Enteromorpha intestinalis* and *E. linza.*	*Cladophora* sp., *Spongomorpha* sp. and other greens.
Barnacles with patches of *Ulva* sp. or *Monostroma* sp. and *Enteromorpha*	Laminarians	Sparse *Porphyra* sp. interspersed with *Balanus* sp. and *E. linza.*	*Mitella* sp. (goose barnacle).
Fucus sp.		Sand.	
		Coraline algae, Reds and often a diatom film. Patches of *Phylospadix* sp. (*Zostera* sp. etc.)	
		Laminarians.	

TABLE III

LOCAL FIELD OBSERVATIONS

Place	Exposure	Slope	Dominant algae	Common Chironomid Species	Chironomid Species Present
1. Otter Pt.	Exposed to Pacific Swell	Steep	*Cladophora* sp.	*P. alaskensis* *S. clavicornis*	*P. alaskensis* *S. marinus* *S. pacificus*
2. Victoria Seawall	Moderate	Steep	*Enteromorpha linza*	*P. alaskensis* *S. marinus* *S. clavicornis*	All four species.
3. Foul Bay	Slight	Slight	Diatoms Mixed Greens *Fucus* sp.	*P. alaskensis* *S. marinus* *S. clavicornis*	*P. alaskensis* *S. clavicornis* *S. marinus*
4. Arbutus Cove	Slight	Moderate	Diatoms Mixed Greens *Fucus* sp.	*P. alaskensis* *S. clavicornis*	*P. alaskensis* *S. clavicornis* *S. marinus*

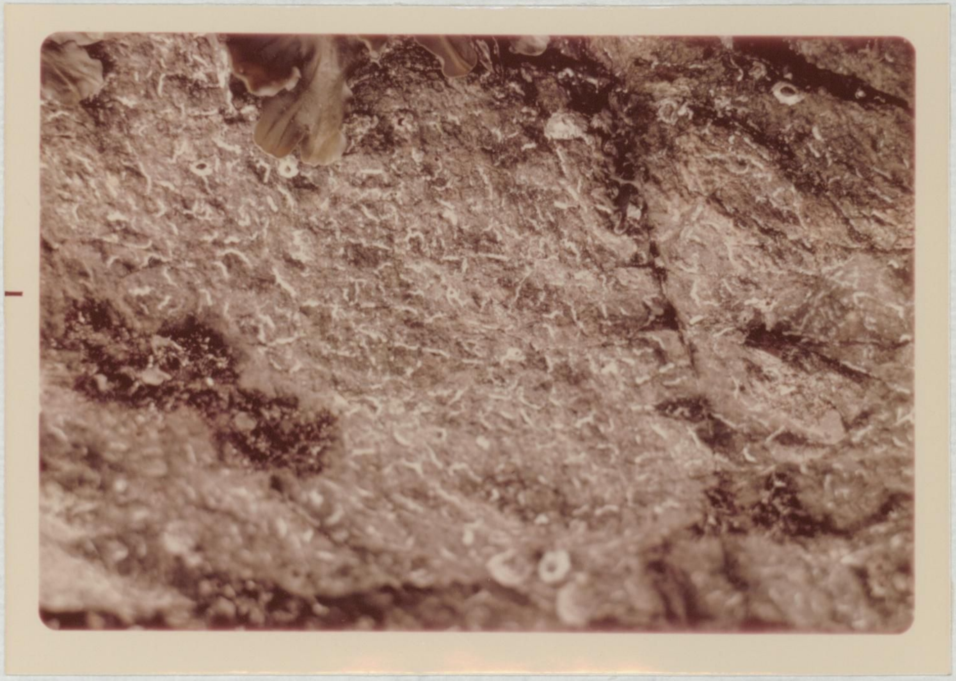
collected at this site. *S. clavicornis* was abundant and when an emergence had taken place they could be collected easily as they ran over the intertidal rocks. This species was also numerous in the fall and on some nights most rocks in the lower intertidal zone were covered with adults. *P. alaskensis*, although present, was out-numbered by the other two species. Again their emergences continued throughout the winter. During the extensive adult emergences of *S. marinus* and *S. clavicornis* in October and November it became difficult to find the larvae of these species.

The green algal cover at Foul Bay beach was patchy at most times of the year (Fig. 14), and the larvae present lived, for the most part, in the diatom cover. Examples of the transient nature of the algal and diatom cover could be found regularly, indicating that though it may provide cover and food for a given period it can soon disappear (Fig. 15). In spite of the transient nature of the algal cover intertidal chironomids were numerous, especially *S. marinus* and *S. clavicornis*. *P. alaskensis* could also be found but in fewer numbers and closer to the low intertidal zone than the other two species. Here also, emergence continued throughout the year with more noticeable numbers of adults appearing in the fall and early winter.

The chironomid population on the seawall confirmed that larvae seem to prefer the vertical sides of boulders and cliffs. This was particularly true of *P. alaskensis* larvae. In addition to the larvae on the seawall there was also a population of all four species living on the rocks further down the shore. Here, in contrast to the wall, *S. clavicornis* and *S. marinus* were more numerous than *P. alaskensis*. Another noticeable occurence was that often when no adults could be found on the seawall

Fig. 14 - Mid littoral at Foul Bay, Victoria. The photograph shows the patchy algal cover (arrows indicate pieces of *Ulva* sp. or *Monostroma* sp.). The wet looking areas are diatom-unicellular algal cover. The ruler is 6" long.

Fig. 15 - Upper mid littoral at Foul Bay, Victoria showing abandoned (mostly) chironomid cases (white lines on the rock).



there was an emergence on the rocks lower down the shore.

The chironomids living on the seawall were the most easily observed of any on the four selected shores. The surface was flat and the algal and diatom growth uniform. Furthermore, the short *Enteromorpha linza* allowed one to see the larval cases that were built amongst this alga. *P. alaskensis* larvae built cases from pieces of *E. linza* cemented by a white silky secretion, probably from the salivary glands. These cases become very sturdy in the later instars and contrasted to those built in culture which were thin-walled and delicate at all stages.

Emergence of *P. alaskensis* occured outside the last instar larval case with the truncated last segment of the pupa inside the front end of the case. After emergence the pupal exuviae could be seen along the seawall with their terminal segments still anchored within the larval case. This observation was not made for any *Saunderia* spp.

It was observed that *P. alaskensis* and *Saunderia* spp. larvae often lived in close association. For example, when late instar *P. alaskensis* larvae were being taken from their cases the cases would have to be broken apart in order to extract the larva. Early instar larvae of *Saunderia* spp. were often found in the outer twinings of the tube and in some cases within the tube itself. *P. alaskensis* was also often found in association with *Balanus glandula* (see Fig. 16). It was discovered that larvae often inhabit the area between the test and the opercular plates of these barnacles. Obviously this niche on the barnacle provides a convenient, protected place for chironomids to build cases. Larvae were also found with tubes built around the base of the barnacle test and the more crowded the barnacles the more frequently the larvae utilized these places for case-building. Occasionally *Saunderia* spp. were found in this

Fig. 16 - Dorsal view of *Balanus glandula* test showing *P. alaskensis* larva which has been living between the test and the opercular plates of the barnacle. (x 12)

Fig. 17 - Nootka Sound showing the typical protected rocky shore zonation. Tidal height approximately 3.0 ft.

association but in the majority of cases it was *P. alaskensis.*

Otter Point was the only exposed beach studied and differed from the others most noticeably in its lack of intertidal species. *P. alaskensis* was the most common intertidal chironomid and the larvae could be found at any time in cases among the *Spongomorpha* sp. or *Cladophora* sp. which cover the rocks. Larvae of *Saunderia* spp. could also be found but they tended to build cases across small crevices on the surface of rocks rather than down in the algal holdfasts as did *P. alaskensis.* The adult behavior differed from that encountered on protected beaches since the greater wave action interfered with the adult's movement over the rocks.

(ii) Range

The B.C. coastline consists of miles of almost identical rocky shoreline. Typically, the protected shores were similar to that which was seen in Nootka Sound (see Figs. 3 and 17). A typical profile of these protected rocky shores was as follows:

1. *Verrucaria* sp.
2. *Balanus* sp. with patches of *Enteromorpha* spp., *Porphyra* sp.
3. *Fucus* sp. and *Balanus* sp.
4. *Mytilis* sp.
5. *Alaria* sp. and *Macrocystis* sp.

Encrusting diatoms are common below *Verrucaria* sp. and corallines are patchy throughout the mid to low intertidal zone.

Exposed shores have some of these zones expanded (i.e. *Verrucaria* sp.). Only two very exposed shores were visited on these trips, Kunghit Island and Anthony Island (Fig. 3). A typical profile of an exposed shore was:

1. *Verrucaria* sp. (much expanded from the sheltered areas)
2. *Fucus* sp. and *Balanus* sp.
3. *Phylospadix* sp.
4. Corallines
5. Patches of *Rhodymenia* sp. and *Spongomorpha* sp.
6. Laminarians.

Again corallines and encrusting diatoms were common.

Generally, it was found that intertidal chironomids were extremely common on all B.C. shores, except sandy ones. Tables IV and V give the data collected and it is evident from these that all shores sampled had at least one species present. Table VI summarizes the species encountered at the various stations visited on both field trips.

On the first trip it was surprising to find that *P. alaskensis* was absent from the Queen Charlotte Islands. Although common at Nootka Sound it was not encountered again until a station was sampled in Johnson Strait (Blenkinsop Bay) (Fig. 3). On the second trip in May 1970, specimens of *P. alaskensis* were taken at Kunghit Island and again at Anthony Island. Both of these stations are on the southern tip of the Queen Charlotte Islands and were the only exposed shores to be sampled.

S. clavicornis was the most common species, the only station at which it was not encountered being Anthony Island. *S. pacificus* was shown to be the rarest species, being taken at only two of the fifteen stations sampled. *P. alaskensis* and *S. marinus* were about equal in distribution and were found at four of the fifteen stations.

C. ABUNDANCE

Fig. 18 shows the stratified random block design used in this experiment along with the nomenclature used in describing it. The

TABLE IV

SUMMARY OF OBSERVATIONS TAKEN DURING THE OCTOBER 1969 FIELD TRIP TO THE NORTHERN B.C. COAST

Station	Exposure	Slope	Dominant algae	Common Chironomid Species	Chironomid Present
Nootka Sd.	Protected	Moderate	*Fucus*	*P. alaskensis*	*P. alaskensis* *S. marinus* *S. clavicornis*
Lyell Is.	Protected	Steep	*Fucus* and some Green Algae	*S. clavicornis*	*S. clavicornis*
Queen Charlotte City	Moderate	Moderate	*Fucus*	*S. clavicornis*	*S. clavicornis*
Barnard Harbour	Protected	Moderate	*Fucus*	*S. clavicornis*	*S. marinus* *S. clavicornis*
Blenkinsop Bay	Moderate	Slight	*Ulva* Red Algae *Fucus*	*P. alaskensis* *S. clavicornis*	*P. alaskensis* *S. marinus* *S. clavicornis*

TABLE V

SUMMARY OF OBSERVATIONS TAKEN ON THE MAY 1970 FIELD TRIP TO THE NORTHERN B.C. COAST

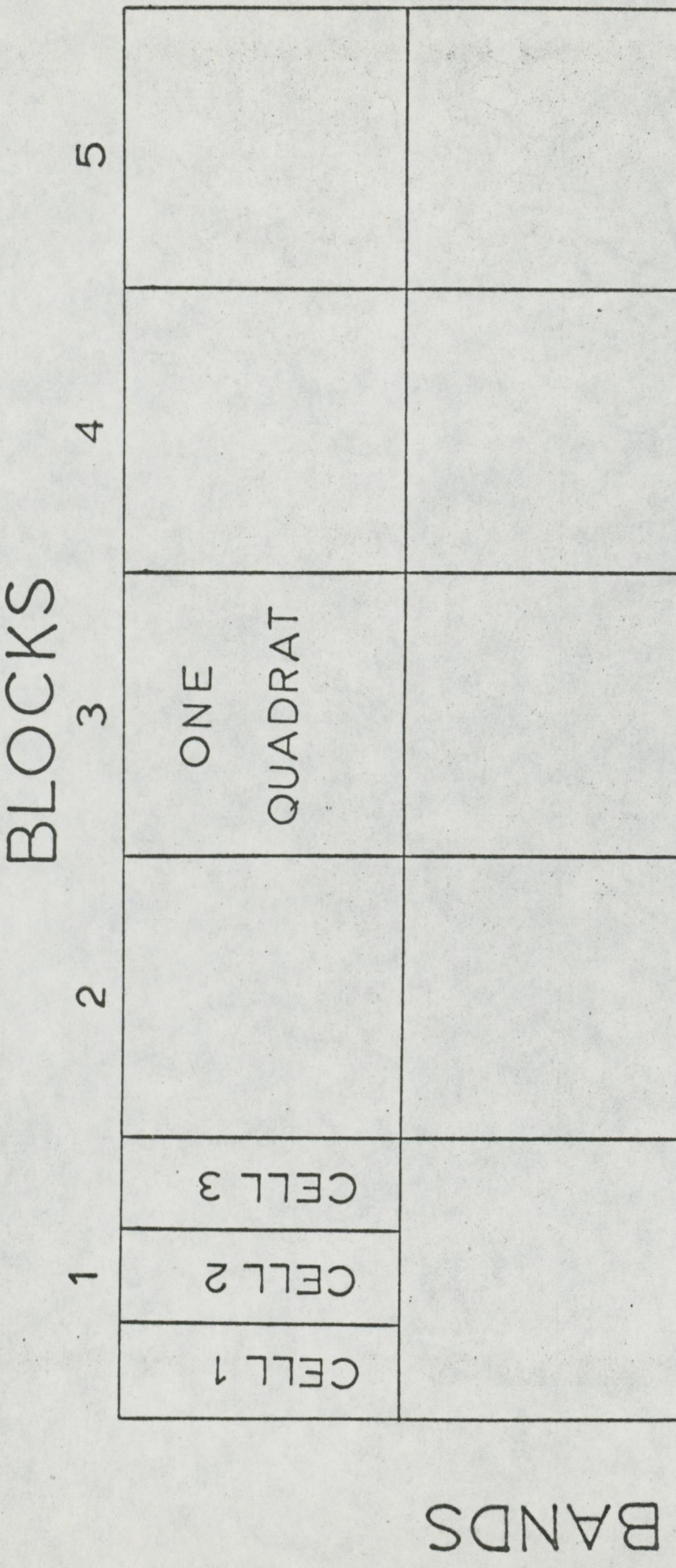
Station	Exposure	Slope	Dominant algae	Common Chironomid Species	Chironomidae Present
Kunghit Is.	Very exposed	Moderate to steep	*Phylospadix* sp., *Fucus* sp. etc. on rocks	*S. clavicornis*	*P. alaskensis* *S. clavicornis*
Gowgaia Bay	Protected	Moderate	*Fucus* sp. etc.	*S. clavicornis*	*S. clavicornis*
Tasu Sd.	(Protected) No data	-	-		*S. clavicornis*
Hibben Is.	Protected	Moderate	*Enteromorpha* sp. *Cladophora* sp.	*S. clavicornis*	*S. clavicornis*
Reynolds Sd.	Protected	Moderate	*Fucus* sp. etc.	*S. clavicornis*	*S. marinus* *S. clavicornis*
Naden Harbour	Protected	Slight	*Fucus* sp. *Ulva* sp.	*S. clavicornis*	*S. pacificus* *S. clavicornis*
Masset Inlet	Protected	Slight	*Fucus* sp. Diatom	*S. clavicornis*	*S. clavicornis*
Hotspring Is.	Moderate	Steep	*Fucus* sp. *Ulva* sp.	*S. clavicornis*	*S. clavicornis* *S. pacificus*
Anthony Is.	Exposed	Steep	*Porphyra* sp. *Ralfsia* sp. *Halosaccion* sp.		*P. alaskensis*

TABLE VI

SUMMARY OF THE SPECIES ENCOUNTERED AT STATIONS VISITED DURING FIELD TRIPS

Stations Sampled	Species Collected			
	P. alaskensis	*S. marinus*	*S. clavicornis*	*S. pacificus*
Nootka Sd.	x	x	x	
Blenkinsop Bay	x	x	x	
Barnard Harbour (Princess Royal)		x	x	
Anthony Is.	x			
Kunghit Is.	x		x	
Gowgaia Bay			x	
Tasu Sd.			x	
Hibben Is.			x	
Dawson Harbour			x	
Shields Bay (Reynolds Sd.)		x	x	
Naden Harbour			x	x
Masset Inlet			x	
Queen C. City			x	
Lyell Is.			x	
Ramsay Is.			x	x

Fig. 18 - Stratified random block design used in sampling chironomid larvae on the Seawall.


BLOCKS
1
2
3
4
5
ONE QUADRAT
CELL 1
CELL 2
CELL 3
BANDS

sampling results were analyzed in two categories (1) data for the three species of *Saunderia* and (2) data for *Paraclunio alaskensis.* Tables VII and VIII present the results for one complete calendar year and Tables IX and X summarize the data showing for each month: (a) the mean number of larvae for each quadrat, (b) the total number of larvae for each block, (c) the total number of larvae for each band, and (d) the total number of larvae for all blocks and bands. Frequency distributions (i.e. number of cells with X number of larvae) have been plotted and the resulting curves are presented in Figs. 19 and 20. Figs. 21 and 22 show inshore water temperatures for each month as compared to the mean larval density (numbers /1.25 in 2) per month calculated from Tables IX and X. Tables XI and XII present a test of fit to the Negative Binomial Distribution of the curves in Figs. 19 and 20. A sample of the method used is outlined in Appendix H.

Table XIII shows the results of an analysis of variance to determine spatial and temporal effects. The results indicated that in all cases there was a significant difference between the months (temporal). Also indicated were the significant difference that existed between blocks for *P. alaskensis*. It was realized when calculating these statistics that the populations being compared varied somewhat from a normal distribution. However, as Li (1964) states, "Non-normality of the population does not introduce serious error in the F-test or in the two-tailed t-test. If the F-table and t-table are used in determining the critical regions, the true significance level is actually larger than the one being specified." Winer (1962) has also stated that "The work of Box (1953) has shown that the sampling distribution of the F ratio is relatively insensitive to moderate departures from normality."

The signficant temporal effects shown in Table XIII were expected

EXPLANATION OF TABLES VII AND VIII

Raw data for larval counts is arranged with the dates of collection in the first column, and each other column indicating one sample point. Each date is listed five times, once for each block and since a maximum of six samples was taken from each block there are at least 3 sets of asterisks in each block.

Dates are coded as follows:

Example 17/06/91
Day ↑ Block #
Month Year
i.e.1969

EXPLANATION OF TABLES VIII TO X

The groups of three asterisks in these tables indicate cells in which no sample was taken and should not be confused with empty cells. They mean that within the design of the experiment no plan had been made to take a sample in these cells. Cells in which no sample could be taken were given the mean for the other cells of the quadrat. An example of this is the contrasting situations where (a) no samples were taken in band 3 because no band 3 existed on that particular date and where (b) three samples were to be taken from a band but on taking the sample it was found that the third random sample point was barren of algal cover. In example (a) asterisks are indicated whereas in (b) the average of the first two random sample points would be used for the third point.

TABLE VII

LARVAL COUNTS OF *SAUNDERIA* SPP. THROUGH 1969-70 SAMPLING

17/06/91	0.	0.	***	0.	0.	0.	***	***	***
17/06/92	0.	0.	0.	1.	2.	1.	***	***	***
17/06/93	0.	0.	***	0.	8.	1.	***	***	***
17/06/94	0.	0.	***	0.	5.	6.	***	***	***
17/06/95	0.	***	***	0.	2.	1.	***	***	***
66/07/91	0.	0.	1.	3.	3.	2.	***	***	***
66/07/92	4.	0.	0.	7.	1.	2.	3.	6.	17.
66/07/93	1.	0.	***	10.	4.	***	8.	10.	***
66/07/94	0.	***	***	1.	18.	24.	20.	9.	***
66/07/95	2.	0.	***	1.	4.	***	21.	14.	***
13/08/91	0.	0.	0.	2.	2.	1.	***	***	***
13/08/92	0.	0.	0.	3.	3.	7.	***	***	***
13/08/93	0.	1.	0.	22.	12.	8.	***	***	***
13/08/94	4.	3.	5.	42.	16.	19.	***	***	***
13/08/95	9.	6.	0.	4.	26.	6.	***	***	***
25/09/91	16.	7.	8.	4.	20.	1.	***	***	***
25/09/92	12.	8.	4.	7.	8.	6.	***	***	***
25/09/93	0.	32.	22.	11.	12.	5.	***	***	***
25/09/94	3.	6.	***	6.	14.	***	21.	0.	***
25/09/95	5.	6.	***	0.	8.	***	24.	5.	***
14/10/91	0.	0.	1.	10.	29.	8.	***	***	***
14/10/92	2.	3.	2.	2.	6.	6.	***	***	***
14/10/93	0.	0.	0.	0.	0.	1.	***	***	***
14/10/94	0.	8.	***	11.	7.	***	5.	11.	***
14/10/95	0.	1.	1.	42.	8.	2.	***	***	***
26/11/91	3.	3.	2.	5.	5.	8.	***	***	***
26/11/92	3.	8.	5.	8.	2.	1.	***	***	***
26/11/93	0.	0.	9.	0.	2.	0.	***	***	***
26/11/94	***	***	***	6.	4.	0.	***	***	***
26/11/95	***	***	***	6.	0.	***	***	***	***
10/12/91	2.	2.	2.	0.	0.	3.	***	***	***
10/12/92	4.	3.	3.	0.	1.	0.	***	***	***
10/12/93	***	***	***	3.	1.	3.	0.	1.	2.
10/12/94	***	***	***	3.	9.	13.	8.	3.	5.
10/12/95	***	***	***	2.	5.	3.	0.	2.	1.
22/01/01	1.	2.	2.	1.	1.	1.	***	***	***
22/01/02	1.	2.	1.	0.	1.	1.	***	***	***
22/01/03	0.	0.	1.	2.	0.	1.	***	***	***
22/01/04	7.	0.	3.	1.	1.	1.	***	***	***
22/01/05	3.	0.	1.	3.	1.	7.	***	***	***
04/02/01	0.	0.	0.	0.	0.	0.	***	***	***
04/02/02	4.	0.	0.	0.	0.	1.	***	***	***
04/02/03	0.	0.	0.	0.	0.	0.	***	***	***
04/02/04	0.	0.	***	0.	0.	***	0.	0.	***
04/02/05	0.	0.	***	0.	0.	***	0.	0.	***
18/03/01	0.	0.	0.	0.	0.	***	***	***	***
18/03/02	0.	0.	0.	0.	0.	0.	***	***	***
18/03/03	0.	0.	0.	0.	0.	0.	***	***	***
18/03/04	***	***	***	0.	0.	0.	***	***	***
18/03/05	***	***	***	0.	0.	0.	***	***	***
23/04/01	0.	0.	0.	0.	0.	0.	***	***	***
23/04/02	0.	0.	0.	0.	0.	12.	***	***	***
23/04/03	0.	***	***	0.	0.	0.	***	***	***
23/04/04	***	***	***	0.	0.	0.	***	***	***
23/04/05	***	***	***	0.	2.	0.	***	***	***
13/05/01	0.	0.	0.	0.	0.	0.	***	***	***
13/05/02	6.	0.	13.	1.	0.	4.	***	***	***
13/05/03	2.	2.	6.	0.	4.	0.	***	***	***
13/05/04	***	***	***	2.	0.	2.	***	***	***
13/05/05	***	***	***	0.	0.	1.	***	***	***
17/06/01	0.	0.	0.	0.	1.	0.	***	***	***
17/06/02	0.	0.	0.	1.	6.	1.	***	***	***
17/06/03	0.	0.	0.	4.	0.	8.	***	***	***
17/06/04	***	***	***	0.	2.	3.	***	***	***
17/06/05	***	***	***	2.	0.	4.	***	***	***

TABLE VIII

LARVAL COUNTS OF *P. ALASKENSIS* THROUGH 1969-70 SAMPLING

17/06/91	1.	0.	***	0.	0.	0.	***	***	***
17/06/92	0.	0.	0.	0.	1.	1.	***	***	***
17/06/93	0.	0.	***	0.	3.	2.	***	***	***
17/06/94	0.	0.	***	0.	2.	6.	***	***	***
17/06/95	0.	***	***	0.	1.	1.	***	***	***
66/07/91	0.	0.	1.	1.	2.	2.	***	***	***
66/07/92	2.	0.	0.	2.	0.	0.	3.	3.	1.
66/07/93	0.	0.	***	1.	1.	***	5.	5.	***
66/07/94	0.	***	***	1.	1.	4.	5.	3.	***
66/07/95	1.	0.	***	1.	3.	***	7.	6.	***
13/08/91	0.	0.	0.	2.	1.	1.	***	***	***
13/08/92	1.	0.	0.	0.	1.	3.	***	***	***
13/08/93	0.	0.	0.	6.	0.	4.	***	***	***
13/08/94	6.	3.	10.	1.	2.	3.	***	***	***
13/08/95	0.	0.	0.	2.	3.	2.	***	***	***
25/09/91	0.	0.	0.	5.	10.	0.	***	***	***
25/09/92	0.	1.	0.	8.	2.	6.	***	***	***
25/09/93	0.	0.	3.	0.	0.	11.	***	***	***
25/09/94	0.	0.	***	14.	8.	***	3.	8.	***
25/09/95	0.	0.	***	0.	3.	***	6.	1.	***
14/10/91	0.	0.	0.	5.	3.	4.	***	***	***
14/10/92	2.	2.	1.	4.	0.	2.	***	***	***
14/10/93	0.	0.	0.	0.	1.	1.	***	***	***
14/10/94	0.	12.	***	6.	7.	***	1.	3.	***
14/10/95	0.	0.	1.	8.	3.	1.	***	***	***
26/11/91	6.	4.	4.	7.	13.	0.	***	***	***
26/11/92	0.	6.	3.	4.	7.	0.	***	***	***
26/11/93	0.	0.	2.	0.	0.	0.	***	***	***
26/11/94	***	***	***	6.	3.	0.	***	***	***
26/11/95	***	***	***	5.	0.	***	***	***	***
10/12/91	1.	1.	0.	0.	1.	1.	***	***	***
10/12/92	1.	0.	0.	0.	1.	0.	***	***	***
10/12/93	***	***	***	4.	0.	4.	1.	0.	3.
10/12/94	***	***	***	2.	6.	9.	3.	0.	1.
10/12/95	***	***	***	0.	0.	1.	0.	1.	1.
22/01/01	6.	2.	2.	1.	0.	2.	***	***	***
22/01/02	3.	4.	0.	1.	0.	4.	***	***	***
22/01/03	1.	0.	2.	5.	2.	3.	***	***	***
22/01/04	9.	1.	7.	7.	3.	2.	***	***	***
22/01/05	6.	3.	3.	3.	1.	10.	***	***	***
04/02/01	0.	0.	0.	0.	3.	2.	***	***	***
04/02/02	2.	0.	0.	4.	0.	0.	***	***	***
04/02/03	1.	0.	3.	0.	0.	0.	***	***	***
04/02/04	0.	0.	***	1.	1.	***	0.	0.	***
04/02/05	0.	0.	***	0.	0.	***	0.	0.	***
18/03/01	0.	0.	0.	1.	0.	1.	***	***	***
18/03/02	0.	0.	0.	0.	0.	0.	***	***	***
18/03/03	3.	1.	0.	0.	0.	0.	***	***	***
18/03/04	***	***	***	0.	0.	0.	***	***	***
18/03/05	***	***	***	0.	0.	0.	***	***	***
23/04/01	0.	0.	0.	0.	0.	0.	***	***	***
23/04/02	0.	0.	0.	0.	0.	0.	***	***	***
23/04/03	0.	***	***	0.	0.	0.	***	***	***
23/04/04	***	***	***	0.	0.	0.	***	***	***
23/04/05	***	***	***	3.	0.	1.	***	***	***
13/05/01	0.	0.	0.	0.	0.	0.	***	***	***
13/05/02	0.	2.	1.	0.	0.	1.	***	***	***
13/05/03	1.	1.	3.	0.	1.	0.	***	***	***
13/05/04	***	***	***	1.	0.	2.	***	***	***
13/05/05	***	***	***	0.	0.	2.	***	***	***
17/06/01	0.	0.	0.	0.	2.	0.	***	***	***
17/06/02	0.	0.	0.	0.	3.	1.	***	***	***
17/06/03	1.	0.	0.	1.	0.	3.	***	***	***
17/06/04	***	***	***	0.	8.	5.	***	***	***
17/06/05	***	***	***	2.	1.	3.	***	***	***

TABLE IX

SUMMARIZED DATA OF LARVAL COUNTS OF *SAUNDERIA* SPP. THROUGH 1969-70 SAMPLING

JUNE 17/69

BLOCKS 1	2	3	4	5	TOTAL	
0.0	0.0	0.0	-0.0	0.0	0.0	BAND 1
0.0	1.333	3.000	3.667	1.000	9.000	2
*******	*******	*******	*******	*******	0.0	3
0.0	1.333	3.000	3.667	1.000	9.000	TOTAL

JULY 15 + 29 AVG

0.333	1.333	0.500	0.0	1.000	3.167
2.667	3.333	7.000	14.333	2.500	29.833
*******	8.667	9.000	14.500	17.500	49.667
3.000	13.333	16.500	28.833	21.000	82.667

SEPTEMBER 25/69

10.333	8.000	18.000	4.500	5.500	46.333
8.333	7.000	9.333	10.000	4.000	38.667
*******	*******	*******	10.500	14.500	25.000
18.667	15.000	27.333	25.000	24.000	110.000

AUGUST 13/69

0.0	0.0	0.333	4.000	5.000	9.333
1.667	4.333	14.000	25.667	12.000	57.667
*******	*******	*******	*******	*******	0.0
1.667	4.333	14.333	29.667	17.000	67.000

OCTOBER 14/69

0.333	2.333	0.0	4.000	0.667	7.333
15.667	4.667	0.333	9.000	17.333	47.000
*******	*******	*******	8.000	*******	8.000
16.000	7.000	0.333	21.000	18.000	62.333

TABLE IX (continued)

NOVEMBER 26/69

2.667	5.333	3.000	*******	*******	11.000
6.000	3.667	0.667	3.333	3.000	16.667
*******	*******	*******	*******	*******	0.0
8.667	9.000	3.667	3.333	3.000	27.667

DECEMBER 10/69

2.000	3.333	*******	*******	*******	5.333
1.000	0.333	2.333	8.333	3.333	15.333
*******	*******	1.000	5.333	1.000	7.333
3.000	3.667	3.333	13.667	4.333	28.000

JANUARY 22/70

1.667	1.333	0.333	3.333	1.333	8.000
1.000	0.667	1.000	1.000	3.667	7.333
*******	*******	*******	*******	*******	0.0
2.667	2.000	1.333	4.333	5.000	15.333

FEBRUARY 4/70

0.0	1.333	0.0	0.0	0.0	1.333
0.0	0.333	0.0	0.0	0.0	0.333
*******	*******	*******	0.0	0.0	0.0
0.0	1.667	0.0	0.0	0.0	1.667

MARCH 18/70

0.0	0.0	0.0	*******	*******	0.0
0.0	0.0	0.0	0.0	0.0	0.0
*******	*******	*******	*******	*******	0.0
0.0	0.0	0.0	0.0	0.0	0.0

APRIL 23/70

0.0	0.0	0.0	*******	*******	0.0
0.0	4.000	0.0	0.0	0.667	4.667
*******	*******	*******	*******	*******	0.0
0.0	4.000	0.0	0.0	0.667	4.667

MAY 13/70

0.0	6.333	3.333	*******	*******	9.667
0.0	1.667	1.333	1.333	0.333	4.667
*******	*******	*******	*******	*******	0.0
0.0	8.000	4.667	1.333	0.333	14.333

JUNE 15/70

0.0	0.0	0.0	*******	*******	0.0
0.333	2.667	4.000	1.667	2.000	10.667
*******	*******	*******	*******	*******	0.0
0.333	2.667	4.000	1.667	2.000	10.667

TABLE X

SUMMARIZED DATA OF LARVAL COUNTS OF *P. ALASKENSIS* THROUGH 1969-70 SAMPLING

JUNE 17/69

BLOCKS 1	2	3	4	5	TOTALS	
0.500	0.0	0.0	0.0	0.0	0.500	BAND 1
0.0	0.667	1.667	2.667	0.667	5.667	2
*******	*******	*******	*******	*******	0.0	3
0.500	0.667	1.667	2.667	0.667	6.167	TOTAL

JULY 15 + 29 AVG

0.333	0.667	0.0	0.0	0.500	1.500
1.667	0.667	1.000	2.000	2.000	7.333
*******	2.333	5.000	4.000	6.500	17.833
2.000	3.667	6.000	6.000	9.000	26.667

AUGUST 13/69

0.0	0.333	0.0	6.333	0.0	6.667
1.333	1.333	3.333	2.000	2.333	10.333
*******	*******	*******	*******	*******	0.0
1.333	1.667	3.333	8.333	2.333	17.000

SEPTEMBER 25/69

0.0	0.333	1.000	0.0	0.0	1.333
5.000	5.333	3.667	11.000	1.500	26.500
*******	*******	*******	5.500	3.500	9.000
5.000	5.667	4.667	16.500	5.000	36.833

OCTOBER 14/69

0.0	1.667	0.0	6.000	0.333	8.000
4.000	2.000	0.667	6.500	4.000	17.167
*******	*******	*******	2.000	*******	2.000
4.000	3.667	0.667	14.500	4.333	27.167

TABLE X (continued)

NOVEMBER 26/69

4.667	3.000	0.667	*******	*******	8.333
6.667	3.667	0.0	3.000	2.500	15.833
*******	*******	*******	*******	*******	0.0
11.333	6.667	0.667	3.000	2.500	24.157

DECEMBER 10/69

0.667	0.333	*******	*******	*******	1.000
0.667	0.333	2.667	5.667	0.333	9.667
*******	*******	1.333	1.333	0.667	3.333
1.333	0.667	4.000	7.000	1.000	14.000

JANUARY 22/70

3.333	2.333	1.000	5.667	4.000	16.333
1.000	1.667	3.333	4.000	4.667	14.667
*******	*******	*******	*******	*******	0.0
4.333	4.000	4.333	9.667	8.667	31.000

FEBRUARY 4/70

0.0	0.667	1.333	0.0	0.0	2.000
1.667	1.333	0.0	1.000	0.0	4.000
*******	*******	*******	0.0	0.0	0.0
1.667	2.000	1.333	1.000	0.0	6.000

MARCH 13/70

0.0	0.0	1.333	*******	*******	1.333
0.667	0.0	0.0	0.0	0.0	0.667
*******	*******	*******	*******	*******	0.0
0.667	0.0	1.333	0.0	0.0	2.000

APRIL 23/70

0.0	0.0	0.0	*******	*******	0.0
0.0	0.0	0.0	0.0	1.333	1.333
*******	*******	*******	*******	*******	0.0
0.0	0.0	0.0	0.0	1.333	1.333

MAY 13/70

0.0	1.000	1.667	*******	*******	2.667
0.0	0.333	0.333	1.000	0.667	2.333
*******	*******	*******	*******	*******	0.0
0.0	1.333	2.000	1.000	0.667	5.000

JUNE 15/70

0.0	0.0	0.333	*******	*******	0.333
0.667	1.333	1.333	4.333	2.000	9.667
*******	*******	*******	*******	*******	0.0
0.667	1.333	1.667	4.333	2.000	10.000

Fig. 19 - Graph showing a frequency distribution for *Saunderia* spp. larvae sampled in 1969-70. (Numbers of larvae plotted against the number of cells containing those larvae.)

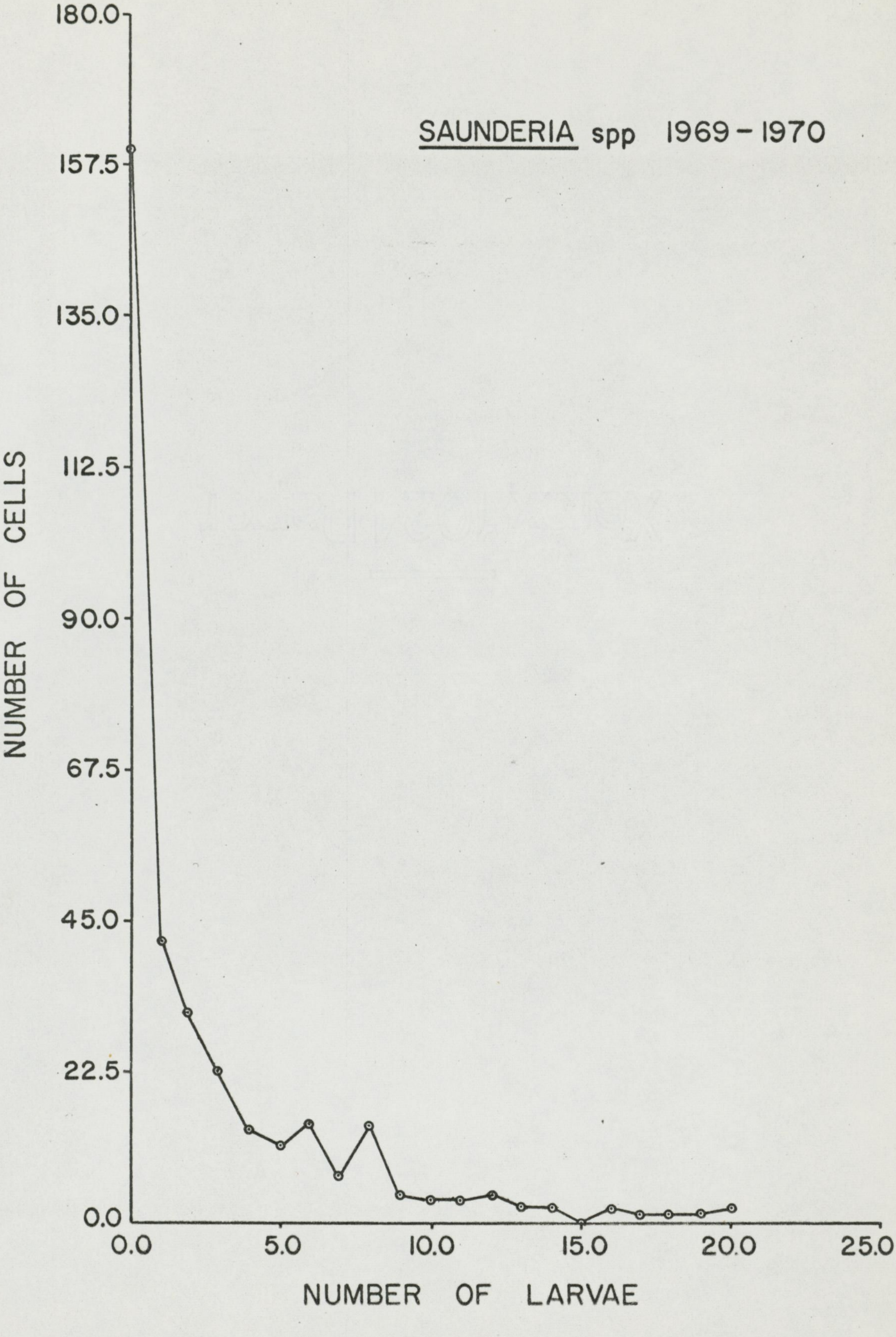

SAUNDERIA spp 1969 - 1970
NUMBER OF CELLS
NUMBER OF LARVAE
180.0
157.5
135.0
112.5
90.0
67.5
45.0
22.5
0.0
0.0
5.0
10.0
15.0
20.0
25.0

Fig. 20 - Graph showing a frequency distribution for *P. alaskensis* larvae sampled in 1969-70. (Numbers of larvae plotted against the number of cells containing those larvae.)

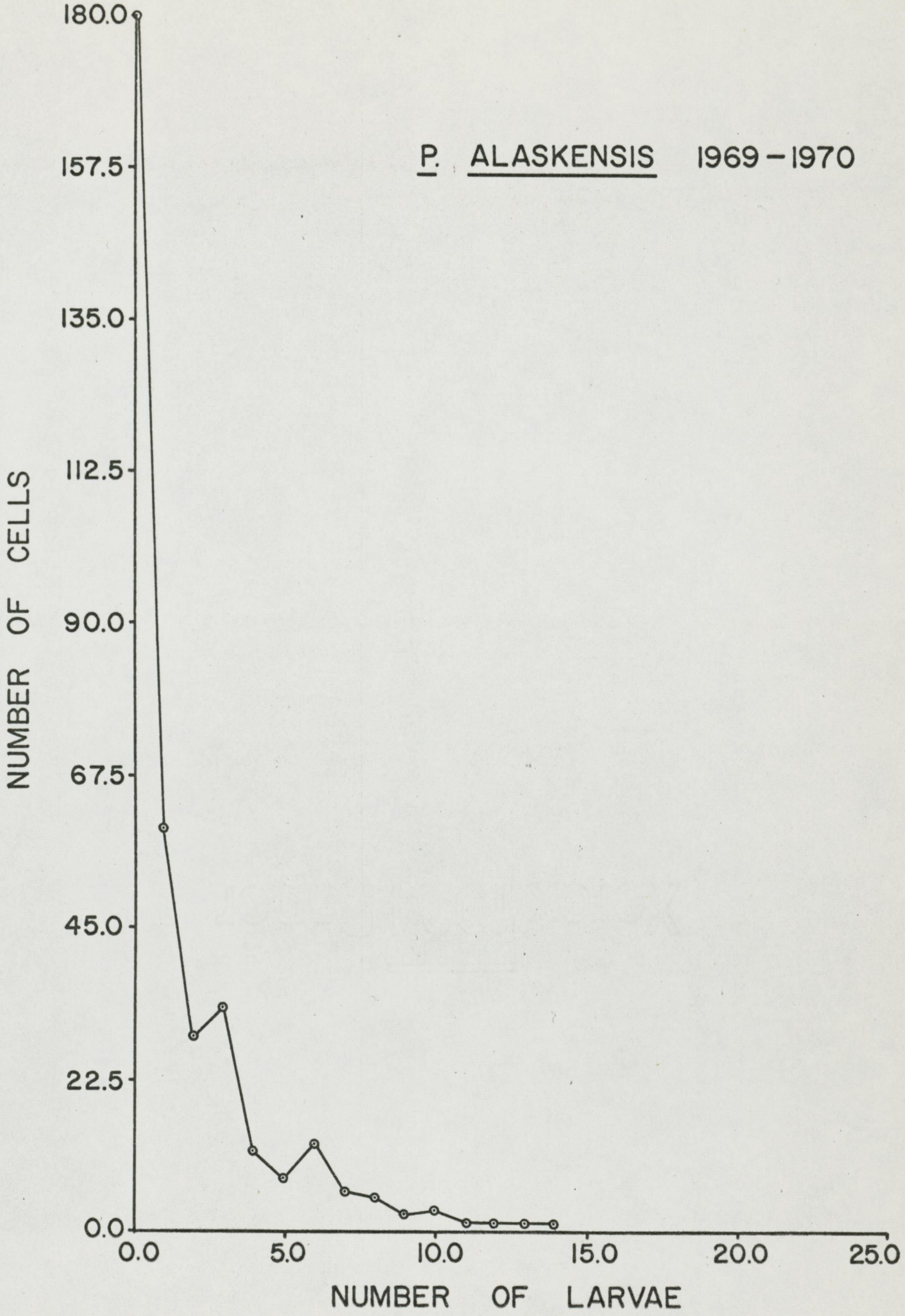

P. ALASKENSIS 1969-1970
NUMBER OF CELLS
180.0
157.5
135.0
112.5
90.0
67.5
45.0
22.5
0.0
0.0
5.0
10.0
15.0
20.0
25.0
NUMBER OF LARVAE

Fig. 21 - Graph showing the mean larval densities of *Saunderia* spp. for each month plotted against the months of the sampling period (June 1969 to June 1970). Also shown is an inshore water temperature against month's curve.

95% confidence limits indicate July, September and October as being significantly different from February, March and April.

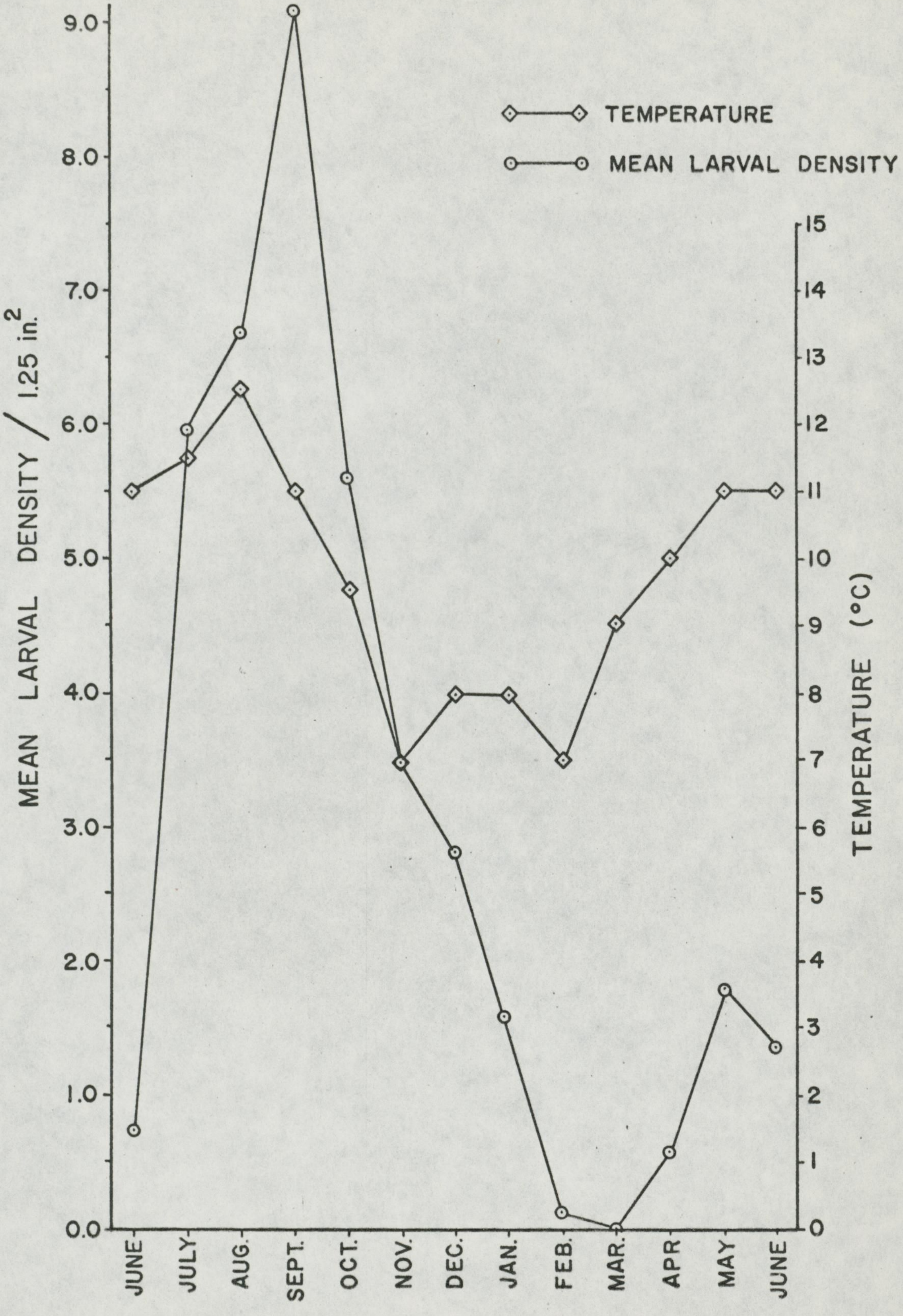

◇—◇ TEMPERATURE
⊙—⊙ MEAN LARVAL DENSITY
MEAN LARVAL DENSITY / 1.25 in.^{2}
9.0
8.0
7.0
6.0
5.0
4.0
3.0
2.0
1.0
0.0
TEMPERATURE (°C)
15
14
13
12
11
10
9
8
7
6
5
4
3
2
1
0
JUNE
JULY
AUG.
SEPT.
OCT.
NOV.
DEC.
JAN.
FEB.
MAR.
APR
MAY
JUNE
MONTHS

Fig. 22 - Graph showing the mean larval densities of *P. alaskensis* for each month plotted against the months of the sampling period (June 1969 to June 1970). Also shown is an inshore water temperature against month's curve.

95% confidence limits indicate September, October, November and January as being significantly different from February, March and April.

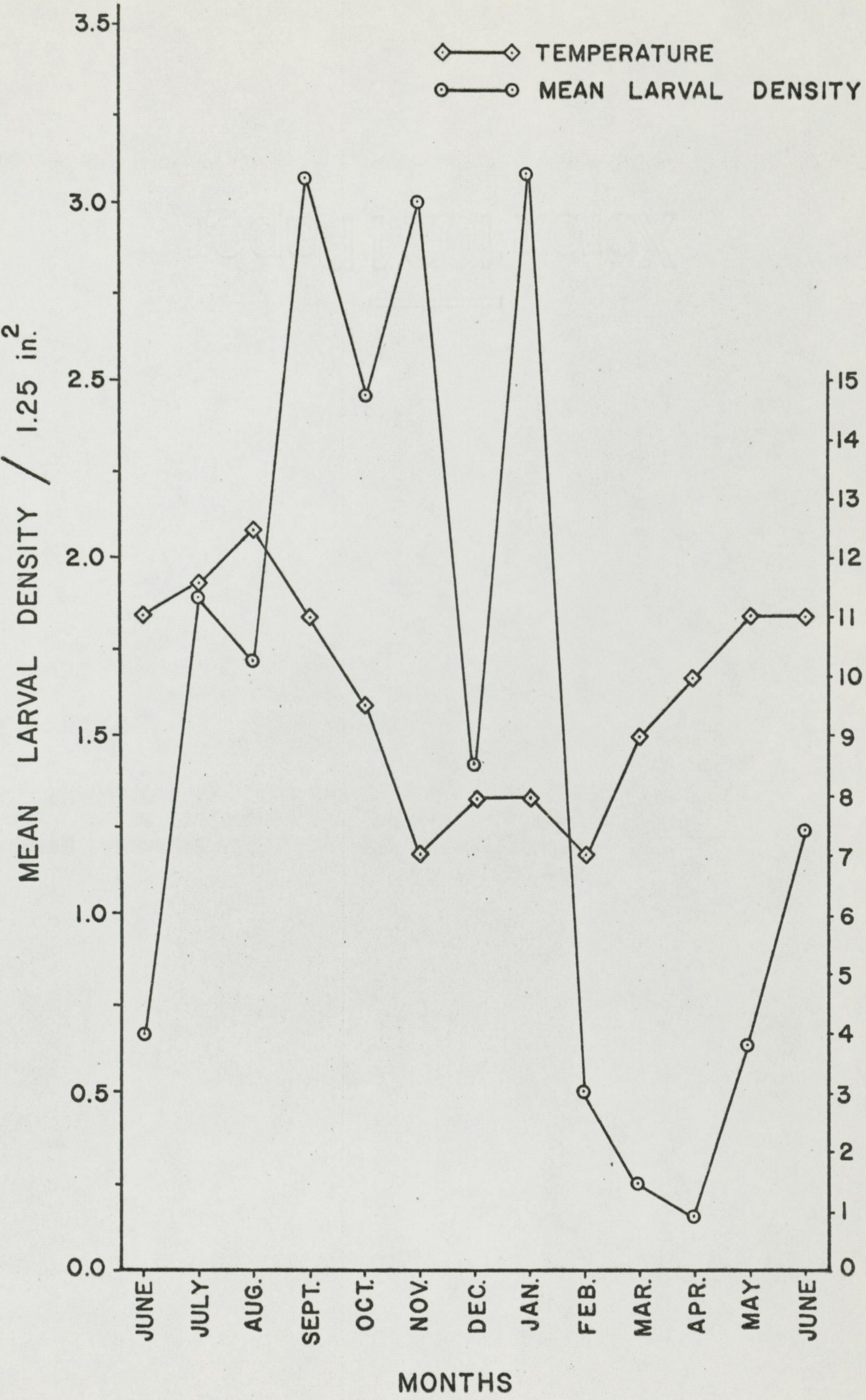

TEMPERATURE
MEAN LARVAL DENSITY
MEAN LARVAL DENSITY / 1.25 in.^{2}
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
TEMPERATURE (°C)
15
14
13
12
11
10
9
8
7
6
5
4
3
2
1
0
JUNE
JULY
AUG.
SEPT.
OCT.
NOV.
DEC.
JAN.
FEB.
MAR.
APR.
MAY
JUNE
MONTHS

TABLE XI

TESTING THE FIT OF DATA FOR *SAUNDERIA* SPP. TO THE NEGATIVE BINOMIAL DISTRIBUTION

x	x^2	Observed Frequency f	Expected Frequency	$\chi^2 = \frac{(f-e)^2}{e}$
0	0	160	168.30	0.41
1	1	42	49.15	1.04
2	4	31	28.92	0.15
3	9	23	19.98	0.49
4	16	14	14.65	0.03
5	25	11	11.23	0.00
6	36	15	8.83	4.31
7	49	7	7.07	0.00
8	64	15	5.73	15.00
9	81	4	4.69	
10	100	3		
11	121	3		
12	144	4		
13	169	2		
14	196	2 25.0	25.34	.005
15	225	0		
16	256	2		
17	289	1		
18	324	1		
19	361	1		
20	400	2		

$\chi^2 = 21.44 = \Sigma\frac{(f-e)^2}{e}$

critical region for

$\chi^2_{.05(17)} = 14.07$

If $\chi = 6$, 7 and 8 are averaged, $f = 12.3$, 12.3 and 12.3 and $\frac{(f-e)^2}{e} = 1.36$, 3.87 and 7.53 respectively. Hence $\chi^2 = 14.89$ as compared to 21.44.

TABLE XII

TESTING THE FIT OF DATA FOR *PARACLUNIO ALASKENSIS* TO THE NEGATIVE BINOMIAL DISTRIBUTION

x	x^2	Observed Frequency f		Expected Frequency	χ^2 $\frac{(f-e)^2}{e}$
0	0	180		179.99	0.00
1	1	60		63.90	.24
2	4	29		36.57	1.57
3	9	33		23.56	3.78
4	16	12		15.94	.97
5	25	8		11.18	.91
6	36	13		7.98	3.16
7	49	6		5.79	.01
8	64	5		4.22	
9	81	2			
10	100	3	14.00	14.28	.01
11	121	1			
12	144	1			
13	169	1			
14	196	1			

$\chi^2 = 10.64 = \Sigma \frac{(f-e)^2}{e}$

critical region for

$\chi^2_{.05(6)} = 12.6$

Therefore accept the hypothesis that the above distribution conforms to a negative binomial.

TABLE XIII

ANALYSIS OF VARIANCE FOR *Saunderia* SPP. AND *P. alaskensis* TO DETERMINE TEMPORAL (MONTHS) AND BLOCK EFFECTS

Saunderia spp.

Source of Variation	D. of F	Sums of Squares	Mean Squares	F Ratios
		Band no. 1		
Blocks	4	7.785	1.946	0.476 N.S.(C.L.=2.61)
Months	12	339.587	28.299	6.925 *
Error	48	196.166	4.087	
Total	64	543.538		
		Band no. 2		
Blocks	4	97.726	24.432	1.73 N.S.(C.L.=2.61)
Months	12	845.208	70.434	4.976 *(C.L.=2.00)
Error	48	679.441	14.155	
Total	64	1622.375		

* = significant at the 5% level.
C.L. = Critical Level - these are approximate.

P. alaskensis

		Band no. 1		
Blocks	4	34.677	8.669	4.745 *(C.L.=2.61)
Months	12	45.474	3.789	2.074 *(C.L.=2.00)
Error	48	87.706	1.827	
Total	64	167.857		
		Band no. 2		
Blocks	4	26.703	6.676	3.243 *(C.L.=2.61)
Months	12	88.490	7.374	3.582 *(C.L.=2.00)
Error	48	98.812	2.059	
Total	64	214.005		

and are illustrated in Figs. 21 and 22. However, the block effects for *P. alaskensis* were investigated using a Student-Neuman-Keuls Test (Sokal and Rohlf, 1969) to determine the blocks between which significant difference(s) existed (Table XIV). This test indicated that block 4 was significantly different from the other blocks at the 0.05 level for both bands 1 and 2.

Finally a Sign Test (Li, 1964) was applied to compare band 1 with band 2 throughout the data. The results of this test are given in Table XVI and show no significant difference between the number of larvae sampled in band 1 (*B. fascopurpurea)* and those sampled in band 2 (*E. linza* and *E. intestinalis)*.

D. FOOD CONSUMPTION

It was found that larvae of both *Paraclunio* and *Saunderia* could successfully feed on *Ulva* sp. or *Monostroma* sp. under laboratory conditions. This observation may not apply in the field since the algae were ground in a mortor and pestel before addition to the cultures. Also evident in culture was the fact that the larvae would also feed upon the ciliate-bacterial film which formed on the bottom of the dishes and adhered to the pieces of algae.

Gut analyses of field-collected larvae revealed that *P. alaskensis* and *Saunderia* spp. fed on both diatoms and green algae, and that diatom feeding was not restricted to early instar larvae (Tables XVI and XVII). There was also strong evidence that larvae of both genera are able to feed selectively on diatoms. This is illustrated in Table XVI where it can be seen that the dominant diatom in the larval guts (*Navicula* sp.) was rare in the substrate sample. Also evident (Table XVII) was the fact that

TABLE XIV

STUDENT-NEUMAN-KEULS TEST TO DETERMINE BETWEEN WHICH BLOCKS A SIGNIFICANT DIFFERENCE EXISTS FOR *P. ALASKENSIS*

Band No. 1

# of Groups Being Compared	2	3	4	5
Q	2.844	3.421	3.764	4.008
L.S.R.	1.066	1.282	1.411	1.502

Blocks	1	2	3	4	5
Means	0.73	0.79	0.61	2.58	1.32
	a	a	a	b	a

Means followed by the same letter are not significant at the 5% level.

Band No. 2

# of Groups Being Compared	2	3	4	5
Q	2.844	3.421	3.764	4.008
L.S.R.	1.133	1.363	1.410	1.597

Blocks	1	2	3	4	5
Means	1.21	1.05	0.85	2.65	1.28
	a	a	a	b	a

Means followed by the same letter are not significant at the 5% level.

TABLE XV

SIGN TEST COMPARING BAND 1 WITH BAND 2 THROUGHOUT THE SAMPLING TIME. MEAN NUMBER OF LARVAE PER THREE CELLS IN BAND 1 WAS COMPARED TO THE SAME IN BAND 2 FOR EACH SAMPLING.

SAUNDERIA SPP.

Block #	χ^2 Value
1	2.00
2	0.00
3	1.60
4	0.33
5	0.00

P. ALASKENSIS

Block #	χ^2 Value
1	0.50
2	1.28
3	0.11
4	0.40
5	0.11

Critical Value = 3.84 for χ^2 at the 5% level and 1 Degree of Freedom.

There are no significant values.

TABLE XVI

GUT ANALYSES OF LARVAE COLLECTED FROM ARBUTUS COVE

Habitat Sample	Collection Date	Dominant Species	Common Species	Rare Species
Arbutus Cove -mid littoral-	May 6, 1970	*Melosira moniliformes*		*Navicula* sp. *Striatella* sp. *Fragilaria* sp.

Larva #	Species	Life Stage	Gut Contents: Algae: Dominant	Common	Rare	Other
1	*P. alaskensis*	late instar	*Navicula* sp.	*Striatella*	*Melosira* sp. *Arachnoidiscus* sp.	
2	*P. alaskensis*	late instar	*Navicula* sp.		*Melosira* sp. *Striatella* sp.	
3	*P. alaskensis*	late instar	*Navicula* sp.		*Melosira* sp. *Striatella* sp.	A few juvenile green cells.
4	*Saunderia* sp.	mid instar	*Navicula* sp.			A few juvenile green cells.
5	*P. alaskensis*	late instar	*Navicula* sp.		*Fragillaria* sp. *Ulothrix* sp. *Melosira* sp. *Cocconeis* sp.	
6	*P. alaskensis*	late instar	*Navicula* sp.	*Fragillaria*	*Melosira* sp. *Cocconeis* sp.	
7	*P. alaskensis*	late instar	*Navicula* sp.		*Melosira* sp. *Cocconeis* sp.	
8	*Saunderia* sp.	late instar	*Navicula* sp.		*Melosira* sp. *Fragillaria* sp. Green sporlings	

TABLE XVI (continued)

GUT ANALYSES OF LARVAE COLLECTED FROM ARBUTUS COVE

Larva #	Species	Life Stage	Gut Contents			
			Algae			Other
			Dominant	Common	Rare	
9	*P. alaskensis*	late instar	*Navicula* sp.	*Fragillaria*	*Cocconeis* sp.	
10	*P. alaskensis*	late instar	*Navicula* sp.		*Melosira* sp. *Cocconeis* sp.	

TABLE XVII

GUT ANALYSES OF LARVAE COLLECTED FROM THE VICTORIA SEAWALL

Habitat Sample	Collection Date	Dominant Species	Common Species	Rare Species
Seawall -high littoral-	May 7, 1970	*Enteromorpha linza*	*Navicula* sp. *Achnanthes* sp. Blue-green algae *Fragillaria* sp.	*Cocconeis* sp. *Licmorphora* sp. *Pleurosigma* sp.

Larva #	Species	Life Stage	Gut Contents: Algae: Dominant	Common	Rare	Other
1	*P. alaskensis*	late instar	*Enteromorpha linza*	*Navicula* sp. *Achnanthes* sp. Blue-greens		*Enteromorpha* - mostly sporlings and younger growing parts.
2	*P. alaskensis*	late instar	*Navicula* sp.	*Enteromorpha linza* *Achnanthes* sp.	*Fragillaria* sp. *Licmorphora* sp.	Low food density.
3	*P. alaskensis*	late instar	*E. linza* (large chunks) *Navicula* sp.	*Fragillaria* sp. *Achnanthes* sp.		High Food density.
4	*Saunderia* sp.	late instar	*Achnanthes* sp.	*Navicula* sp.	*Fragillaria* sp.	
5	*Saunderia* sp.	mid to late	*Achnanthes* sp.			Gut almost empty.
6	*P. alaskensis*	late instar	*E. linza*		*Navicula* sp. *Achnanthes* sp.	Big chunks of *E. linza* mostly young sporlings.
7	*P. alaskensis*	late instar	*E. linza*		*Navicula* sp. *Achnanthes* sp. *Melosira* sp.	
8	*Saunderia* sp.	late instar	*E. linza*			Small chunks younger parts.

TABLE XVII (continued)

GUT ANALYSES OF LARVAE COLLECTED FROM THE VICTORIA SEAWALL

Larva #	Species	Life Stage	Gut Contents			
			Algae			Other
			Dominant	Common	Rare	
9	*Saunderia* sp.	late instar	*Achnanthes* sp.		*Navicula* sp. *Licmorphora* sp.	All diatoms.
10	*P. alaskensis*	late instar		*E. linza* *Achnanthes* sp.	*Navicula* sp.	

P. alaskensis preferred the younger parts of green algae (*E. linza* in this case.

E. FOOD CHAIN ASSOCIATIONS

The way in which chironomids fit into the intertidal food chain is of general interest although few experiments were designed to answer this question. Some insight was obtained from hours of observing these animals on the shore. It would seem obvious that the adults since they fly, are additions to the terrestrial food chains.

Some evidence in support of this statement was found while observing swallows (Hirudinidae) flying parallel to the seawall, behavior that was observed only when adult chironomids were emerging. In the intertidal habitat mites and sculpins were observed to feed on both adults and larvae of these genera. The results of gut analyses on tide pool sculpins (cottids) is presented in Table XVIII.

TABLE XVIII

GUT ANALYSES OF TIDE POOL SCULPINS

Date Collected	Species of Sculpin	Collection Site	No. of Insects in Fish Stomach			
			P. alaskensis		*Saunderia* spp.	
			Adults	Larvae	Adults	Larvae
1969						
Mar. 2	*O. maculosus*	Otter Point	1	-	-	-
Mar.10	*O. maculosus*	Foul Bay	-	7	-	14
Mar.10	*O. maculosus*	Foul Bay	-	6	-	6
Apr. 3	*Oligocottus* sp.	Otter Point	1	-	-	1
Apr. 3	*Oligocottus* sp.	Otter Point	2	-	2	1
May 6	*O. maculosus*	Foul Bay	-	-	1	-

Each of the above dates indicates the gut analysis of one fish.

No pupae were found in these analyses.

DISCUSSION

A. SPECIES IDENTIFICATION

The eggs of *Saunderia* spp. and *P. alaskensis* differ both morphologically and in the way in which they are deposited. Members of *Saunderia* lay their eggs in a mass surrounded by a gelatinous matrix which becomes attached to the substrate by means of an adhesive area. The eggs of *P. alaskensis*, on the other hand, are laid singly or in small clumps and are deposited into or onto the substrate. Since it is generally conceeded that insects evolved from a terrestrial myriopod stock (MacKerras, 1950) and then invaded freshwater, and since freshwater species of Chironomidae generally lay their eggs in gelatinous masses while those of terrestrial species are laid singly or in clumps, it may be hypothesized that in the two genera studied here we have convergence from different habitats. It is possible that *Paraclunio* spp. adapted to marine life from a terrestrial habitat whereas *Saunderia* spp. evolved from a freshwater stock. The "brown-green" colour that is characteristic of the eggs of *P. alaskensis* permits further ecological speculation. Ostensibly it seems that this colour functions to conceal the eggs. However, since the colour is not acquired until about a week after oviposition the camoflage hypothesis is less acceptable. It is possible, therefore, that this colour is a product of the hardening of the egg chorion which acts to protect the developing larva just as the gelatinous covering does in *Saunderia* spp.

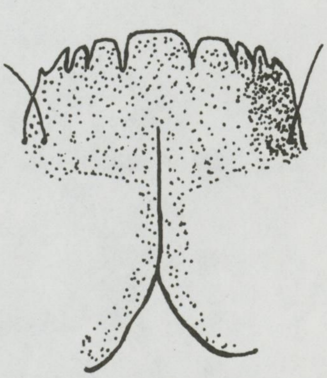
The larvae of *P. alaskensis* upon emergence are active and immediately begin moving about on the substrate while those of *Saunderia* spp. remain relatively inactive for a few days within the gelatinous matrix before breaking out. Comparison of the labial features of the larvae with those presented by Saunders (1928) (Fig. 23) resulted in some disagreement as to which larvae were associated with the adult stages. The results of this study revealed that *S. marinus* from culture corresponded closely in labial features to the larva described by Saunders as *S. (Camptocladius) pacificus*, while *S. clavicornis* from culture corresponded closely in labial features to those presented as *S. (Camptocladius) marinus*. Cultured *P. alaskensis* agreed with the drawings of Saunders. Although *S. pacificus* was not cultured some larvae were collected which were tentatively identified as this species. The labial features corresponded closely to those presented by Saunders (1928) as *S. (Camptocladius) clavicornis*, similarities being evident in the accentuated roundness of all labial teeth. However, these larvae do not show the medial tooth projecting as far anteriorly as portrayed by Saunders. These larvae cannot be positively associated with *S. pacificus* although, by elimination, this relationship can be hypothesized. Many intertidal habitats were examined in this study and no new species were discovered. If this larva does belong to a yet unknown adult it would seem that this adult is rare. The developmental times of 4, 5 and 7 months for *S. clavicornis*, *S. marinus* and *P. alaskensis* respectively should be considered only as approximations of those occurring naturally. Developmental time periods recorded in culture were variable, but where natural conditions cannot be duplicated exactly there are many possible factors which could have given these results. For example crowding in some cultures could have contributed to this variability, for it has been shown that where crowding occurs in chironomid populations there is a corresponding decrease in feeding activity (Kajak and Warda, 1968) which could, in turn, effect

Fig. 23 - Drawings of the labium attributed to

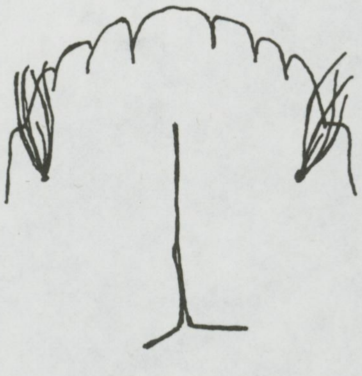
(a) *P. alaskensis*
(b) *S. marinus*
(c) *S. clavicornis*
(d) *S. pacificus*

by Saunders (1928).

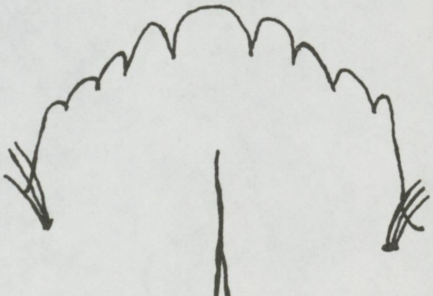
a



b



c



d

growth rates and thus generation time. In addition, the temperature was fixed during culturing at 10°C., which is not a natural phenomenon.

The cultured pupae of *S. marinus* and *S. clavicornis* agreed with Saunders descriptions. *P. alaskensis* pupae were especially distinctive with their truncated terminal abdominal segment and could hardly be confused with *Saunderia* spp. Saunders (1928) has proposed that this truncated terminal segment of the pupa of *P. alaskensis* is used as "a piston in the (larval) tube to force the pupa to the surface when ready to emerge". However, it was found that *P. alaskensis* was not able to emerge from the water surface even though prior to emergence the pupae floated to the surface. Adult emergence in a large number of marine chironomids (*Allochironomus crassiforceps* Kieffer, *Clunio* spp., etc.) occurs from the water surface and while their habitat is still under water. (Hashimoto, 1957; Palmen, 1962; Olander and Palmen, 1968). Emergence of this type occurs in the two cultured species of *Saunderia*. Unfortunately no information on emergence has been published for species closely related to *P. alaskensis*. It would seem however that because of the size of *P. alaskensis*, which is much larger than most chironomids, the surface tension of the water is one of the barriers against surface emergence. Many times in the laboratory adult *P. alaskensis* were observed to emerge almost completely only to have a wing, leg, or some other part of its body become attached to the water surface. It is hypothesized that this is due to the animal's weight which is such that it allows appendages to break the surface tension but the animal does not then have the strength to free itself. It is proposed that rather than being used to force the pupa from the tube the terminal disc is instead used to anchor the pupa to the tube's entrance. Pupal exuviae have been found in large numbers on the seawall with their anterior parts projecting from the larval tubes and the posterior segments still anchored within the tube. It is likely that this arrangement gives the emerging adult the extra stability and leverage that is needed for a swift emergence.

One of the basic differences between the adults of the two genera is body size. There is, however, some seasonal variation in the size of *P. alaskensis*. Saunders (1928) gives the range for males of this species as 6.6 mm body length in spring to 3.2 mm in late summer, which is in accord with data collected here. This phenomenon has also been reported from Japan for *Clunio tsushimensis* Tokunaga (Hashimoto, 1968) which, like *P. alaskensis*, propogates itself continuously throughout the year. Hashimoto found that "the mean monthly body length of *C. tsushimensis* varies under the influence of annual changes in the temperatures of the sea" and that there is a time lag of approximately one month between a change in temperature and a change in body size. He also found that the summer and winter forms could be readily reproduced in the laboratory by manipulating the temperature. This was not tested in the case of *P. alaskensis*.

No such marked size differences were noticed in *Saunderia* spp. even though these species reproduce throughout the year and presumably are subject to the same temperature influences as *P. alaskensis*. Perhaps this effect is much less marked in *Saunderia* spp.

As mentioned earlier the four species studied fit into Hashimoto's (1962) two categories of "Flying" and "Walking" types. This hypothesis proposes a progressive adaptation to the marine environment from swarming types such as *S. pacificus* and *S. marinus* to non-swarming "Walking" types such as *S. clavicornis* and *P. alaskensis*. This progressive specialization is reflected in the male antennae of the four species where a shortening and broadening of the terminal antennal segment occurs with a corresponding reduction in the number of setae on the antennae (Fig. 24). There is little doubt that these modifications are related to the loss of the swarming habit in *P. alaskensis* and *S. clavicornis*.

B. DISTRIBUTION

Hashimoto (1962) states "In general, the habitat of marine chironomids is restricted to the intertidal zone of the rocky shore. (Sic) Sandy beach never harbors marine chironomids." This statement has been verified for *P. alaskensis* and *Saunderia* spp. Their tube building and food preferences would seem to eliminate pure sandy shores as a suitable habitat.

P. alaskensis and *S. clavicornis* are the most ubiquitous of the four species occurring commonly at all four beaches. In fact, these two species have been found to be the most highly modified for intertidal life and therefore would be expected to be most commonly encountered.

By far the largest emergences of adults occurred at night and in the Fall. *S. clavicornis* was observed on the intertidal rocks in vast numbers and as described for *Clunio* spp. "the rocks were covered with powdery 'snow'" (Tokunaga, 1935). This was not as evident with *S. marinus* which tends to fly more. Often an emergence of adults occurred on the rocks offshore from the seawall when there was no emergence on the seawall. Palmén and Lindeberg (1959) state that "the emergence of those species that inhabit a wide range of depths with often very different temperature conditions extends over a considerable period of time, the individuals of shallow-water populations emerging much earlier than those

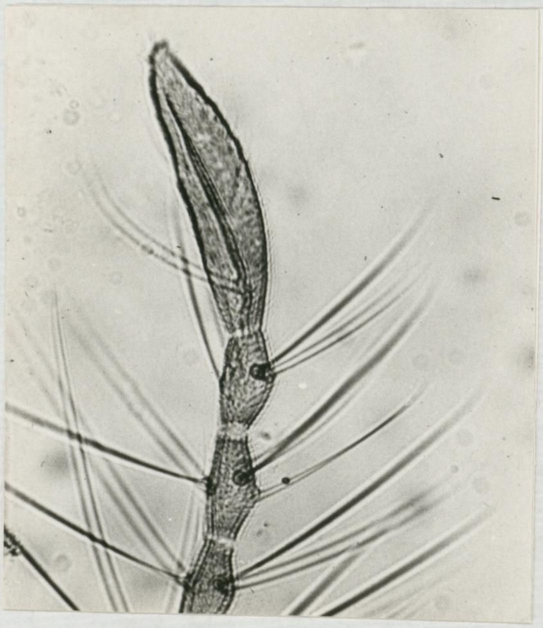
Fig. 24 - Photographs showing the terminal antennal segments of the males of:

A. P. *alaskensis*
B. S. *clavicornis*
C. S. *marinus*
D. S. *pacificus*

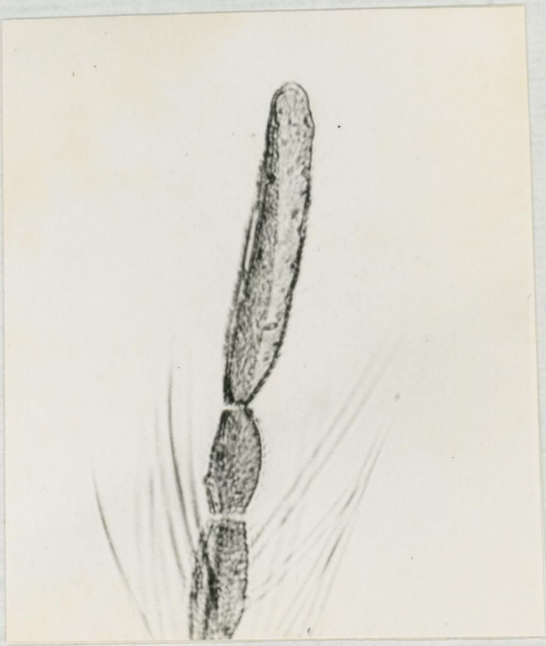
(x 200)

A

B



C



D

which live in deeper waters." Palmen (1962) also states "there is a clear correlation between the water temperature and the onset and subsequent course of emergence." This "temperature-emergence" hypothesis which states that with an increase in cumulative day-degrees accelerated emergence occurs,could, by extrapolation, explain the situation that one finds at the seawall. The population inhabiting the rocks off the wall would be exposed to a much different temperature regime. According to Miller (1941), Mundie (1957) and Palmen (1962) the onset of emergence in Chironomidae is correlated with the sum of the cumulative day-degrees and although no data is available for the populations at the seawall a considerable difference between the two would be expected.

Exposure does not appear to determine the presence or absence of these insects on a given shore. It may, however, drastically effect their emergence times and location on the shore due to differing temperature regimes and the spray zone associated with increased exposure.

It appears that these insects are very adaptable in terms of habitats and food sources. Exposed shores differ markedly in green algae present but do not limit the occurrence of the larvae. The necessity for adaptability is obvious when one considers the transient nature of the algae on any one shore throughout a year.

The distributional and ecological data collected along the B.C. coast confirmed a number of hypotheses that had been formed from local observations. For example, it is now obvious that *S. clavicornis* is common on both exposed and sheltered shores. In addition as long as the shore is rocky and not exclusively sand these animals are likely to be present. Only *P. alaskensis* and *S. clavicornis* were collected on exposed shores, *S. marinus* and/or *S. pacificus* being absent. It is also significant that *S. clavicornis* and *P. alaskensis* have evolved in the direction of "sexualisomorphic walking specialization". That is, they fit into Hashimoto's (1962) "Walking Type" category and in addition the sexes have become more alike in secondary sexual characteristics. According to Hashimoto (1962) this type of specialization occurs where flight is not favourable, as on rocky, windy shores. Sexual isomorphism is not as evident in the males of *S. marinus* and *S. pacificus* where the antennae and palps are longer and the sensory hairs more numerous than those of the females.

Specialization can be related to distribution, the two most specialized species, *P. alaskensis* and *S. clavicornis* being encountered most often and on the most diverse types of shores. *S. marinus* is intermediate and is found on protected shores while *S. pacificus*, the least modified, is rare and is seldom encountered.

C. ABUNDANCE

Until the present study little data were available for larval densities in marine Chironomidae. In certain areas *Chironomus atrella* (Townes) lives in protected coves of low salinity and Anderson and Hitchcock (1968) have reported larval densities of 4316/ft.^{2} in mud dredges taken in July. This figure is comparable with maximum densities found for *Saunderia* spp. of 4838/ft.^{2} collected in the Fall at the Victoria seawall. *P. alaskensis* has been found to reach a maximum density of 1613/ft.^{2}. Stuart (1941) found maximum densities of approximately 425/sq.ft. for *Cricotopus fucicola* Edwards, a brackish water chironomid found only in the high intertidal pools on the Scottish coast.

The most obvious results of the analysis of variance carried out on the seawall population are the significant F values which indicate a significant fluctuation in the larval populations within the year.

The non-significant block effect for *Saunderia* spp. indicates a relatively uniform distribution while block effects for *P. alaskensis*, when analysed with a Student-Neuman-Keuls Test (See Table XIV), indicate only block 4 as being significantly different (Figs. 25 and 26). The significance of block 4 having a larger larval density can perhaps be explained by the association between *B. glandula* and these larvae. Block 4, and to a smaller extent block 5, had a larger population of barnacles which started as "spat" in August and September, 1969. It can be seen from the summarized data that larger scores in block 4 begin in September and the trend continues into January, 1970.

Also to be considered is the question of whether or not the larvae prefer one band over another. The two algal bands are characterized by *Bangia fascopurpurea* (one of the few high intertidal Rhodophyceae) and *Enteromorpha linza*. A Sign test showed that for both genera of Chironomidae there was no significant preference for either band. Saunders (1928) stated that red algae were unfit food for these larvae so it must be assumed that the diet consisted largely of diatoms - a food source shown to be utilized by these larvae. These results indicate that the type of alga is not such an important factor governing the distribution of larvae as was previously thought.

It has been shown that the distribution of *P. alaskensis* larvae in the sample area is described closely by a negative binomial distribution ($\chi^2\ .05^{(6)} = 10.64$). The data for *Saunderia* spp. also fits the negative binomial even though the $\chi^2_{(10)}$ value of 21.44 is much above the critical $\chi^2_{(.05,10)}$ value of 14.07. If one considers individual χ^2 values in

Fig. 25 - Graph showing the mean number of *P. alaskensis* larvae (calculated for the 13 month sampling period) in band 1 plotted against each block.

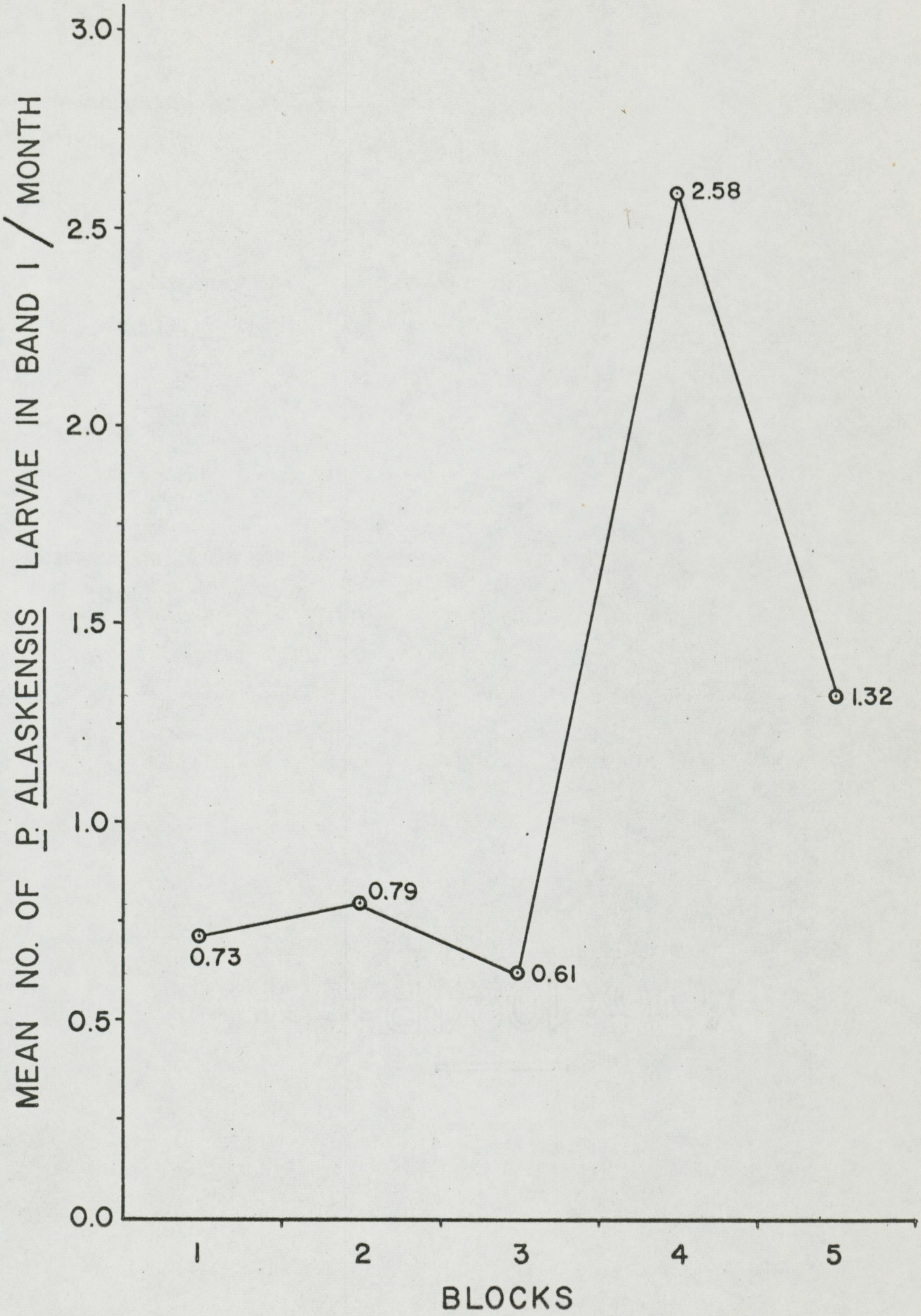

MEAN NO. OF P. ALASKENSIS LARVAE IN BAND I / MONTH
3.0
2.5
2.0
1.5
1.0
0.5
0.0
1
2
3
4
5
BLOCKS
0.73
0.79
0.61
2.58
1.32

Fig.26 - Graph showing the mean number of *P. alaskensis* larvae (calculated for the 13 month sampling period) in band 2 plotted against each block.

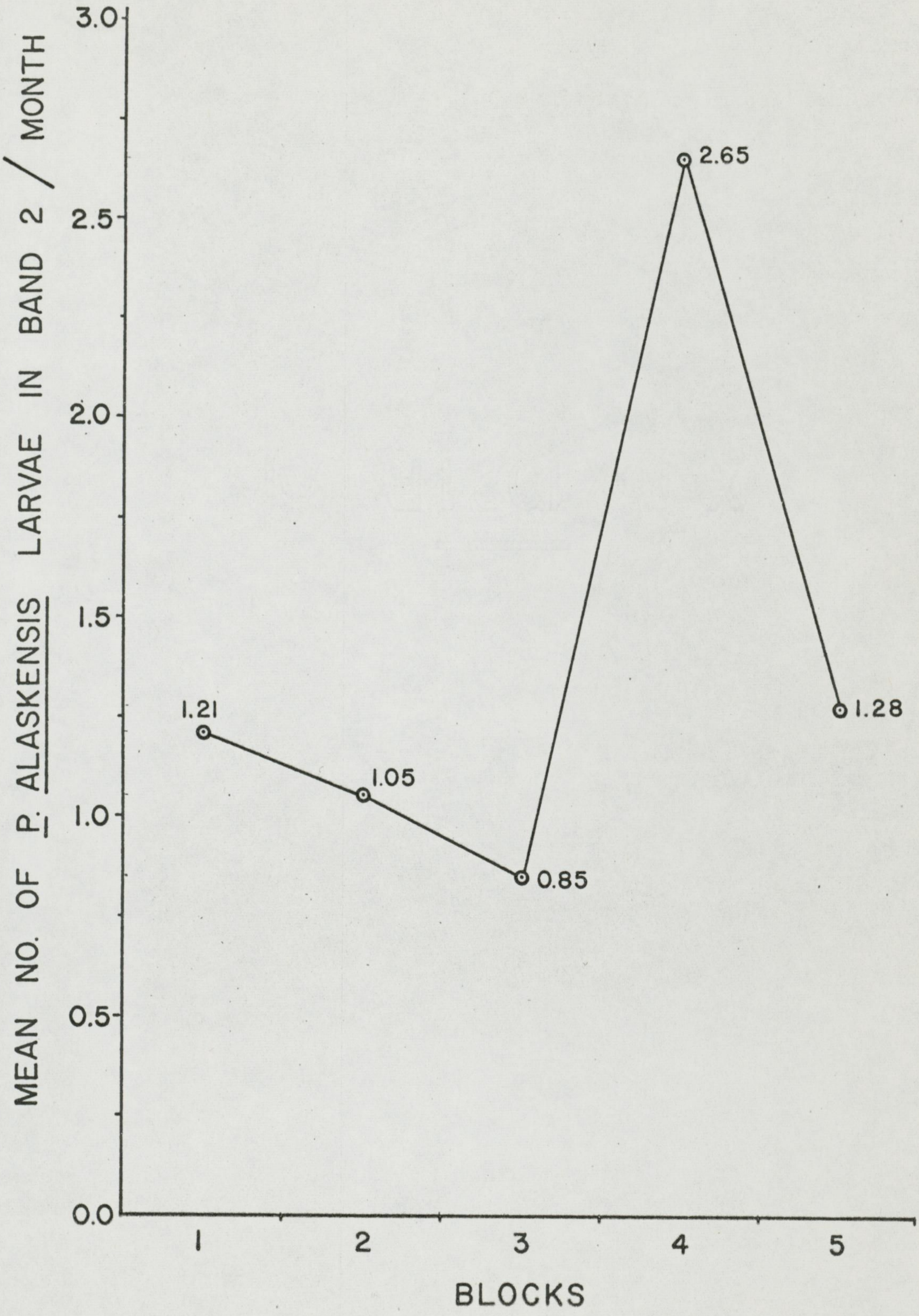

MEAN NO. OF P. ALASKENSIS LARVAE IN BAND 2 / MONTH
3.0
2.5
2.0
1.5
1.0
0.5
0.0
1.21
1.05
0.85
2.65
1.28
1
2
3
4
5
BLOCKS

Table XII (far right column) one value, namely the frequency observed of 15 for x = 6, contributes 70% to the $\chi^2_{(10)}$ value of 21.44. In fact, the averaged frequencies for x = 6, 7 and 8 yield a $\chi^2_{(.05,10)} = 14.89$ which approaches the critical value of 14.07. It is proposed that this distribution is still acceptable as conforming to a negative binomial distribution.

The negative binomial is by no means new to Entomology. "Most commonly in ecological studies the variance will be found to be larger than the mean, that is, the distribution is contagious, the population is clumped or aggregated. Many contagious insect populations that have been studied can adequately be expressed by the negative binomial distribution" (Southwood, 1966). The negative binomial indicates a contagious or clumped population as compared to the Poisson distribution which indicates a random occurrence of the population. The negative binomial is described by two parameters; the mean and the exponent K, where K is a measure of the amount of contagion. Generally K has a value of about 2, higher values indicating an approach to randomness; K values of less than 2 indicate a higher degree of contagion (Southwood, 1966). A modification of Bliss and Fisher's (1953) method was used to test the fit of data to this distribution (Appendix H). Once K has been calculated it is then possible to calculate the mean size of a clump using Arbous and Kerrich's (1951) formula:

$$\lambda = \frac{\bar{x}}{2K} \nu$$

where $\bar{x}$ = the mean, ν is a function with a χ^2 distribution with 2K degrees of freedom and λ = the number of individuals in the aggregation for the probability level, here taken as 0.5. Southwood (1966) points out that contagion, as suggested by a fit to the negative binomial, may be due either to active aggregation of the animals or to environmental pressure. "Dr. R.E. Blackith has suggested that if mean size of a clump is calculated using Arbous and Kerrich's (1951) formula and this is found to be less than 2 then the 'aggregation' would seem to be due to some environmental effect and not to an active process. Aggregations of two or more insects could be caused by either factor." (Southwood, 1966). Table XIX shows that for both genera values of k are less than 2 indicating that the larval contagion is due to some environmental factor(s). A possible cause of larval contagion, given that it is due to environmental pressures, could be the availability of tube-building sites. It was observed that larvae often build tubes in a crack, depression or any small irregularity in the rock surface. Perhaps the larvae need surface irregularities onto which they can attach the secretions from the salivary glands that are used for case building. The environmental pressure would not seem to lie in food availability since this is uniformly available.

There is little known on population fluctuations in intertidal chironomid larvae. Large fluctuations throughout the year corresponding with the mass adult emergences could, however, be expected. If the species were univoltine one would expect a relatively constant larval population with a sudden drop in density near the time of pupation and adult emergence. The density would then increase after the eggs had been laid and the new larval population emerged. If a species is multivoltine, however, one would expect larval population fluctuations throughout the year according to the number of generations per annum. For example, consider a population of a species that is multivoltine, as are the four species under study here.

TABLE XIX

APPLICATION OF ARBOUS AND KERRICH'S (1951) FORMULA TO DATA FOR *SAUNDERIA* SPP. AND *P. ALASKENSIS*

$\hat{k}$ for *Saunderia* spp. = 0.33 (calculated as in Appendix 1)
$\hat{k}$ for *P. alaskensis* = 0.45 (calculated as in Appendix 1)

Saunderia spp.

$$\lambda = \frac{\bar{x}}{2k}\gamma = \frac{2.5364}{2 \times 0.33}(\gamma)0.455 = \underline{1.749}$$

γ is a function with a χ^2 distribution with 2k degrees of freedom and was taken as 1 (.45 x 2), at the 5% level.

P. alaskensis

$$\lambda = \frac{\bar{x}}{2k} = \frac{1.5859}{0.90}\ 0.455 = \underline{0.82}$$

γ is given the value of 1 as described above for *Saunderia* spp.

Since this species is growing in the larval stages all year its growth rates will vary according to the temperature (Olander and Palmen, 1968). The winter generations, growing at lower temperatures, will take a longer time to develop from egg to adult than those growing during the spring or summer. If there are a number of generations in the population at a time (multivoltine) this could result in two groups of larvae emerging as adults at approximately the same time even though one group had been laid months earlier than the other. This phenomenon could be visualized as occurring in larvae that were laid as aggs in late winter (December or January) and another group in spring or early summer (April or May). The former, to start with, would have slow larval development whereas the latter group would have accelerated development in all stages. It is feasible that the emergence of these two generations would be only one month apart even though the eggs were deposited four months apart. It can be seen from this example that if there are a number of generations in the population, all developing in different stages, then one could expect large emergences of adults at certain times of the year and hence larger populations of larvae at certain times of the year.

Figs. 21 and 22 show the fluctuations that would be predicted by the above hypothesis. In addition they show a temperature correlation with larval density. Thus the maximum inshore water temperatures occur in August and the maximum larval populations in September; the minimum water temperatures in November to February and the minimum larval populations in January to April. The graph for *Saunderia* spp. is more uniform than for *P. alaskensis* but generally this correlation can be sean in both genera.

There is another possible explanation for the large population fluctuations described in this study (Kajak, 1970, Personnal Communication). Going back to the hypothetical larval population it would be expected of a univoltine species that larval densities would be relatively stable, except for a gradual decline in numbers due to mortality, up until the time of emergence. This concept when applied to a multivoltine species is different, however, since there are generations developing at different times of year. In this case one would expect mortality rates to vary during the year along with the varying environmental pressures (temperatures, predators, tides, etc.). Hence one might find a summer generation with a low mortality rate while a late fall generation would have a high rate. In these cases one could predict variations in larval density as seen in Figs. 21 and 22.

In order to test these two hypotheses more information on the number of generations of larvae in the population at one time, the density of adult emergences throughout a year, and the rate of growth of larvae at varying temperatures is necessary.

D. FOOD CONSUMPTION

The most complete recent work on chironomid feeding is that of Walshe (1951) who describes the various feeding mechanisms of chironomid larvae. The feeding habits of *P. alaskensis* and *Saunderia* spp. correspond most closely to Walshe's description of feeding in "plumosus-type larvae" (forms related to *Tendipes plumosus*). She describes feeding as consisting of "frequent extensions of the body out of either of the entrances of the glass tubes and with their mouth-parts and anterior prolegs scraping up particles of mud in the vicinity. Occasionally larvae ate particles which had dropped into the tubes." (Glass tubes were used in which the larvae built their cases.)

The discovery that P. *alaskensis*, S. *marinus* and S. *clavicornis* could successfully feed on *Ulva* sp. is interesting from two aspects. In the natural habitat these larvae are rarely found in *Ulva* sp. which is too foliose and provides little cover and few niches for tube construction. Secondly it provides evidence that these animals are feeding directly on the green algae and not just using it as cover.

There have been few investigations of chironomid feeding in which the contents of the alimentary tracts of the larvae have been compared to the floral composition of the substrate. Kajak and Warda (1968) have shown that larvae are able to select algae from the sediment and that even certain groups of algae can be selected. The selection of algae is not determined by their digestibility or easy assimilation, since only diatoms are easily digested (Kajak and Warda, 1968). The gut analyses of this study confirm these findings and indicate that larvae of these genera feed on green algae when available although their main food source is diatoms.

E. FOOD CHAIN ASSOCIATIONS

The way in which insects fit into the overall ecology of the intertidal environment is of special interest. The mechanism behind the functioning of ecosystems is of prime importance today and in order to understand the system one must also understand the component parts of that system. Food chains are one of the most important ecological pathways since it is through these that one species most effects another.

There are a number of important predators of intertidal chironomids the most important of which are mites, sculpins and young salmon (Annan, 1958).

Marine mites (family Halacaridae) make up twenty-three known genera of which at least eleven exist on the northern Pacific coast (Light, et al., 1961) and many are predatory species inhabiting almost every conceivable marine environment. Paterson (1970) has reported that freshwater mites are significant predators of chironomid larvae and it can be inferred that the same phenomenon exists in the marine environment.

It has been shown in this study that intertidal sculpins are also important predators of chironomid larvae and adults. Nakamura (1966, Personal Communication) conducted an extensive study of the diet of *Oligocottus maculosus*, a common tide-pool sculpin, and found chironomid larvae to be one of its major food items. Annan (1958) reports the feeding of young pink, chum and spring salmon on various intertidal chironomid larvae and pupae. The length of these fish ranged from 4.0 to 9.5 cm and therefore had newly migrated from freshwater. Data for the month of July indicated that up to 26% of the salmon examined had Chironomidae predominant in the stomach contents. It is not surprising that these insects are chosen by certain fish when one considers the importance of chironomid larvae in the diet of freshwater fishes.

In summary, the intertidal chironomids on the B.C. coast are worthy of further study both from the ecological point of view and from economic aspects. Little is known about salmon once they leave their freshwater habitat and it is possible that these insects play an important role in their early life.

CONCLUSIONS

1. All life stages of *Paraclunio alaskensis* and *Saunderia* spp. can now be identified from morphological characteristics. The larval instars can easily be separated by differences in labial characteristics.
2. *P. alaskensis* and *Saunderia* spp. can be cultured (in filtered seawater) under laboratory conditions and can be fed fragments of algae (*Ulva* spp., *Monostroma* spp.).
3. It is proposed that *Saunderia* spp. adapted to the intertidal environment from a freshwater species of chironomid while *P. alaskensis* from a terrestrial one.
4. Adults of *Saunderia* spp. emerged successfully from the surface of cultures while *P. alaskensis* adults were unsuccessful in surface emergence.
5. *P. alaskensis* has four larval instars and a developmental time of 204 days at 10°C. *Saunderia* spp. have four larval instars and *S. marinus* has a developmental time of 150 days, *S. clavicornis* 110 days at 10°C.
6. The truncated terminal abdominal segment of the *P. alaskensis* pupa probably serves as an anchor to hold the pupa at the entrance of the larval case during adult eclosion.
7. The four species of chironomids show, morphologically, a progressive adaptation to the intertidal environment. *P. alaskensis* and *S. clavicornis* are the most fully adapted, *S. marinus* intermediately and *S. pacificus* the least adapted.
8. The larvae studied occur on a variety of different types of shores but are never found on exclusively sand beaches.

9. Shore exposure was not found to determine the presence or absence of these insects.
10. Adult emergences occur throughout the year but are most extensive in the Fall.
11. *S. clavicornis* is the most ubiquitous of the species studied while *S. pacificus* is the most rare.
12. The range of the species studied has been found to include the Queen Charlotte Islands.
13. The distribution of the larvae of *Paraclunio* sp. and *Saunderia* spp. within their habitat is contagious and this is probably due to environmental factors rather than active aggregation of the larvae.
14. It is hypothesized that there are a number of overlapping generations per year and that large fall emergences are due mainly to the variable life span of the insects under variable temperature regimes.
15. Larval densities of 4316/ft.^{2} were recorded at the Victoria Seawall for *Saunderia* spp. and 1613/ft.^{2} for *P. alaskensis*.
16. The larvae of the four species feed on green algae and diatoms. It has been demonstrated that they can select certain groups of diatoms from the substrate.
17. Important predators of these intertidal chironomids are: mites, sculpins, and salmon fry.

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APPENDIX A

LARVAL MEASUREMENTS FROM LARVAE SACRIFICED FROM CULTURES OF *S. MARINUS, CLAVICORNIS,* AND *P. ALAKENSIS*

The larval instar measurements were taken with the hope that the instars of each species could be separated by head capsule width and length. "Dyar demonstrated that the head capsule of caterpillars increases in width with each molt by a geometrical progression, and once the factor is established for a species, this can be used as a criterion to determine larval instars" (Patton, 1963). This technique has also been used for instar determination in Chironomidae (Oka and Hashimoto, 1959; Anderson and Hitchcock, 1968).

Larvae were periodically removed from cultures that could spare them and generally 10 was the sample size. Three measurements were taken: head capsule length, head capsule width and body length. (See Oka and Hashimoto, 1959 for details of measurements.)

First instar measurements are presented for *P. alaskensis*, *S. marinus* and *S. clavicornis*. Later instar measurements are shown for *S. marinus* only.

Genus or Species	Instar	Mean Body Length	Mean Head Length	Mean Head Width	Sample Size
P. alaskensis	1st	0.072 mm	0.015 mm	0.012 mm	10
P. alaskensis	late 1st	0.157 mm	0.016 mm	0.013 mm	7
S. marinus	1st	0.061 mm	0.009 mm	0.008 mm	10
S. marinus	1st	0.053 mm	0.008 mm	0.007 mm	10
S. marinus	4th	0.582 mm	0.042 mm	0.033 mm	6
S. clavicornis	1st	0.077 mm	0.008 mm	0.007 mm	10

APPENDIX B

MOUNTING TECHNIQUES USED IN STUDYING THE LARVAE AND ADULTS OF *SAUNDERIA* SPP. AND *P. ALASKENSIS*

Larvae were mounted using the following method:

1. CLEARING - The larva was placed in a vial containing 10% KOH. If the specimen had been preserved in alcohol it was washed in distilled water before being macerated in the KOH. The time interval that the larva was left in KOH varied with the size of the larval head capsule (approximately four hours with second instar larvae to overnight with prepupal larvae).
2. WASHING - The larva was then transferred to distilled water and left for about two hours.
3. MOUNTING - The larva was mounted in Turtox CMC-10 after the body had been separated from the head (the body was generally immersed in light green or fast green stain for a few seconds). After briefly washing in distilled water, the body and the head capsule were mounted on the same slide and made permanent with ringing compound.

The older method of dehydrating through alcohols after maceration in KOH and mounting in Canada balsam was not used due to the dehydrating effect of the alcohols which collapse and distort the larval body, a process that is much reduced by CMC-10 mounting medium.

Adults were mounted using the following method:

1. CLEARING - The adult was macerated in 10% KOH until the body and head were almost transparent.
2. DEHYDRATING - The wings were removed and dehydrated through 70%, 95% and 100% ethanol rinses.
3. MOUNTING - The head, thorax and abdomen were briefly immersed in light green or fast green stain, washed in distilled water and mounted separately on a slide in CMC-10.

The wings were then cleared in cedar wood oil for about 15 minutes, in xylene for 15 minutes, and then mounted in Canada balsam.

APPENDIX C

KEY TO THE LARVAE OF *Saunderia marinus, clavicornis, pacificus** and *Paraclunio alaskensis*

1. Robust larva with the head capsule having a noticeable square-cut appearance in dorsal view. A dark brown to black color noticeable around the mouthparts and posterior edge of head capsule (occiput). Labial plate with the medial tooth having a distinctly "flaired" point. (Fig. 27)

   Paraclunio alaskensis Coquilette

   Head capsule usually less than the width of the first thoracic segment and lacking the "square-cut look" of *P. alaskensis*. Labium without flaired medial tooth.

   Saunderia spp. Sublette 2

2. Labial plate (labium) with rounded medial tooth. Four flanking teeth with their axes sloping toward the medial tooth. (Fig. 8)

   S. marinus Saunders

   Labial plate with medial tooth almost "squared-off" at the apex and the four flanking teeth not sloping toward the medial tooth. Teeth of the labium generally farther separated from each other than in *S. marinus*. (Fig. 8)

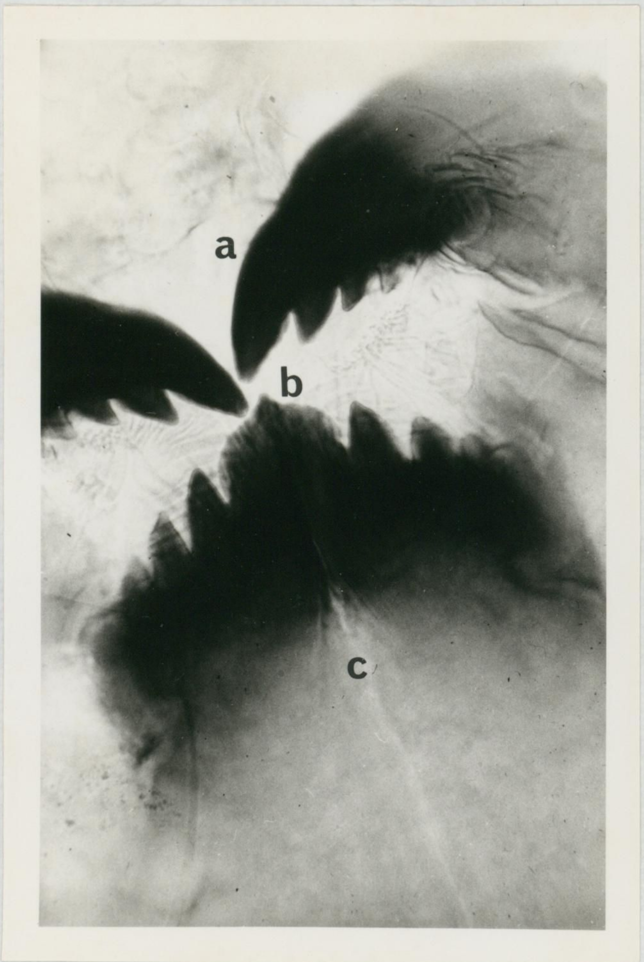
   S. clavicornis Saunders

* Labial plate with all teeth distinctly rounded. Medial tooth approximately as tall as flanking teeth. Teeth generally widely separated. (Fig. 8)

S. pacificus Saunders

* (Identification of *S. pacificus* is provisional upon association with the adult stage. This was not accomplished in this study).

Fig.27 - Photograph showing the mouthparts of a *P. alaskensis* larva showing:
(a) mandibles
(b) flaired medial tooth of the labium
(c) labium.
(x 200)


a
b
c

APPENDIX D

KEY TO MALE PUPAE OF *SAUNDERIA MARINUS, CLAVICORNIS, PACIFICUS AND PARACLUNIO ALASKENSIS*. MODIFIED FROM SAUNDERS (1928)

1. Terminal abdominal segment truncated as in Fig. 9.

Paraclunio alaskensis Coquillett

Terminal abdominal segment not truncated 2

2. Head rounded in profile (Fig. 28) 4

Head pointed in profile (Fig. 28) 3

3. Male genitalia in a conical process, only slightly exposed (Fig. 28)

Saunderia pacificus Saunders

4. Genital segment hardly covered by dorsal rectangular plate with two sharp points on the posterior margins (Fig. 28)

Saunderia clavicornis Saunders

Genital segment slightly covered by a rounded dorsal plate with no poihts (Fig. 28)

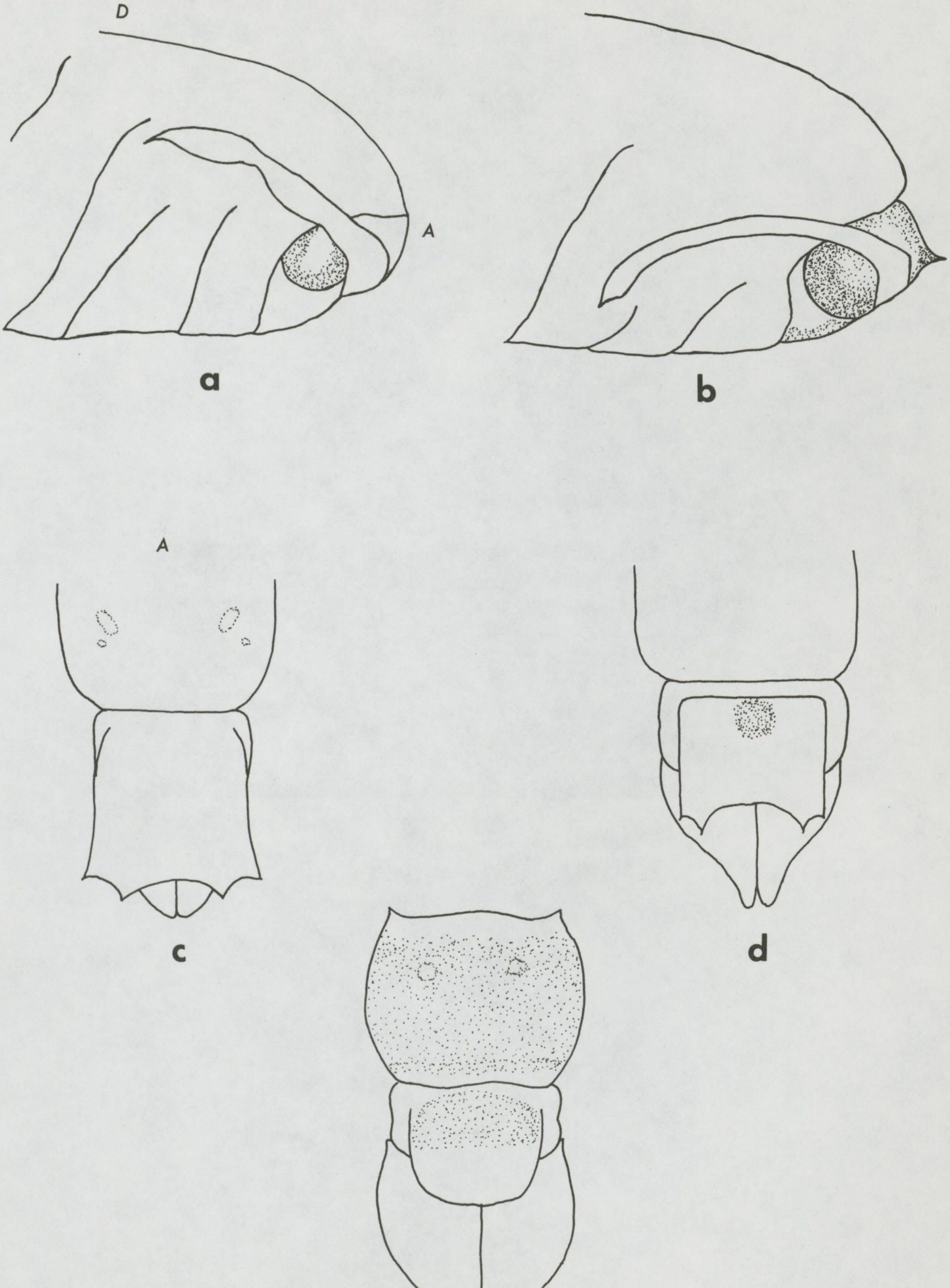
Saunderia marinus Saunders

Fig. 28 - Drawings showing:

- (a) male pupal head of *S. clavicornis*
- (b) male pupal head of *S. pacificus*
- (c) genital segments of the male pupa of *S. pacificus*
- (d) genital segments of the male pupa of *S. clavicornis*
- (e) genital segments of the male pupa of *S. marinus*.

(Drawings modified after Saunders, 1928)

A = Anterior
D = Dorsal


D
A
a
b
A
c
d
e

APPENDIX E

KEY TO THE ADULT MALES OF *SAUNDERIA MARINUS, CLAVICORNIS, PACIFICUS* AND *PARACLUNIO ALASKENSIS*

1. Antennae reduced to nine or fewer segments 2

Antennae with more than nine segments 3

2. Body length from anterior tip of thorax to end of the abdomen 3.2 to 6.6 mm. Antennae eight segmented with the terminal segment short and swollen. (Fig. 24). Small dark pigment spot on the postgenae behind the compound eyes. Palps one segmented.

Paraclunio alaskensis Coquillett

Body length as measured above 1.5 to 1.9 mm. Antennae nine segmented and with the sensory setae reduced. Terminal antennal segment moderately swollen. (Fig. 24). Palps four segmented.

Saunderia clavicornis Saunders

3. Antennae thirteen or fourteen segmented with terminal segment only slightly swollen (Fig. 24). Claspers with a stout chitinous peg on the inner distal surface. (Fig. 10).

Saunderia pacificus Saunders

Antennae generally thirteen segmented but variable. Terminal segment unswollen and elongated (Fig. 24). Claspers without chitinous peg on the inner distal surface. (Fig. 10).

Saunderia marinus Saunders

APPENDIX F

MISCELLANEOUS OBSERVATIONS FROM CULTURES OF *SAUNDERIA* SPP. AND *P. ALASKENSIS*

(a) FEEDING.

Larvae, especially of *Paraclunio alaskensis*, were observed on a number of occasions feeding on pieces of *Ulva* sp. (Chlorophyceae) which had been introduced to the culture. The algal sheet was held between the mandibles and the labial plate and with the later instar *Paraclunio* a noticeable piece of algae was taken at each attempt. Feeding was not confined to larger pieces of algae as larvae were observed to feed on the diatom and ciliate film that formed on the bottom of the culture dishes.

(b) MOVEMENT.

Larvae were frequently observed moving about outside of their cases and their movement was accomplished by means of bodily extension and contraction in conjunction with the use of the anterior and posterior pseudopods that gripped the substrate. The larvae were never observed to swim with the characteristic whipping movement of freshwater chironomids. The movement away from the larval cases was not associated with any particular activity i.e. feeding, molting etc. Often the larvae would move back into their tube if disturbed. In some cases interruption was followed by commencement of case-building movements.

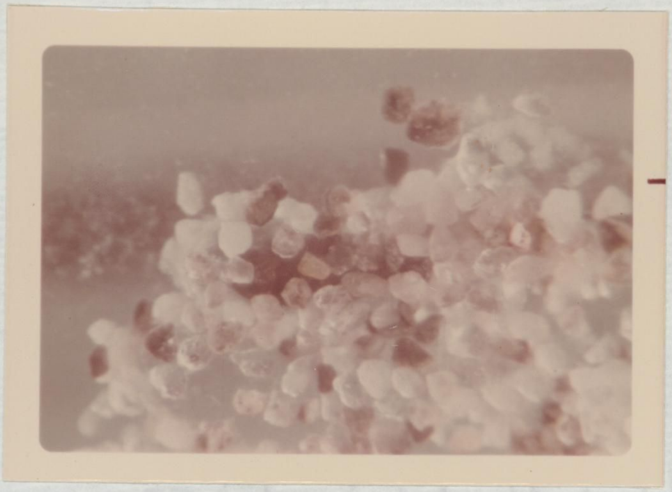
On one occasion a late instar *P. alaskensis* larva, was observed making rhythmic movements while inside its tube. These consisted of "S" shaped waves passing from the posterior to the anterior of the animal's body and upon introduction of ground *Ulva* sp. the green algal cells were observed to pass into the posterior end of the tube.

(c) CASE-BUILDING

Tube or case-building was observed a number of times and consisted of the following sequence of events:

1. The larva began a rhythmic movement of its head capsule and thorax from one side to the other. While this movement was being carried out the larva's body was anchored to the substrate by the posterior pseudopods. Initially there were no visible secretions from the larval mouthparts nor any attempt on the part of the larva to move pieces of the substrate.
2. After continuing the above motion (the time varied from one larva to the next), the larva began secreting a number of silky, whitish threads from its mouthparts. Larvae were often observed extending their cases or "repairing" them by use of these threads. Larval cases were generally many times the larval length and often had ends or corners in them (see Fig. 29). The materials used to build the cases were variable. If no sand or algae was present the case was built into the diatom-ciliate film on the bottom of the culture dish and fecal pellets were combined with this to form the tube. If algae were present then the case would be constructed from small fragments of this material. If a sheet of algae happened to be curled into a tube, this served equally well, with some addition inside and on each end of silk threads and detritus (Fig. 29). Sand was also often used for case-building. The later instar larvae tended to use sand and when used, the particles were bound together by the secretions described above. The case was attached to the substrate and occasionally pieces of algae were incorporated (Fig. 29). Tubes were often abandoned by larvae and apparently this occurred when the larva had molted and a larger case

<u>Fig. 29</u> - Photographs of the larval cases of *Saunderia* spp. and *P. alaskensis* in cultures.
A = a sand case (x 12)
B = an algal case with additions of sand (x 12)
C = a fecal case (x 6).



A

B

C

was needed or when food in the vicinity of the case became scarce. It was noticed many times that larvae would build cases extremely close to one another. It was often difficult to tell whether there were two separate cases or one case with two larvae. This phenomenon was observed mostly in early instar larvae.

APPENDIX G

CULTURE RECORDS FROM THE REARING OF *SAUNDERIA* SPP. AND *PARACLUNIO ALASKENSIS*

Culture #	Species	Time for eye spots to appear	Time to case building	Egg dev. time	Larval Instars				Duration of Pupal Stage
					#1	#2	#3	#4	
1	*S. marinus*	16 days	-	22 days	-	-	-	-	-
3	*S. marinus*	-	11 days	9 "	36 days	19 days	-	-	5-10 days
6	*S. marinus*	8	-	11	-	-	-	-	-
7	*S. marinus*	6	-	9	-	-	-	-	-
9	*S. marinus*	-	-	15	43	17	18	36 days	46
11	*S. clavicornis*	-	-	14	44	13	15	17	7
2	*P. alaskensis*	15	24	23	37	40	58	56	-
5	*P. alaskensis*	11	9	16	33	-	-	-	-
8	*P. alaskensis*	16	-	21	40	42	20	61	17
10	*P. alaskensis*	12	-	15	-	-	33	-	-
				MEAN DEVELOPMENTAL TIMES					
Saunderia marinus		10	11	13	39	18	18	36	27
					Total developmental time = 151 days				
Saunderia clavicornis				14	44	13	15	17	7
					Total developmental time = 110 days				
Paraclunio alaskensis		14	16	19	37	41	31	59	17
					Total developmental time = 204 days				

APPENDIX H

AN EXAMPLE OF THE METHOD USED TO FIT THE LARVAL FREQUENCY DATA OF THIS STUDY TO THE NEGATIVE BINOMIAL DISTRIBUTION. THE METHOD IS MODIFIED FROM BLISS (1951). THE DATA USED IN THIS EXAMPLE IS THAT COLLECTED FOR *P. ALASKENSIS* LARVAE

x (#s of larvae)	f (frequency of cells containing x)	Negative Binomial Expected Frequency	χ^2 $\frac{(f-e)^2}{e}$
0	180	179.99	0.000
1	60	63.90	0.238
2	29	36.57	1.567
3	33	23.56	3.782
4	12	15.94	.974
5	8	11.18	.905
6	13	7.98	3.156
7	6		.008
8			
9			
10			
11	14.00	14.28	0.005
12			
13			
14			

$$\chi^2 = \Sigma\frac{(O-E)^2}{E} = 10.64$$

Critical value for $\chi^2_{.05(6)} = 12.6$

The following steps are used for the above calculations and results:

Step 1 $\Sigma fx = 563$

Step 2 $\Sigma fx^2 = 3208$

Step 3 $\Sigma f = 355 = (N)$

Step 4 $\bar{x} = \frac{\Sigma fx}{\Sigma f} = 1.5859 = M$

Step 5 $= \frac{\Sigma fx^2 - \frac{(\Sigma fx)^2}{N}}{N-1} = \frac{3208 - \frac{(563)^2}{355}}{354}$

$= 6.54$

and $S = 2.462$

At this point it can be seen that because S^2 is 4 times as great as $\bar{x}$ the Poisson distribution does not fit this data.

The general form of the equation describing the negative binomial distribution is as follows:

$$Px = \frac{(k + x - 1)!}{\bar{x}!\ (k - 1)!} \frac{R^x}{g^k}$$

were P_x = the probability that an observational unit x will contain 0, 1, 2 ... individuals, $R = p/g = \bar{x}\ (k + \bar{x})$, p and g are expected proportions in two categories with $g + p = 1$ and k is a positive exponent.

Step 6. In order to try and fit the data to this equation one must attempt to estimate k by $\hat{k}_1$

$$\hat{k}_1 = \frac{\bar{x}^2}{s^2 - \bar{x}} = \frac{1.59^2}{6.54 - 1.59} = .565$$

For this $\hat{k}_1 = .565$ to have 90% or better efficiency the following inequality must hold:

$$\frac{(k + \bar{x})\ (k + 2)}{\bar{x}} > 15$$

$$\frac{(.51 + 1.59)\ (.51 + 2)}{1.59} = 3.31$$

Since the inequality does not hold this method is not suitable.

Step 7. A second attempt to estimate k by $\hat{k}_2$: it is best to use the approximate $\hat{k}_1 = .51$ obtained in step 6 and the method is to find a $\hat{k}_2$ which solves the following equality: (where fo is the number of zero x's)

$$\hat{k}_2 \log\left(1 + \frac{\bar{x}}{\hat{k}_2}\right) = \log\left(\frac{N}{Fo}\right)$$

$$= \log\left(\frac{355}{180}\right)$$

$$= \log(1.97)$$

$$= 0.294$$

Now first try: $\hat{k}_2 = .51$

($\hat{k}_1$ from step 6 which should be reasonably close to the solution)

$$.51 \log\left(1 + \frac{1.5859}{.51}\right)$$

$$= .51\ (.61384$$

$$= .313$$

Since .313 > .294, select a smaller $\hat{k}_2$

Now try $\hat{k}_2 = .40$

$$.40 \log(1 + \frac{1.5859}{.40}) = .40 \log(4.97)$$

$$= .278$$

Since $.278 < .294$ one can try a larger $\hat{k}_2$ or interpolate.

Trying $\hat{k}_2 = 0.45$

$$.45 \log(1 + \frac{1.5859}{.45}) = .45 \log(4.53)$$

$$= .295$$

Thus k is approximately 0.45

Step 8. Agreement with the negative binomial distribution can be tested having established that $\hat{k}_2 \approx .45$

$\phi_o = \frac{N}{g^k}$ where ϕ_o is the expected relative frequency for $x = o$

$$p = \frac{\bar{x}}{k} = \frac{1.5859}{.45} = 3.52$$

$$g = 1 + p = 4.52$$

therefore $\phi_o = \frac{355}{4.52^{.45}}$

$$\log \phi_o = \log 355 - .45 \log 4.52 \quad = 2.255$$

and ϕ_o = antilog $2.255 = 179.99$

and therefore the expected number of zeros is 179.9

For ϕ_1 calculate:

$$\phi_1 = \frac{(k + x - 1)}{x} .R\ \phi_o$$

$$= \frac{(k + 1 - 1)}{1} .R\ (179.9)$$

Since $R = \frac{\bar{x}}{\bar{K} + \bar{x}} = 0.789$

and $\phi_1 = (.45)\ (0.789)\ (179.9)$

$= 63.90$

$$\phi_2 = \frac{(.45 + 2 - 1)}{2} (0.789)\ (63.9)$$

$= 36.57$

and so on to $\emptyset_{14}$.

Step 9. Now compute a χ^2 value by $\Sigma\frac{(f - e)^2}{e}$ which, in this case is to 10.64 and since the critical region for $\chi^2_{.05(6)} = 12.59$ it can be concluded that the data conforms to the negative binomial distribution.

VITA

Surname: MORLEY Given Names: RICHARD LORNE

Place of Birth: WINNIPEG, MAN. Date of Birth: MARCH 24, 1945.

Educational Institutions Attended, with Dates of Entering and Leaving:

UNIVERSITY OF VICTORIA, FACULTY OF ARTS AND SCIENCE	1963 - 1967
UNIVERSITY OF VICTORIA, FACULTY OF GRADUATE STUDIES	1968 - 1971

Degrees, Diplomas, Etc. Awarded with Dates and Names of Institutions:

B.Sc.	1967	University of Victoria

Honors and Awards:

1968	University of Victoria Graduate Scholarship
1968	University of Victoria Teaching Assistantship
1969	University of Victoria Graduate Fellowship
1969	University of Victoria Teaching Assistantship

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