THE SPECIATION AND SUCCESSION OF ZOOPLANKTON

IN ESQUIMALT LAGOON, BC

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The speciation, abundance and seasonal succession of the zooplankton in Esquimalt Lagoon was studied during 1978 and part of 1979. A brief comparison with the zooplankton in adjacent waters was also made.

The lagoon is characterized by a low species diversity and a population which is dominated in the spring and early summer by the copepod _Acartia clausii_ and to a lesser extent barnacle nauplii and the cladoceran _Podon_. Only very low numbers of other species are found at other times of the year.

The increase in zooplankton population in the spring coincides with the spring phytoplankton increase together with a warming trend. The decline of the population in July appears to be associated with fish predation, a reduction in fecundity due to temperature and adverse conditions in the sediment which inhibit egg hatching.
1. Introduction

An important goal of ecological research is to gain an understanding of how organisms of a community interact with each other and their environment. Since environments are generally very complex such studies are an enormous task. In order to simplify this situation and make it feasible (within manpower limitations) certain selected environmental parameters are measured as a function of time. These are followed until trends can be recognized and then specific aspects of the interaction of the community with the environment are studied in detail.

The purpose of this study is to provide base-line data on the zooplankton community in Esquimalt Lagoon and on certain selected environmental parameters. The zooplankton, secondary producers, are an important link in the marine food chain which leads from phytoplankton, primary producers, ultimately to fish and man. Because of the proximity of Esquimalt Lagoon to DND Establishments and the possible interaction of these establishments with the marine environment, it was important to obtain base-line data for the lagoon.

In this regard, the requirements were to establish:

(i) the nature of the species of zooplankton present
(ii) their relative abundance
(iii) their seasonal succession
(iv) the relationships, if any, between the zooplankton community and the selected physical, chemical and biological parameters.

This study, although presented as a separate report, was carried out in conjunction (for the major proportion of time) with a study of the phytoplankton of Esquimalt Lagoon. A report on the phytoplankton will follow and relationships between the two trophic levels may become more evident.

Some detailed descriptions of the seasonal distribution of plankton in the waters of Southern Vancouver Island have been reported by other investigators. In 1977 Chester et al described the seasonal distribution of plankton in the Strait of Juan de Fuca. A summary of biological oceanographic observations in the Strait of Georgia was prepared by Stephens et al (1969). These major water masses may influence the biota of Esquimalt Lagoon, particularly the Strait of Juan de Fuca. However,
to date, the ecology of Esquimalt Lagoon has not been described.

The physical and chemical environment of Victoria Harbour, Gorge and Portage Inlet, which are in close proximity to Esquimalt Lagoon were described by Meikle et al (1969). However, no information on the zooplankton is available for these locations. Jakle's Lagoon, which is similar to Esquimalt Lagoon, is located at the southern end of the San Juan Island, Washington. This is situated to the north of Puget Sound. The zooplankton population dynamics of this lagoon have been fully described by Landry (1978).

Lagoon type situations afford the possibility of studying zooplankton community interactions in a relatively closed ecosystem. Problems such as sampling the same population through time are minimized, depending upon the tidal flushing, relative to other marine environments. Esquimalt Lagoon is a small tidal lagoon approximately 2 kilometers long and 0.8 km wide at its widest point. It has a maximum depth of approximately 3.5 m and the average depth is about 2.5 m.

2. Material and Methods

Routine sampling was started in the latter part of February, 1978 at three stations (A, B, C, Figure 1).

The sampling intervals were: every fifth or sixth day from February to June, 1978; twice a week from July to November, 1978; once a week from December, 1978 to February 1979; and twice a week from March to May 1979. The reason for the variable sampling frequency was that plankton metabolisms change seasonally with temperature. Growth and reproduction are faster during the summer months, thus shorter sampling intervals were necessary to follow population changes.

On May 25, July 24 and October 17, 1978 zooplankton samples were collected at Station D outside of the lagoon. (Fig. 1).

From February through June, 1978, temperature, nitrate, nitrite and chlorophyll a were sampled at each station in conjunction with routine zooplankton samples. The temperature readings were obtained at one-meter depth intervals at each station using a hand-held thermometer (Fig. 2). The various readings were obtained by lowering the thermometer to the required depth and then sending a plexiglass tube down
the line trapping the water around the thermometer. A few minutes were allowed for the thermometer to reach equilibrium temperature before hauling it to the surface. Nitrate, nitrite and chlorophyll analyses were done on integrated water samples taken at each station. The integrated water samples were obtained by lowering a weighted one-inch Tygon tube through the water column to within .2 meters of the bottom. The top was then stoppered and the tubing hauled up, stoppering the bottom before it broke the surface. The nitrate and nitrite determinations were carried out as described in Stickland and Parsons (1972). In vivo Chlorophyll concentrations were determined using a Turner Model 111 fluorometer.

Beginning in July, 1978, the sampling program was expanded to assist a concurrent phytoplankton study. Salinity, submarine light, phosphate and ammonia determinations were added to the sampling program. Chlorophyll concentrations were determined by 90% acetene extraction, (Stickland and Parsons (1972) as well as by in vivo fluorescence. Both temperature and salinity were measured at 1 m intervals using a Beckman RS5-3 portable salinometer. All nutrient and chlorophyll samples were collected at one-meter depth intervals using a Masterflex portable peristaltic pump. These samples were then filtered through glass fibre filters (Gelman type A/E) and analyzed for nitrate, nitrite, ammonia, and phosphate using the method described by Stickland and Parsons (1972). Light measurements were taken at one-meter depth intervals at each station using a Kahsico Model 268.WA310 underwater Irradiometer.

3. Zooplankton Sampling

Zooplankton were collected using a simple conical net with a length of 140 cm and a mouth diameter of 30 cm. From February, 1978 to January, 1979 a 280µ mesh net was used at all stations. When a 202µ mesh net became available this was used from January 11, 1979 to February 26, 1979 at all stations and then from February 26 to May 31 at stations A and C. During this last period a 28µ mesh net with a 53µ cod-end was used at Station B only. The change to a much smaller mesh size was used to investigate the naupliar and juvenile stages of the copepod community.
The zooplankton collections were from vertical hauls. The net was slowly lowered to the bottom (allowing it to collapse), pausing for a minute to allow the water column to equilibrate, then hauled to the surface quickly. The net was back washed with sea water and the zooplankton collected in the cod-end were washed into a jar and fixed with 4.5% formalin.

Aliquots of each sample were counted using a Bogarov plankton tray under a Wild M4 dissecting microscope. The aliquot size was adjusted using a Plas-Labs plankton splitter so that at least 100 of each of the dominant species were counted. Concentrations in numbers per cubic meter were computed from volume of water filtered in each vertical net haul.

The nauplii and juveniles (copepods) collected with the 28μm mesh net were separated into 2 classes of nauplii and 5 stages of copepodites. The two classes of nauplii were distinguished solely by size; NI being any nauplius smaller than .19 mm and NII any nauplius larger than .19 mm. The copepodite stages were separated according to size, number of legs, and sex. CI has 2 pairs of legs (.36 mm - .48 mm), CII has 3 pairs of legs (.48 mm - .57mm) CIII has 4 pairs of legs (.55mm - .70mm), CIV has 5 pairs of legs with the 5th pair of legs not fully developed (♂: .67mm - .82mm; ♀: .71mm - .84mm), and CV being fully developed adults (♂: .76mm - 1.10mm; ♀: .82mm - 1.21mm).

All of the different species found in any of the hauls were classified as follows. Each separate species was given a reference number and samples were kept in 4.5% buffered formaldehyde. Most of these were then carefully drawn, logged, and identified.

4. Results
4.1 Physical Parameters

The highest daily tides in the Esquimalt Lagoon occur during the winter months; from November to February. The difference between the highest and lowest daily tides is shown in Fig. 3. The greatest tidal exchange occurs during these months. Tidal exchange follows somewhat of a bimonthly cycle. Scrimger (1960) found that typical tidal exchange was approximately 35% of the total lowtide volume per cycle. The mean tidal range is .64m (Mehta, 1974).
The salinity of the lagoon, from the point of view of zooplankton viability, does not differ significantly from that of the external waters (Strait of Juan de Fuca). This is most likely due to the 20-35% of tidal exchange per cycle and the small freshwater input. Five small streams empty directly into the lagoon. A halocline exists throughout the year with the exception of the occasional windy days which thoroughly mix the water column. The salinity values generally range from 29.5°/oo at the surface to 32.0°/oo nearer the bottom. A thin brackish layer occurs at the surface after a rainfall. These values may be compared to the surface values observed in the Strait of Juan de Fuca of 28°/oo to 32°/oo (Chester et al, 1977).

Temperatures of the lagoon exhibit large seasonal changes (Fig 4). Temperatures were as high as 21°C in early August, 1978 and as low as -1°C in mid-January, 1979. There were periods during December and January, 1979 when ice covered as much as two-thirds of the lagoon. The ice made it impossible to follow our rigorous sampling program.

During the summer months large temperature gradients occurred which gradually broke down in the fall and inverted in the winter months Fig. (4). The temperature of the lagoon is warmer in summer than the water outside at Station C and colder in the winter. On July 24th, 1978 the water at Station A was > 16.6°C from the surface to 2m and 13.5°C at 3m. At station D the temperature was 14.8°C at Om, 11.0°C at 1m and 10°C at 3m.

Chlorophyll a values were relatively high throughout most of the year (Fig. 5 a,b,c), the highest values occurring during September and October, 1978 (20-120 mg/m³) with the lowest values in January and February, 1978, 1979 (~ 1.0 mg/m³). Without considering 'food-selectivity' this was the only time of the year when the chlorophyll a values were low enough to be a possible limiting factor of zooplankton growth. However, it should be noted that during this period there appeared to be a fair amount of detritus in the samples.

Although phytoplankton was not sampled for species composition until the beginning of July, 1978, large quantities of chain-forming diatoms were caught in the zooplankton net in May, June and July 1978. From July, 1978 to June, 1979 the seasonal succession of diatoms and other phytoplanktonic species has been established (Watanabe and Robinson, in preparation). Diatoms were dominant in early spring, a succession of alternating species of dinoflagellates and diatoms...
occurred in late spring and summer, a dense red tide (Gymnodinium sanguineum) occurred in the fall, microflagellates and one bloom of diatoms grew in winter with a few periods of very little growth in between. All of the nutrient data will be published in the phytoplankton report as there is no direct correlation with the zooplankton community. The nutrient data indicated some degree of eutrophication in the lagoon and helped substantiate the observation of high phytoplankton biomass.

4.2 Seasonal variation of zooplankton

Table 1 lists all the species of the zooplankton community found in the lagoon in order of abundance.

_Acartia clausii_ was by far the dominant species in Esquimalt Lagoon during the entire sampling period. It was the only copepod which multiplied to a significant population size ($8 \times 10^4/m^3$, Table 1) although there were several other species of copepods which appeared in low numbers periodically.

The cladoceran, _Podon_ ($\leq 1.5 \times 10^4/m^3$) and a species of barnacle nauplii ($\leq 1.8 \times 10^4/m^3$) were the only other species of zooplankton that grew to bloom conditions. These species co-existed all having peak growth periods which corresponded with the spring phytoplankton increase in March through June. Many of the other species were found throughout the year in low numbers, but these species also showed slight seasonal changes. For example; crab zoeae were found in late spring and throughout the summer but were virtually non-existent in fall and winter. _Pseudocalanus minutus_ and _Acartia longiremurus_ were found throughout the year in low numbers but showed slight increases in early spring and late fall ($\leq 10^3/m^3$). _Obelia_ was found in late summer and early fall but rarely found at any other time of the year. _Evadne_ was only found in late summer and early fall, shrimp zoeae were found only in late spring and _Oiolopluera_ were found only in summer. _Centropages abdominales_ occurred year round but appeared slightly more in late summer. Chaetognaths were found only in spring and fall and in general appeared in a poor state of health. The remaining species on the list appeared very infrequently such that no trends could be recognized. The two unidentified species of copepod appeared only very rarely in the lagoon.

Since there is a 20-35% tidal exchange between the lagoon and the...
of *A. clausii*, from November, 1978 to January, 1979 was relatively low (0.5-3x10^3/m^3). In February, 1979 a small increase in population occurred, reaching a peak of 11.0x10^3/m^3 at Station C. The major blooms of this species occurred in March, April, May and June in 1978 and March, April, and May in 1979. Populations reached peak values of up to 5x10^4/m^3 in April, 1978 at Station B and 8.7x10^4/m^3 in May, 1979 at Station B. The summer levels of *A. clausii* were relatively low 1x10^3/m^3 at all three stations with the exception of Station C where in August two blooms occurred which had peak values of 1.6x10^4/m^3 and 5.8x10^3/m^3.

The 1979 spring bloom of *A. clausii* appears to be greater than that in 1978. This coincides with the higher concentrations of Chlorophyll a in 1979 than in 1978. However this may well be a sampling artifact since a much smaller (202μ) mesh was used in 1979. It is possible that a proportion of the adults may have been lost in 1978 through the larger mesh (280μ). This is of minor interest in this investigation which is primarily concerned with the occurrence and timing of each species within the sampling period.

(b) Taxonomy

The identification of *A. clausii* is not clear cut because the subgenus *Acartiura*, of which *A. clausii* is a member, is in somewhat of a state of revision. Bradford, (1976) has looked at many Acartia species around the world and has found slight differences within the same species. She has partially revised the *Acartiura* subgenus. However, that is not to say that her revision will be universally accepted. Carillo et al (1974) have found that when *A. clausii* from the east coast of North America were interbred with *A. clausii* from the west coast no viable offspring were produced. This would indicate that the two populations have diverged enough to be classified separately.

In order to clarify the identification of the lagoon species as *A. clausii* a close examination of the 5th pair of legs of the adult male and female was made (Fig. 10 a, b). The photographs do not show all the spines on the legs which is due to the positioning of the leg on the slide and the fact that the microscope can only focus in one plane. However, further observation Fig. 11, b showed the lagoon species to be
the same *A. clausii* Giesbrecht as described in Brodski (1950) and Bradford (1976) Figure 12.

(c) **Spermathecal sacs**

Throughout the study the percentage of adult females that had spermathecal sacs attached to the genital segment was followed. This was done in order to see if there was a correlation between the number of sperm sacs and subsequent population change.

It was found that at all times approximately 94% of the females had attached sperm sacs and this was independent of female abundance.

(d) **Size**

Although copepod sizes were not routinely measured there was a noticeable seasonal variation. The adults found in winter were significantly larger than those found in summer.

(e) **Sex ratio**

Figure 13 gives a comparison of the number of adult male to female *A. clausii* during the sampling period in Esquimalt Lagoon. Considerable seasonal variations in the sex ratio were observed. Female to male ratios of 1/1 and 3/1 being found in March and August, 1978 respectively. In general the female appeared to be the dominant form throughout the sampling period, with the exception of May, 1979 when the male was the dominant form.

(f) **Stages**

Figure 14 shows the 1979 spring blooms of *A. clausii* fractionated into nauplii and copepodite stages. From February to May the nauplii and copepodite stages exhibited three peaks in abundance which shifted through the stages as back cohorts matured. The alternate pattern of shading distinguishes the different cohorts. The adult stage is not shaded as there is bound to be a mixture of cohorts due to the longer lifespan of the adult than the individual stages.

5. **Discussion**

5.1 **Population**

Although there is a reasonable number of different species in Esquimalt Lagoon it would appear that the environmental conditions are such that, in general, most species are unable to out-compete the single dominant species *Acartia clausii*. Species such as *Pseudocalanus minutus*, *Oikopleura* sp., and chaetognaths which are brought into the lagoon from outside by tidal exchange do not appear to reproduce in
this new situation to any appreciable extent. Only the cladoceran Podon and to a lesser extent Obelia, barnacle nauplii and crab zoeae occurred in the spring in numbers comparable to A. clausii. The distinctive feature of the lagoon during the sampling period was that the zooplankton, predominantly A. clausii, were found in high numbers from March to June, 1978 and then were virtually absent for the balance of the year, until March, 1979. This is somewhat surprising in view of the fact that the chlorophyll a values were very high from June to November, (Fig. 5 a) and visual observation indicated large amounts of detritus were also present. Exchange with the water of Royal Roads (Strait of Juan de Fuca) would have been expected to supply at least one external species which could fill this empty niche. The factors which may lead to the above situation are discussed below.

Acartia clausii is widely distributed throughout the Northern Hemisphere in shallow coastal waters Brodskii (1950), Carter (1965), and Bradford (1976), and its presence in Esquimalt Lagoon is no surprise as it has been observed in other local waters. Landry (1978) has recently completed an in-depth study of this particular species in Jakle’s Lagoon, Washington. With the exception of minimal tidal flushing in Jakle’s Lagoon the two environments are quite similar; shallow (4m), minimal fresh water input, salinity range 25-35°/oo, winter temperature range 4-5°C and late summer maximum of 20-21°C. A. clausii has been documented as being a winter-spring species Conover (1956), Jeffries (1962) and Anraku (1964), appearing in early December, reaching a maximum in May and disappearing in July or early August in Long Island Sound. Landry (1978) however, reported A. clausii as being a spring-early summer species in Jakle's Lagoon, Washington which agrees with the observations in Esquimalt Lagoon. Further, Conover (1956), and Jeffries (1952) found a biannual succession of A. clausii and A. tonsa which did not occur in the Lagoon. In somewhat deeper waters Carter (1965) found A. clausii and Pseudocalanus minutus, the major species found outside of Esquimalt Lagoon co-existing in the same water. The positively phototactic A. clausii inhabiting the upper 4m and P. minutus being below the thermoclines at around 10m. The shallowness of the lagoon (4m) together with the large thermoclines which exist in the late spring and early summer presumably inhibits P. minutus and possibly other species. Those
species which are negatively phototactic are found in deep water
during the day and come to the surface to feed at night (Raymont, 1963).
Many other species have various patterns of vertical migration, the
cause of which is not fully understood. Thus, the outside waters,
which are considerably deeper, could harbour many vertical migrators
which couldn't live in the shallow water of the lagoon.

Exactly what limits the growth of *A. clausii* during the summer
and winter in the lagoon is not altogether clear. However, some of the
factors which must be considered include: salinity, temperature, competi-
tion, predation, food abundance and type and internal rhythms.

5.2 Salinity

Salinity may be eliminated as a factor since seasonally it does not change to any appreciable extent in the lagoon. Also, *A. clausii*
is an euryhaline species able to withstand a broad range of salinities.
Crandell and Horacek (1973) found *A. clausii* in Big Lagoon California
where the salinity was as low as 15°/oo.

5.3 Tidal exchange

Ketchum (1954) notes that the rate at which a planktonic organism must reproduce in order to maintain itself in an estuary is determined by the circulation and tidal exchange rate. Barlow (1955) has found that during part of the year in certain areas of Great-Pond, a small estuary near Woods Hole, an *Acartia* population could not reproduce fast-enough to maintain itself as the circulation was too vigorous. The tidal cycles of Esquimalt Lagoon (Fig. 3) follow a very similar bi-monthly pattern during and after an *A. clausii* bloom. In the summer the high tide occurs at midnight and the low tide at mid-day. Tidal flushing of the surface feeders at night is thus not considered significant. Whilst tidal exchange may thus reduce the population another factor must control the seasonal cycle.

5.4 Temperature

Temperature has been shown to have a large effect on copepod growth and reproduction. Kasahara et al (1975 b) have suggested temperature is the most important factor affecting the hatching of the resting eggs of *Tortanus forcipatus*. Johnson and Miller (1973) found that temperature played a major role in the decline of *A. tonsa*. Further it
has been shown that *A. clausii* is abundant only when the temperature is less than 18°C. Landry (1978), Jeffries (1962), Anraku (1964), and Conover (1956). Anraku showed that *A. clausii* had an optimum respiration and feeding rate at approximately 15°C and suggested that temperatures above 18°C may limit metabolism and thus population size. Conover (1956) found that the respiration rate of *A. clausii* increased with temperature until about 20°C, followed by a sharp decrease.

Uye and Fleminger (1976) found that the optimum temperature for *A. clausii* reproduction was 14°C, and that hatching was confined to a smaller range of salinities as the temperature increased. Landry (1975 a) showed that under summer conditions copepods collected during the winter at 8-10°C produced offspring that developed faster at every stage than those collected during the summer (15-20°C). With excess food development rates increased with temperature until approximately 20°C. All of the evidence suggests that temperature is an important factor in copepod growth and reproduction. The Lagoon data (Fig. 4) agrees with this evidence in that *A. clausii* is only abundant at temperatures less than 18°C, the highest numbers occurring in the temperature range 10-16°C. However, the decline of *A. clausii* in Esquimalt Lagoon occurred at temperatures between 15 to 17°C. It is thus reasonable to assume that temperature was not the causative factor.

5.5 Competition

Competition may be eliminated as a factor since no other species in the lagoon reaches a population which could compete significantly with *A. clausii* Fig 9.

5.6 Food abundance and type

Marshall and Orr (1955) found a direct correlation between food abundance and number of eggs produced per female *Calanus*. They found that starved copepods produced very few eggs, if any, and that as food availability increased, egg production increased up to a maximum level. In an annual cycle the chlorophyll a levels in the lagoon (Fig. 5) are rarely low enough to limit zooplankton production. The lower values of chlorophyll a (0.8-1 mg/m³) occur in January-February and may account for the low winter population of *A. clausii*, but the summer values (4-100 mg/m³) are far from limiting. However, it may not be the quantity
of food (concentration of chlorophyll a) but rather the type of food which may be significant. *A. clausii* may not be able to feed on the particular phytoplankton species which are present during the summer-winter period. Allan (1977) found that *A. clausii* nauplii exhibited no food selection whereas all copepodites showed some food selectivity. Wilson (1973) indicated food selectivity according to size of prey for *A. tonsa*. Marshall and Orr (1955) observed food selectivity in *Calanus*. With any of these studies on food selectivity two or more food sources were available and the copepods favoured one in particular. However, this is not to say that the copepods would not feed on the other food type had the selected one not been present. Wilson (1973) fed a population of *A. tonsa* a variety of different sized plastic beads (7-70μ) which they ingested selectively according to size. These studies indicate that copepods tend to feed on any available food source and when two or more food types are available they feed selectively on one of them. Two or three weeks after the decline of the *A. clausii* population a very thick red tide occurred which lasted for approximately three months (Watanabe, L. and Robinson, MG. CMSL Manuscript Report No. 79-7). The organism which was responsible for the red tide, *Gymnodinium sanguineum* is a naked dinoflagellate which may be too large (70μ) to be ingested by *A. clausii*. Other small flagellates (~10μ) were present however, in abundant numbers (9.1x10^5/m^3) at the same time as an alternate food source. Nival (1976) found that adult *A. clausii* had an almost 100% filtration efficiency in this size range.

Further, during the period of the red tide, a large amount of detritus was visible. Strickland and Parsons (1962) concluded that ocean detritus in the northeastern Pacific is composed of a sufficiently diverse group of compounds to serve as a potential source of food for marine organisms. Baylor and Sutcliffe (1963) concluded that particulate organic matter must be considered as a possible if not an important source of food for marine organisms. Roman (1977) demonstrated with *Acartia tonsa* that detritus can be assimilated by copepods. Poulet (1976) found that detritus often comprised more than 90% of the food ingested by *Pseudocalanus minutus* in natural sea water. Detritus being extremely
available in the lagoon should definitely be considered as a possible food source.

Hodgkin & Rippingale (1971) found A. clausii to be both herbivorous and carnivorous. In fact they concluded that animal food is probably an essential part of their diet. They have found that A. clausii can prey on other species at such a rate that in a mixed population they may prevent recruitment of the other species to adults. Landry (1978) showed that in the absence of food A. clausii copepodites became cannibalistic, eating nauplii.

As the Esquimalt Lagoon is highly productive in terms of a large variety of plant material it seems highly unlikely that amount or type of food limits A. clausii during the summer and fall, although it may during the winter.

5.7 Predation

Predation of zooplankton by small fish is an important link in the marine food chain. In Jakle's Lagoon, Landry (1978) found that four different species of fish fed heavily on an A. clausii population during at least part of the spring and summer months. Although actual data was not obtained in Esquimalt Lagoon it was interesting to note that the decline of the spring bloom of A. clausii seemed to coincide with a large increase in the fish population. In July of 1978 and 1979 there were many calm mornings where fish risings could be seen across the entire lagoon. There was also a very noticeable increase in the fish population near the jetty (Fig. 1). Herring came into the lagoon in large numbers to spawn in April. The live bearing perch appear in large schools in July and August and the young, which feed on A. clausii (Landry, 1978) are seen in large numbers. Both of these species are found in Jakle's Lagoon and it is likely that the other species, particularly the three spined Stickleback, which feeds heavily on A. clausii, is also present in Esquimalt Lagoon. Landry correlated changes in the abundance of A. clausii with the life-cycle of the three spined Stickleback. In May he found that a sharp increase in copepodid and adult mortality coincided with the observed hatching of young Sticklebacks and the possible restimulation of the feeding of adult fish. In May to June predation was reduced by both the aggregation of young fish in shallow areas, where A. clausii is not abundant, and the seasonal die-off...
of mature fish. A dramatic reduction in copepod population occurred in July and August due to the schooling of young fish in the deeper areas of the lagoon. Thus, an increase in fish predation in July most probably accounts for the significant decrease in the population of A. clausii in Esquimalt Lagoon (Figures 9, a, b, c). The occurrence of a significant population of A. clausii at Station C in August may result from decreased fish predation due to the fish moving to deeper water. Station C (2m) is somewhat shallower than the other Stations (3 to 4m).

5.8 Fecundity

In order to try to understand the seasonal cycle of zooplankton in the lagoon, egg production must be considered. Landry (1978) found that the production of A. clausii eggs increased with increase in female size and temperature over the range of 5-20°C. At temperatures greater than 20°C there was a sharp decrease in egg production. He also found that A. clausii fecundity rates were highest during early spring, due to an optimum temperature and female size relation, and decreased in summer. Although temperatures were favourable in summer, smaller female size offset the temperatures, thus lowering the fecundity rate. The potential fecundity in May was calculated to be about 23 eggs/female/day dropping to 19 eggs/female/day in June and about 14-15 eggs/female/day in July, August and October. However, he concludes that the fecundity is not variable enough between cohorts to control the timing of seasonal changes in abundance.

Not until recently have copepod eggs been found in sea bottom muds; Kasahara et al (1974, 1975 a, b) found eggs of 6 species of calanoid copepods in the Seto Inland Sea, Japan. As many as 3 x 10^6/m^2 A. clausii eggs were discovered. Landry (1978) also found clausii eggs with estimates as high as 9x10^6/m^2. His lab. experiments showed that A. clausii eggs sink approximately 3 meters per hour. Since the Esquimalt Lagoon has a maximum depth of 3.5-4.0 meters and the hatching of the eggs takes longer than a day, all of the eggs must hatch from the sediment (assuming the effects of wind mixing etc. are ignored).

When A. clausii eggs are trapped in the sediment the factors which inhibit hatching are darkness, temperature and lack of oxygen (Kasahara et al, 1974, '75, Uye and Fleminger 1976, Landry, 1978). They suggest
that this resting period in the sediment is an important part of the life cycle in that the eggs maintain the species during periods of low abundance (Kasahara et al) found that eggs that had been in the bottom mud for 160 days were still viable.

In Esquimalt Lagoon in January and February the high tidal exchange must mix up the water enough to free the eggs from the dark conditions of the sediment. The sediments are assumed to be anoxic as occasionally anoxic conditions are found in the bottom water in the late summer. (Robinson, M.G. Unpublished results). However, later on in the summer the higher temperature must inhibit the hatching. Kasahara et al (1975) found temperature to be the most important factor in the hatching of resting eggs of Tortanus forcipatus. Uye and Fleminger (1976) showed that with A. clausii, as the water temperature rises over 18°C, hatching is confined to a smaller salinity range around 34‰. As the salinity of the lagoon is always below 34‰ it is most probable that the eggs remain dormant until the temperature is appropriate for some hatching to take place to maintain a breeding stock. Many eggs are thought to be lost by decomposition due to bacteria and fungi (Uye and Fleminger, 1976) and by burial in the sediment. (Landry, 1975).

A. clausii is known to survive winter temperatures of 1°C but metabolism in the winter is slow. It takes two weeks for an egg to develop into an adult female at 20°C but more than 60 days at 5°C (Landry, 1978). Release of the eggs from the sediment in January to February by the high tidal exchange would thus appear as a population increase in March to April as has been observed. Fig. 9.

5.9 Sex ratio

Seasonal variations in the sex ratio of adult A. clausii have been well documented (Marshall, 1949, Digby, 1950, Conover, 1956). Males have been found to outnumber females during part of the spring bloom while females consistently outnumber males during the rest of the year. In Esquimalt Lagoon the males rarely outnumbered the females during the 1978 bloom but did so during the 1979 bloom, Figure 13. Conover (1956) suggests that the males are not as efficient with respect to growing and respiration as females. Thus, any unfavourable
environmental conditions would favour the female population. This could explain why, during periods of low abundance, (assumed due to environmental conditions) 60% of the A. clausii population in the lagoon is female.

During most of May, 1979, males accounted for up to 70% of the population. This may in part be due to the faster development time of males (Landry, 1975). Landry also found that during the Spring and Summer females experienced a higher rate of mortality than males.

6. Conclusion

In terms of its zooplankton population Esquimalt Lagoon is characterized by a low species diversity and a spring to early summer dominance by the copepod *Acartia clausii*. The appearance of this copepod in late February coincided with the Spring bloom of phytoplankton. Large numbers of *A. clausii* (up to $80 \times 10^3/m^3$) are found in March through June and then, with the exception of Station C, decline in July. The numbers are very low ($<1 \times 10^3/m^3$) right through the summer, fall and winter.

The only other zooplankton which occur in significant numbers are barnacle nauplii and the cladoceran *Podon*. They both occur and decline at about the same time as *A. clausii*.

All of the species found outside of the lagoon are found inside but, with the exceptions above, in low numbers. Esquimalt lagoon maintains its own ecosystem with an environment significantly different from that of the deeper external waters. Tidal exchange can introduce external species into the lagoon but, even with the abundance of phytoplankton and an absence of competition, these species do not appear to reproduce and fill the empty niche in the summer and fall. This is not too surprising since it takes only one of many parameters to inhibit population growth. The most important of these are considered to be restrictions due to the shallow water column (3m) and high summer temperatures.

Due to its dominance in the lagoon and its ecological importance in the Northern Hemisphere the control of the life cycle of *A. clausii* is of some interest. An interaction of several factors appear to regulate the seasonal cycle of this species. The occurrence of its peak
abundance in spring has been well documented and the conditions in the lagoon are very favourable for growth. However, what factors limit population growth during the remainder of the year seem to vary with location.

The initial decrease of *A. clausii* populations in July can only be explained by fish predation and the increase in temperature of the water column. The temperatures in August were close to the critical thermal maximum for adults. Further, when temperatures reach approximately 20°C the salinity range for egg hatching is around 34‰ which never occurs in the lagoon. Egg hatching in the fall when the temperature decreases may be inhibited by the anoxic conditions thought to prevail in the sediments. Anoxic bottom water has been observed at this time of the year.

During the winter months a combination of a fairly low phytoplankton biomass and the cold temperature, which reduce the rates of metabolism, growth and development, are thought to limit the population. An increase in tidal exchange during these months would also decrease the population.

The spring population increase of *A. clausii* is thought to be seeded by the small breeding stock of adults which is present during the winter. In Spring, an increase in temperature increases metabolism and an increase in phytoplankton biomass occurs.

These conclusions are based on a somewhat limited amount of data and a lot of information from other sources. Some conclusions should be substantiated further. In particular the areas which should be examined in more detail are:

(i) The seasonal cycle of the eggs of *A. clausii* in the lagoon sediment;

(ii) the possibility that the red tide in the Fall is somehow toxic to *A. clausii*;

(iii) the speciation, population and seasonal succession of fish in the lagoon together with their diet in terms of predation on *A. clausii*. 
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and the development of life stages of the marine copepod Acartia 

- 1975(c) Dark inhibition of egg hatching of the 

- 1978 : Population dynamics and production of a 
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Oliver and Boyd. 195 p.


8. Acknowledgements

The authors wish to express their thanks to Mr. Grant Gardner, Institute of Ocean Sciences Patricia Bay for assistance with the identification of some zooplankton species. They are also indebted to Ms. L. Watanabe for many helpful discussions and assistance with the sampling program.

Financial assistance from the Federal FLIP program in the form of a salary for one of us (T.B.) enabled the bulk of this work to be carried out. The final phase was funded by CRAD Contribution No. 3610-624.
Fig. 1. Sampling stations in Esquimalt Lagoon (A, B, C) and Royal Roads (D)
Fig. 2. In situ Temperature Probe
Fig. 4. Temperature profiles in Esquimalt Lagoon. February 1978 to June 1979.
Fig. 5a. Concentration of Chlorophyll-a in Esquimalt Lagoon at Station A. February 1978 to June 1979.
Fig. 5b. Concentration of Chlorophyll-a in Esquimalt Lagoon at Station B, February 1978 to June 1979.
Fig. 5c. Concentration of Chlorophyll-a in Esquimalt Lagoon at Station C. February 1978 to June 1979.
Fig. 6. Benthic organisms of Esquimalt Lagoon

Specimen #270

POLYCHAETE
- 50 Segments
- Dark Brown colour (Light Brown appendages)
- Protrusion of head region can retract in or extend out
Specimen #408

AMPHIPOD (GAMMARID)

- Small compound eyes
- All (but one) appendages uniramous
- Chelate appendages
- Light brown - beige colour
- Note: First large leg biramous
- Found in bottom sample

Fig. 7a. Benthic organisms of Esquimalt Lagoon
Specimen #407

AMPHIPOD (GAMMARID)
- Small eyes
- All appendages uniramous
- Chelate appendages
- Sort of light brown - beige colour
- Found in bottom sample

Fig. 7b. Benthic organisms of Esquimalt Lagoon
Specimen #416

AMPHIPOD (CAPRELLID)

- Small compound eyes
- Found in bottom sample benthic-attached
- Light brown colour
- All appendages chelate and uniramous

Fig. 7c. Benthic organisms of Esquimalt Lagoon
Specimen #415

AMPHIPOD (HYPERID)

- Found in bottom sample
- Light brown - beige colour
- Swimming feet biramous
- Large compound eye

Fig. 7d. Benthic organisms of Esquimalt Lagoon
specimen #366

COPEPOD (CYCLOPOID)

- Female has slightly swollen genital segment
- Light brown to white
- Red eye spot
- No other dark internal structures
- 4th leg modified and on first segment of urosome
- No 5th leg
- Urosome a little over 1/2 body length
- Found in bottom sample
- Often sacs on prosome
- Sometimes setae on one uropod of telson longer than other one

Fig. 8. Benthic organisms of Esquimalt Lagoon
Fig. 9a. Seasonal succession of zooplankton in Esquimalt Lagoon. February 1978 to May 1979. Station A.
Fig. 9b. Seasonal succession of zooplankton in Esquimalt Lagoon. February 1978 to May 1979. Station B.
Fig. 9c. Seasonal succession of zooplankton in Esquimalt Lagoon. February 1978 to May 1979. Station C.
Fig. 10a. Male 5th segment

Fig. 10b. Female 5th segment
Fig. 11a. Male 5th segment and urosome

Fig. 11b. Female 5th segment, urosome and attached sperm sac
Fig. 12. *Acartia clausii* Giesbrecht (from Brodski & Bradford)
Fig. 13. Seasonal succession of adult male and female *Acartia clausii* in Esquimalt Lagoon - Station C. Feb. 1978 to May 1979.
Fig. 14. Cohort analysis of *A. clausii* in Esquimalt Lagoon, Spring 1979. Naupliar and Copepodite stages.
TABLE 1: Zooplankton species found in the Esquimalt Lagoon in approximate order of abundance.

<table>
<thead>
<tr>
<th>SPECIES REFERENCE #</th>
<th>DESCRIPTION</th>
<th>MAX ABundance (^*) (#/m(^3))</th>
</tr>
</thead>
<tbody>
<tr>
<td>357</td>
<td>Acartia clausii</td>
<td>83,491</td>
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<tr>
<td>334</td>
<td>Podon sp.</td>
<td>14,968</td>
</tr>
<tr>
<td>319</td>
<td>barnacle nauplii</td>
<td>17,653</td>
</tr>
<tr>
<td>326</td>
<td>barnacle larvae</td>
<td>468</td>
</tr>
<tr>
<td>271</td>
<td>polychaete juveniles</td>
<td>1,419</td>
</tr>
<tr>
<td>359</td>
<td>Psuedocalanus minutus</td>
<td>395</td>
</tr>
<tr>
<td>356</td>
<td>Acartia longiremus</td>
<td>1,720</td>
</tr>
<tr>
<td>132</td>
<td>Obelia sp.</td>
<td>821</td>
</tr>
<tr>
<td>567</td>
<td>Oikopleura sp.</td>
<td>416</td>
</tr>
<tr>
<td>437</td>
<td>Crab zoeae</td>
<td>382</td>
</tr>
<tr>
<td>361</td>
<td>Centropages abdominales</td>
<td>304</td>
</tr>
<tr>
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<td>Evadne sp.</td>
<td>960</td>
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<tr>
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<td>156</td>
</tr>
<tr>
<td>354</td>
<td>unidentified copepod</td>
<td>129</td>
</tr>
<tr>
<td>130, 131, 133-6</td>
<td>various spp. of medusae</td>
<td>156</td>
</tr>
<tr>
<td>256</td>
<td>chaetognaths</td>
<td>29</td>
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<tr>
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<td>Metridia pacifica</td>
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<tr>
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<td>186</td>
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</table>

\(^*\) on any given date with 202\(\mu\) or 280\(\mu\) mesh net.
TABLE II: Comparison of zooplankton populations inside and outside of the lagoon on three different dates.

(a) Vertical haul. May 25, 1978 (Note: Used 202μ bongo net)

<table>
<thead>
<tr>
<th>SPECIES #</th>
<th>DESCRIPTION</th>
<th>#/m³</th>
<th>% pop.</th>
<th>SPECIES #</th>
<th>DESCRIPTION</th>
<th>#/m³</th>
<th>% pop.</th>
</tr>
</thead>
<tbody>
<tr>
<td>352</td>
<td>Various copepodite stages</td>
<td>2,229</td>
<td>38.9</td>
<td>357</td>
<td>Acartia clausii</td>
<td>4,340</td>
<td>74.5</td>
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<td>359</td>
<td>Pseudocalanus minutus</td>
<td>1,975</td>
<td>34.5</td>
<td>352</td>
<td>Various copepodite stages</td>
<td>810</td>
<td>13.9</td>
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<tr>
<td>319</td>
<td>Barnacle nauplii</td>
<td>1,072</td>
<td>18.7</td>
<td>334</td>
<td>Podon sp.</td>
<td>212</td>
<td>3.6</td>
</tr>
<tr>
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<td>Unidentified copepod</td>
<td>169</td>
<td>3.0</td>
<td>271</td>
<td>Polychaete juveniles</td>
<td>116</td>
<td>2.0</td>
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<td>356</td>
<td>Acartia longiremus</td>
<td>56</td>
<td>1.0</td>
<td>319</td>
<td>Barnacle nauplii</td>
<td>96</td>
<td>1.7</td>
</tr>
<tr>
<td>364</td>
<td>Cyclopoid copepod</td>
<td>56</td>
<td>1.0</td>
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<td>Pseudocalanus minutus</td>
<td>77</td>
<td>1.3</td>
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<td>Barnacle larvae</td>
<td>28</td>
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<td>Podon sp.</td>
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<td>356</td>
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<td>.6</td>
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<td>.5</td>
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<td>.3</td>
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<td>.5</td>
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<td>Chaetognaths</td>
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<td>.5</td>
<td>460</td>
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(TOTALS: 5,728 100.1)

<table>
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<th>SPECIES #</th>
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<th>% pop.</th>
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<tr>
<td>352</td>
<td>Various copepodite stages</td>
<td>2,229</td>
<td>38.9</td>
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<tr>
<td>359</td>
<td>Pseudocalanus minutus</td>
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<td>319</td>
<td>Barnacle nauplii</td>
<td>1,072</td>
<td>18.7</td>
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<tr>
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<td>Unidentified copepod</td>
<td>169</td>
<td>3.0</td>
</tr>
<tr>
<td>356</td>
<td>Acartia longiremus</td>
<td>56</td>
<td>1.0</td>
</tr>
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<td>364</td>
<td>Cyclopoid copepod</td>
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<td>1.0</td>
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<td>326</td>
<td>Barnacle larvae</td>
<td>28</td>
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<td>.5</td>
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(TOTALS: 5,826 99.8)
TABLE II: Comparison of zooplankton populations inside and outside of the lagoon on three different dates.

(b) Vertical haul, July 24, 1978.  (Note: Used 202μ bongo net)

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<tr>
<td>356</td>
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<td>25.8</td>
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<td>Obelia sp.</td>
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<td>5.9</td>
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<td>5.9</td>
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<td></td>
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<td><strong>TOTALS</strong>:</td>
<td><strong>93</strong></td>
<td><strong>100.0</strong></td>
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</table>
TABLE II: Comparison of zooplankton populations inside and outside of the lagoon on three different dates.

(c) Vertical haul, Oct 17, 1978. (Note: Used 202μ bongo net)

<table>
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<td>35</td>
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<td>361</td>
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<td>Acartia longiremus</td>
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<td>359</td>
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<td>567</td>
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